

RESEARCH ARTICLE

Pest suppression potential varies across 10 bioenergy cropping systems

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Abstract

Top-down suppression of herbivores is a fundamental ecological process and a critical service in agricultural landscapes. Adoption of bioenergy cropping systems is likely to become an increasingly important driver causing loss or gain of this service in coming decades. We measured natural pest suppression potential in ten model bioenergy crops in a long-term experimental array by deploying plasticine sentinel caterpillar mimics, which record imprints from predator attacks. Cropping systems included three intensive annual row crop systems and a range of simple perennial monocultures and more complex polycultures. We compared attack rates across the ten cropping systems and assessed differences over time within a growing season and between the ground level and canopy. We found strong differences in attack rates across cropping systems, usually with more attacks in perennial crops than annuals. However, outcomes varied in space and time, both within and among cropping systems. Birds and small mammals were responsible for most, and sometimes all, attacks in annual crops and were most important early in the season. Chewing arthropod attacks increased over the course of the growing season and were responsible for most attack events in perennial systems. In late summer there were almost no attacks in annual crop canopies, while attack rates in perennial canopies at the same time were quite high and were carried out almost entirely by chewing arthropods. Our results underscore the lack of trophic complexity in annual bioenergy cropping systems relative to perennials. They also illustrate the dramatic changes in predator activity and predation intensity that occur both seasonally and between the ground and plant canopy. Policies and practices that increase the footprint of annual crops for bioenergy are likely to cause a deficit in pest suppression services at local and landscape scales.

KEYWORDS

bioenergy, ecosystem service, grassland, pest suppression, predation, sentinel prey

INTRODUCTION

Predation is an integral ecosystem function that structures communities and maintains biodiversity (Paine, 1966). In agricultural landscapes, it is a highly valued ecosystem service, as natural enemies of herbivores limit their impact on crops, improving yields and/or reducing insecticide use. The classic valuation of this natural pest suppression service is \$4.5 bn/y (Losey & Vaughan, 2006; \$6.7 bn/y adjusted for inflation). Natural pest suppression is also highly spatially and temporally variable; the abundance, diversity, and effectiveness of natural enemies depends on management at both field and landscape scales (Crowder et al., 2010; Haan et al., 2020; Martin et al., 2019; Muneret et al., 2018).

It is important to consider how future changes to agricultural landscapes will affect pest suppression. One change anticipated in coming decades is the increased use of bioenergy crops grown as renewable alternatives to fossil fuels (Robertson et al., 2017). Nearly all credible scenarios for addressing the climate crisis require expanded use of bioenergy (IPCC, 2018), suggesting these types of crops, in one form or another, will become increasingly prominent features of agricultural landscapes over the course of the 21st century.

There are a wide variety of cropping system types that could become mainstream, and their effects on pest suppression will depend on which crops are adopted and how they are incorporated into landscapes. Some options are traditional high-input row crops; for example, in the US, ~40% of corn yield is already allocated to ethanol fuel production (USDA ERS 2022), and sorghum varieties are being explored as alternatives to corn (Moore et al., 2021). However, increasing the footprint of annual crops like corn for bioenergy reduces biodiversity, dismantles the trophic complexity required for adequate natural pest suppression, and results in increased insecticide use (Landis et al., 2008; Lark et al., 2020, 2022; Meehan et al., 2011).

Beyond traditional row crops, there are several candidate low-input perennial systems being considered or developed for bioenergy applications in North America. These include *Miscanthus*, an exotic clonal grass that forms dense and highly-productive thickets (McCalmont et al., 2017; Moore et al., 2021), and cultivars of native prairie grasses like switchgrass and big bluestem which have been developed for bioenergy applications (Casler et al., 2018; McLaughlin & Kszos, 2005). Other perennial systems are more biodiverse and ecologically complex. For example, reconstructed native prairie can be used as a feedstock (Tilman et al., 2006), and there are several short-rotation coppicing systems using willow, poplar, or other fast-growing woody plants that can host diverse

communities of organisms depending on management (Baum et al., 2012; Vanbeveren & Ceulemans, 2019).

Compared to annual crops like corn, the impact of perennial crops on biodiversity, ecosystem processes, and pest suppression is more complicated to assess as they have not yet been deployed widely on the landscape and their net effects depend on which ecosystems they replace. In general, perennial crops are more biodiverse than annual systems but less diverse than natural reference systems (Immerzeel et al., 2014; Núñez-Regueiro et al., 2021; Tudge et al., 2021). Pest suppression in perennial bioenergy systems also tends to be much stronger than in annuals (Werling et al., 2014). Net effects of perennial bioenergy crops on both biodiversity and natural pest suppression services could be positive in contexts where they replace annual crops on marginal lands (Donnison et al., 2021; Werling et al., 2011, 2014).

To determine the potential of a range of bioenergy cropping systems to influence pest suppression, we used plasticine sentinel caterpillars (Howe et al., 2009; Low et al., 2014) to quantify attack rates and census communities of attacking organisms. These caterpillar mimics are made of moldable material that records imprints when attacked by other organisms, allowing investigators to quantify attack rates and identify the types of organisms responsible for them. This approach has been used successfully in a variety of other studies to assess predation rates and biocontrol potential (Howe et al., 2009; Lövei & Ferrante, 2017; Roslin et al., 2017).

While it is generally expected that pest suppression will be poor in annual bioenergy crops and improved in complex perennial systems, there are many perennial crop types that could be adopted and their relative strengths and weaknesses in this regard have not been assessed. Additionally, relatively little texture has been added in terms of how pest suppression services vary in space and time within these cropping systems. Therefore, we (1) asked how predation varies among ten candidate bioenergy cropping systems planted in a long-term experimental array, and (2) assessed variation over time (within a growing season) and space (near the ground vs. in the plant canopy) within each of them. Our specific expectations were (1) attack rates will be higher in perennial crops than in annuals (as shown by previous studies), but that various perennial systems will also differ from one another; (2) differences between cropping systems are not static and will change as the season progresses; (3) predation pressure will be vertically stratified (i.e., differ between the ground level and the crop canopy); and (4) communities of organisms responsible for attacks will turn over along all of these axes.

METHODS

Data from this study were collected in 2021 in the Bioenergy Cropping Systems Experiment, a long-term experiment established in 2008, at Kellogg Biological Station, Michigan State University, USA. This array is a randomized complete block design containing 5 replicates of each of 10 bioenergy cropping system types (summarized in Table 1). Each plot measures 28 × 40 m and is surrounded by mowed turf. For details about the array and its management history see <https://lter.kbs.msu.edu/research/long-term-experiments/glbrc-intensive-experiment/>. Among the 10 cropping system types in the experiment, there were three annual monocultures: corn (*Zea mays* L.), sorghum (*Sorghum bicolor* L. Moench photoperiod-sensitive hybrid ES5200), and a second sorghum variety (photoperiod-insensitive hybrid TAM17900) with a fall-planted cereal rye cover crop (*Secale cereale* L. var. Wheeler). There were also four low-diversity perennial systems. These included *Miscanthus* × *giganteus*, a vegetative grass that produces dense bamboo-like thickets, and two treatments containing switchgrass (*Panicum virgatum* L. var. Cave-in-rock), a perennial prairie grass native to North America that has been cultivated for bioenergy applications. One of these was newly seeded into cover crop residue and establishing during the year of data collection, while the other was made up of mature, established stands. There was also a treatment containing five native prairie grass species (*Panicum virgatum* L., *Andropogon gerardii* Vitman, *Sorghastrum nutans* (L.) Nash, *Elymus canadensis* L., *Schizachyrium scoparius* (Michx.) Nash). Finally, complex perennial polyculture treatments included reconstructed prairie (18 species; 6 grasses, 9 forbs, 3 legumes, and limited volunteers), successional volunteer

vegetation (a mix of warm and cool season grasses, grassland/prairie forbs, and a variety of volunteer herbaceous and woody species), and a short-rotation poplar coppicing system (*Populus* 'NM6', a hybrid between *P. nigra* and *P. maximowiczii*) with a diverse volunteer understory. The poplar treatment was coppiced in 2014 and replaced in 2019; thus, the stand was in its third year of growth during the study with stems ~2–3 m in height. Species lists for each treatment are available at <https://lter.kbs.msu.edu/wp-content/uploads/2012/05/GLBRC-Species.pdf>.

Sentinel caterpillars were made of unscented moldable green plasticine (Van Aken). Caterpillars were produced using a sugar paste extruder and were 3 mm in diameter and 15 mm long, mimicking a generic Geometrid moth larva. We attached them with glue (Gorilla Glue) to wooden kabob stakes (15 cm length), which were stuck in foam gardening knee pads at ~2 cm intervals to keep caterpillars separated and placed in cardboard boxes or coolers for transport (Appendix S1, Figure S1.1).

Sentinel prey were deployed for two periods each during June, July, and August (June 2–4 and June 7–9, July 19–21 and July 21–23, and August 23–25 and August 25–27) in every plot in the experimental array. Each plot contained three sampling stations (see <https://lter.kbs.msu.edu/maps/images/glbrc-station-flags.pdf>). In each instance we placed two caterpillars at each sampling station, each positioned approximately 1.4 m northwest or southeast of the station. They were left in place for approximately 48 h before retrieval and were placed and retrieved in the same order to standardize exposure time. We deployed caterpillars both near the soil surface and in the plant canopy (Figure 1). For the soil surface location, stakes were placed in soil so the caterpillar was ~4.5 cm above the soil surface. In row crops, we placed them directly adjacent to plant

TABLE 1 Overview of ten bioenergy cropping system treatments included in the experimental array.

Cropping system	Category
Corn (<i>Zea mays</i>)	Annual
Sorghum (<i>Sorghum bicolor</i> hybrid ES5200)	Annual
Sorghum (<i>Sorghum bicolor</i> hybrid TAM17900) with fall-seeded rye cover crop (<i>Secale cereale</i> var. Wheeler)	Annual
<i>Miscanthus</i> (<i>Miscanthus</i> × <i>giganteus</i>)	Simple perennial
Switchgrass (<i>Panicum virgatum</i> var. Cave-in-rock; establishing stand)	Simple perennial
Switchgrass (<i>Panicum virgatum</i> var. Cave-in-rock; mature stand)	Simple perennial
Native grass mix (5 species)	Simple perennial
Reconstructed prairie (6 grasses, 9 forbs, 3 legumes, plus volunteers)	Complex perennial
Successional vegetation (unseeded, volunteer species)	Complex perennial
Poplar (<i>Populus</i> 'NM6') with diverse understory	Complex perennial

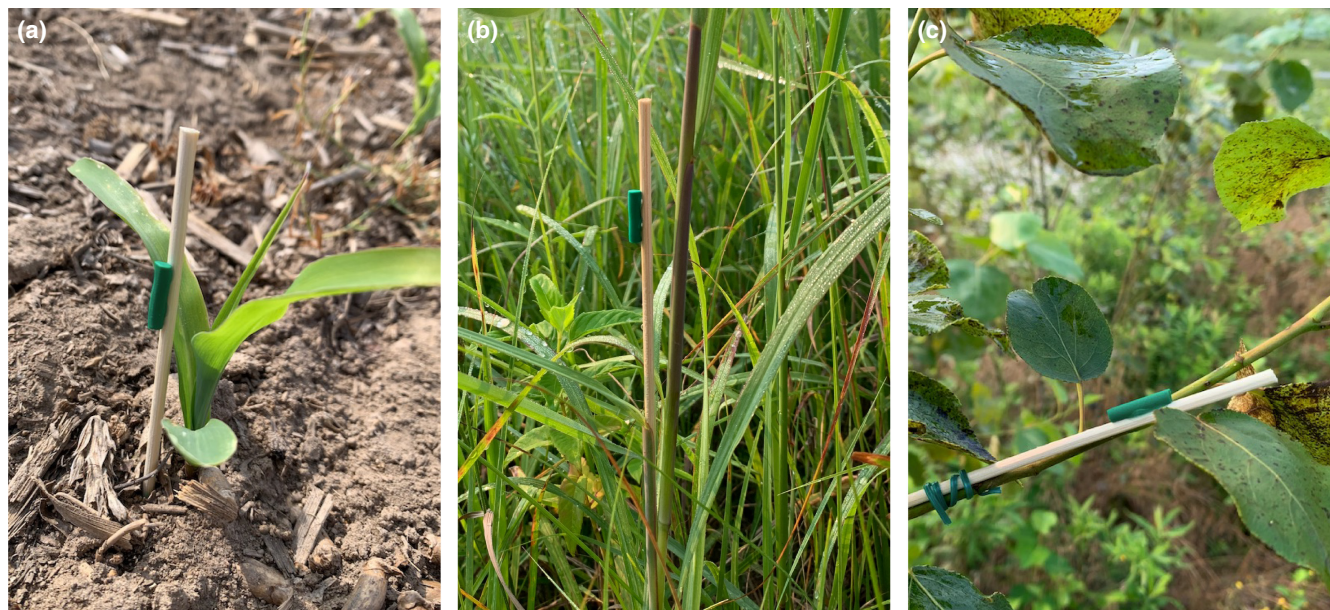


FIGURE 1 Plasticine sentinel caterpillars (a) staked in soil, (b) inserted in a grass leaf sheath, and (c) fastened to a stem with wire.

stems (Figure 1a). In perennial systems, we disturbed vegetation structure minimally but at times rearranged thatch so it would not touch the caterpillar. In June, all caterpillars were staked at the soil surface, as most vegetation was still low and no canopy had formed. Then, in July and August, at each station we placed one caterpillar at the soil surface and fastened the other (positioned southeast of each sampling station) in the plant canopy. In newly-establishing switchgrass plots, caterpillars were not deployed on June 7–9 because of a pesticide application. Additionally, in this treatment, in July we deployed a caterpillar along the soil surface at each sampling station but not in the canopy, as it consisted mainly of grass blades, rather than reproductive stems, offering little structural support.

When placing caterpillars in the canopy we fastened them toward the top of plants, up to approximately 180 cm height if the canopy was taller (this occurred mostly in August). We placed canopy caterpillars on a plant as close as possible to the point 1.4 m SE of each sampling station, but precise locations were constrained by availability of plant structures that could support the caterpillar, and if needed we adjusted the caterpillar's position by up to ~0.5 m to the nearest tall stem near the top of the canopy that could support them. When placing caterpillars on corn, sorghum, *Miscanthus*, and prairie grasses, we secured the stake by inserting it in a leaf sheath (Figure 1b). When caterpillars were attached to woody species or forbs, we used flexible green wire or tape to fasten the stake to a stem or twig (Figure 1c). We marked locations with field flags or tape so we could find and recover the caterpillars but offset them from

the sentinel prey by 10–30 cm to minimize potential effects on predators.

In all, we deployed 1740 plasticine sentinels. Of these, 9 were subsequently discarded due to handling or labeling issues. Additionally, 20 were unable to be relocated. We suspect they were removed, stake and all, by birds or mammals but since this is impossible to confirm we omit them.

Plasticine caterpillars were evaluated for evidence of attacks in the laboratory using stereo microscopes. To avoid observer bias, all evaluations were performed by the lead author. Caterpillars were judged as having no evidence of attack, as having been attacked by small mammals, birds, chewing arthropods, or having been probed by a proboscis or ovipositor (we did not distinguish between these two). Figure 2a–d show representative photos of each type of attack. We also recorded whether the sample had been impacted by contact with vegetation or handling. In cases where this type of damage was severe enough to obscure potential attack marks by predators (>30% coverage), we omitted the sample ($n = 3$). Thirteen caterpillars were removed entirely from their stakes with no definitive marks left behind. We suspect this was due to birds or mammals but categorized these as 'unknown'.

Statistical analyses were carried out in R version 4.2.2. To test for differences in attack frequencies, we built binomial generalized linear mixed models (GLMMs) using the R package *lme4* (Bates et al., 2015). Since data collected in June focused only on the ground level, we modeled these data separately with a fixed effect for cropping system type and a random effect for replicate (this factor accounts

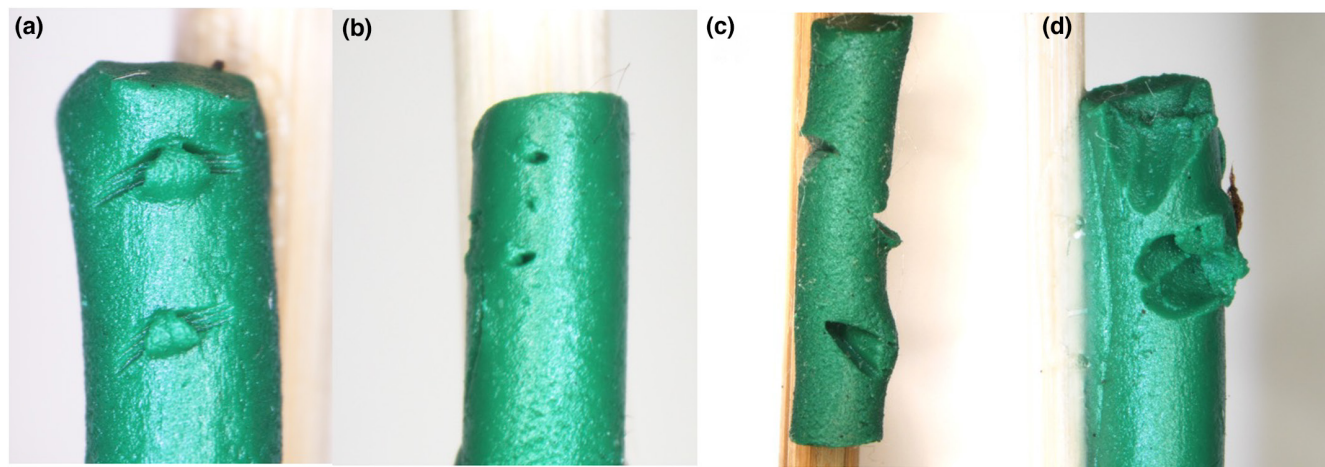


FIGURE 2 Examples of marks left by (a) chewing arthropods, (b) arthropod proboscis or ovipositor, (c) bird beak, and (d) rodent teeth.

for spatial differences within the array, as replicates were grouped). We compared this to a null model containing only the random effect, using QAICc. Then, for data collected in July and August, we built a GLMM with cropping system type, month, and stratum (ground or canopy) as fixed effects, as well as the interaction terms between stratum and treatment, and treatment and month. We included replicate as a random effect as in the model for June. We compared this model to all its possible subsets, again using QAICc, using the R package *MuMin* (Bartoń, 2022). Next, we tested if communities attacking the caterpillars differed, using Permutational Multivariate Analysis of Variance (PERMANOVA) with the *adonis2* function in the R package *vegan* (Oksanen et al., 2022). Models were structured with the best set of predictor variables identified during model selection above (but including replicate as a fixed effect as this procedure does not accommodate mixed-effect models). The model used a Bray–Curtis dissimilarity index and 999 permutations.

RESULTS

Out of the 1705 plasticine caterpillars we recovered and assessed, 496 (29.0%) contained identifiable attack marks from vertebrates or arthropods (in addition to the 13 which were removed entirely from their stakes and classified as ‘unknown’). Attack rates were highly variable; in some settings (e.g., corn and sorghum canopies) there were very few or even zero attacks, while in others, 60% or more of the caterpillars were marked (Figure 2). Calculating across time and stratum (i.e., vertical position), predation pressure varied more than four-fold among habitat types, with 48 h attack frequencies ranging from 11.7% in corn to 48.9% in the native grass mix. Attack rates also increased in general as the season progressed, with 20.1%

TABLE 2 Models of attack frequencies as functions of crop type, month, and/or stratum, and their interactions using comparisons based QAICc, comparing the two possible models from June and the top four models for data collected in July and August. For June, the model including habitat type strongly outperformed the null model. For July/August, the model with all terms and interactions strongly outperformed all others. All models also included a random effect for replicate.

Time period	Model terms included	Δ QAICc	Weight
June	Intercept + crop	0	1
	Intercept	37.02	0
July/August	Intercept + crop + month + stratum + crop: month + crop: stratum	0	0.998
	Intercept + crop + month + stratum + crop: stratum	12.63	0.002
	Intercept + crop + stratum + crop: stratum	25.73	0.000
	Intercept + crop + month + crop: stratum	28.22	0.000
	Intercept + crop + month + stratum + crop: month		

of caterpillars attacked in June, 28.5% in July, and 38.1% in August. Finally, when a canopy had formed (July and August), attack rates were higher on average near the ground (39.1%) than in the canopy (27.3%).

Model comparison revealed that attack frequencies varied strongly by crop type, by stratum within a crop, and over time, and furthermore that these variables interacted strongly (Table 2, Figure 3). First, in June, attack frequencies differed strongly by crop type (i.e., the model including crop type as a predictor strongly outperformed the null model). Then, in July and August, attack frequency

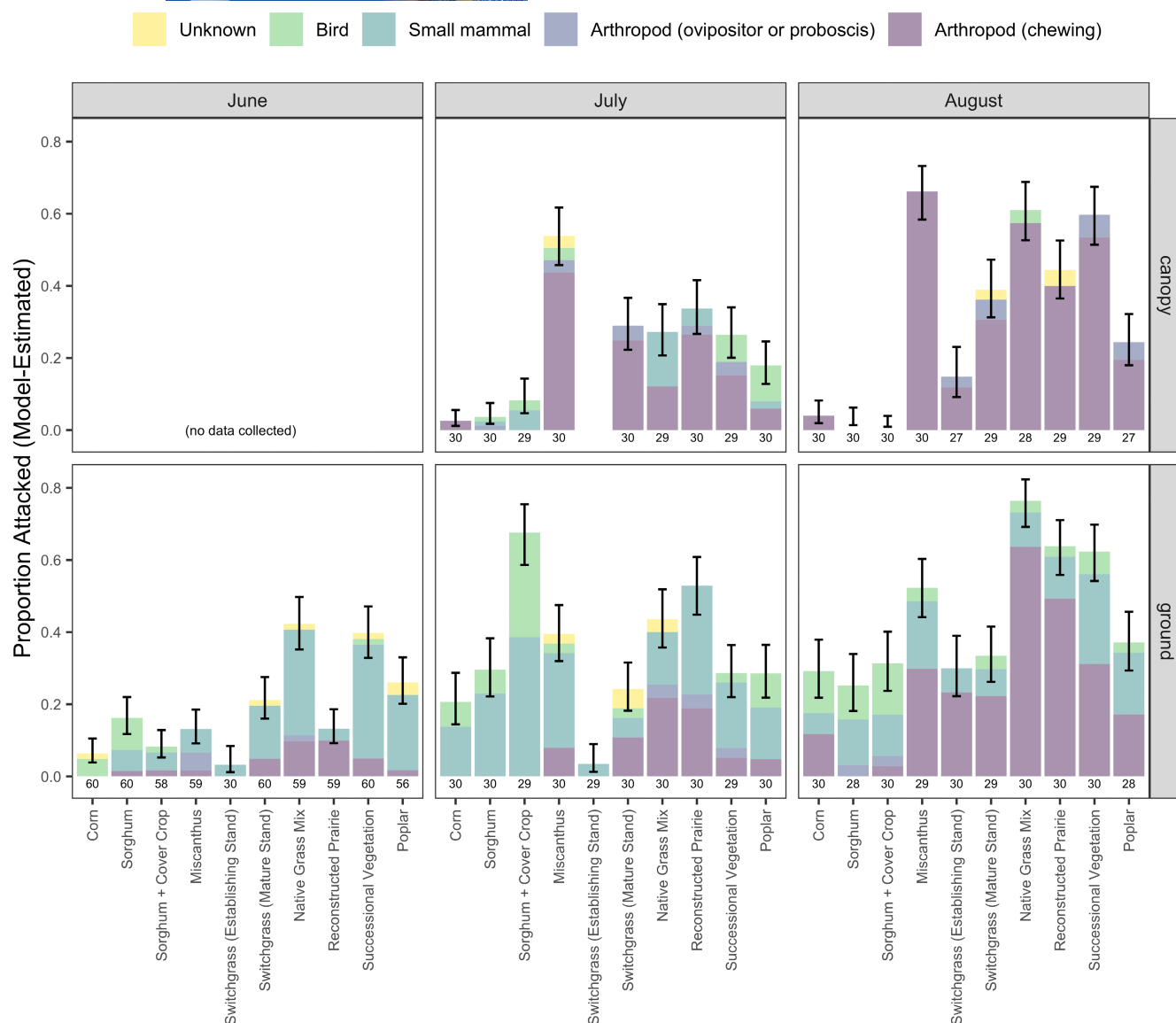


FIGURE 3 Modeled attack rates on plasticine caterpillar mimics and identities of attackers in bioenergy crops varied strongly among cropping systems, changed over the course of the growing season, and were vertically stratified. Bars represent generalized linear mixed model-estimated means; error bars denote 1 SE from the mean. Bars are stacked to show the proportion of attacks in each circumstance that were caused by arthropods, birds, small mammals, or unknown causes. Sample sizes are shown below each bar. In August at the canopy level we show model-estimated mean attack rates in sorghum treatments but in reality zero attacks occurred (hence no stacked bars).

differed between crop types, between the ground and canopy, from month to month, and their interactions. That is, while attacks generally increased from July to August, the effect of crop type also differed between the 2 months (or, equally, temporal change was stronger in some crops than in others). Similarly, overall attacks were significantly lower in the canopy than on the ground, but this difference also varied from crop to crop. For example, attacks much rarer in annual crop canopies than along the ground but were often comparable between strata within perennial crops (Table 2, Figure 3).

When we asked how the community composition of attackers differed, results mostly paralleled those

describing attack frequency but with fewer interactions (Table 3). In June, community composition differed strongly by treatment. In July and August, community composition differed significantly between cropping system treatments, between the 2 months, and with position in the canopy (it also differed by replicate within the array). However, interaction terms were not significant. That is, while attacker communities turned over strongly between cropping systems, over time, and were vertically stratified, the effect of cropping system was consistent over time, and the community differences between canopies and the ground level did not differ strongly from crop to crop.

TABLE 3 The types of attack marks that plasticine caterpillars bore after 48 h differed by habitat type, over time, and with vertical position.

Time period	Predictor	df	Pseudo-F	p
June	Treatment	9	2.52	<0.01
	Replicate	4	1.54	0.11
July–August	Treatment	9	6.63	<0.01
	Sampling period	1	10.69	<0.01
	Stratum	1	20.32	<0.01
	Replicate	4	2.62	0.01
	Treatment: sampling period	9	1.37	0.126
	Treatment: stratum	9	1.44	0.10

DISCUSSION

We found strong differences in top-down pressure attributable to cropping system type, changes over time, vertical stratification, and the interactive effects of these variables. We also found strong spatial and temporal turnover in the types of organisms responsible for these attacks. In line with our expectations, attack rates in annual crops (corn and sorghum) were generally lower than in perennial systems, and there was also substantial variation among perennial systems with these patterns changing from month to month. Attack rates also differed between the ground level and canopy, but this varied across cropping system types.

The highly interactive effects of cropping system type, time, and strata make it difficult to outline broad-brush conclusions or interpret differences using pairwise contrasts. However, combining information about attack rates and the organisms responsible reveals the following narrative (Figure 3). In June, attacks were relatively infrequent, driven mostly by vertebrates, and were substantially higher in a few perennial habitats (native grass mix, successional vegetation), often with contributions from both vertebrates and arthropods. In July, attack rates increased in most treatments. Near the soil surface, rates were usually similar between annual crops and perennial systems, although they were driven only by vertebrates in annual systems. Patterns in the canopy differed; attack rates were very low in annual crops but markedly higher in perennial systems, where primarily chewing arthropods were very active. These patterns became more exaggerated in August. Near the soil surface, attack rates in corn and sorghum were moderate and usually driven by vertebrates, whereas chewing arthropods accounted for more attacks in perennial systems, and some perennial habitats had very high attack rates. In the canopy, few to no attacks occurred in annual systems while chewing arthropods were very active across most perennial habitats.

While we found predation pressure was often weaker in corn and sorghum than other crops, there were also strong differences between perennial systems. Ignoring

variation over time and strata, overall attack rates were very low in establishing switchgrass stands (12.9%), which is unsurprising since it was newly seeded at the beginning of the study. Attack rates were highest in the native grass mix (48.9%), and in general ranged from between a quarter and half of caterpillars being attacked (26.9% in poplar, 28.1% in mature switchgrass stands, 37.1% in reconstructed prairie, 39.9% in *Miscanthus*, and 42.9% in successional vegetation).

There was no obvious pattern to account for why some perennial systems in our study had higher attack rates than others. In general, the abundance and diversity of many groups of organisms can increase with plant species richness (Haddad et al., 2009; Scherber et al., 2010), and in an agricultural context, diversified systems tend to have more natural enemies, fewer herbivores, and reduced crop damage (Letourneau et al., 2011). One recent study (Hertzog et al., 2017) found predation usually increased with plant diversity (although only at ground level and not higher in vegetation). We found no such pattern; while bird and arthropod diversity increased with plant diversity in this experimental array (N. L. Haan, unpublished data; Appendix S2), the pattern did not extend to predation rates. This was exemplified by the *Miscanthus* system, which was species-poor compared to most other perennial systems, but where in our study attacks by both small mammals and chewing arthropods were frequent. Similarly, the poplar system contained the most plant species (Appendix S2, Table S2.1), but predation rates were often lower than in simple, less-diverse systems. Pest suppression services—at least in the way we assessed them—were generally elevated in perennial systems compared to annuals, but were not enhanced in more biodiverse perennial systems relative to simple perennial crops.

The vertical stratification of predation risk we documented is in general agreement with other studies. In a multi-country study, Ferrante et al. (2019) deployed plasticine caterpillars in corn and found attack rates along the ground were around double those in the canopy (although this varied geographically). We observed the same pattern but it was much more stark; across

corn and sorghum crops, in July/August the overall raw attack rate along the ground was 33.9% compared to just 3.9% in the canopy. Hertzog et al. (2017) also found higher attack rates on multiple types of sentinel prey, including plasticine caterpillars, along the ground compared to higher in vegetation (in this case, sentinels were placed lower than in our study, halfway up plant shoots). They assessed predation across a plant diversity experiment with plots containing a gradient from 1 to 60 meadow species and found that stratification was more pronounced when plant diversity was high. In contrast, in our study within the perennial systems there was little difference in attack rates between the ground (41.3%) and canopy (38.5%; Figure 3).

One of the most striking findings in this study was the complementary roles of vertebrates and invertebrates in attacking simulated herbivores. Both groups were active in perennial systems but in annual crops this process was carried almost entirely by vertebrates. While birds and small mammals were able to compensate for the lack of arthropod activity along the ground level in these crops, they were all but absent in the canopy and nearly all sentinel caterpillars remained unscathed. It is intuitive that small mammals are more active along the ground than in crop canopies, but more surprising that birds were focused on the ground in these systems as well, despite often perching in the canopy.

In a concurrent study we censused communities of multiple taxa in the same array (N. L. Haan, unpublished data), which can provide context for results of this study. The small mammal community was made up of mice (*Peromyscus* spp.) and ground squirrels (*Ichthyomys tridecemlineatus* Mitchell), which were common throughout most of the array, and meadow voles (*Microtus pennsylvanicus* Ord) and shrews (*Sorex cinereus* Kerr), which were almost entirely limited to perennial systems (Appendix S2, Table S2.2). Nearly all marks left by mammals appeared to be from mice and/or meadow voles, but we occasionally found larger dentition marks that looked like ground squirrels or tiny, pointed imprints left by shrews. The bird community in the array was dominated by common seed and/or insect-feeding species including (in descending order of abundance) red-winged blackbird (*Aegialius phoeniceus* L.), American goldfinch (*Spinus tristis* L.), song sparrow (*Melospiza melodia* Wilson), and mourning dove (*Zenaida macroura* L.).

Marks left by chewing arthropods were diverse, although we did not attempt to identify them beyond establishing that they were produced by arthropod mandibles. We suspect most marks were caused by ants; these were shallow and often numerous and occurred both on the ground and in the canopy. However, we also often found deep slashes that could have been produced by jumping

spiders, ground beetles, predatory wasps, ground beetles, or orthoptera. In some cases, we found marks from two long, thin mandibles on the end of the caterpillar (possibly lacewing larva), while in other cases there were several larger slashes through the middle of the body.

Mobile organisms move between habitat types in agricultural landscapes, spilling over along edges or collecting resources from combinations of habitats (Tscharntke et al., 2005, 2012). Our data were collected in an experimental array with plots that are smaller than typical crop fields (0.11 ha, 28 × 40 m, separated by 15 m mowed turf on all sides), and results need to be interpreted in this context. Compared to a realistically scaled landscape there were more edges and more potential for organisms in high-quality habitats to spill over into species-poor communities, and the array was situated in a species-rich landscape at a biological station. We interpret this as meaning the differences in attack rate we measured are conservative, since they occurred where the potential for natural enemy spillover from high to low-quality habitats was elevated.

Plasticine caterpillars, like any single method, provide a limited picture of overall predation patterns. They may be passed over by predators that use chemosensory or movement-related cues, or spectral cues that come from live prey but not plasticine, or if they use ambush-style attacks or webs. Plasticine may also record marks from probing organisms that would not be lethal to a real insect. Some predators respond similarly to live and plasticine sentinel prey (Ferrante et al., 2017), but in general, attack rates on plasticine sentinels tend to be lower (Lövei & Ferrante, 2017). Two new studies have also found artificial prey can underestimate attacks by invertebrates more severely than those by vertebrates (Nimalrathna et al., 2023; Zvereva & Kozlov, 2022). Disparities between attack rates on live prey vs. artificial sentinels can also change strongly within a season and do so inconsistently depending on the predator group in question, leading to misleading conclusions about the relative importance of various predator groups. Therefore, while methods used in our study provide a meaningful first comparison of predation across these cropping systems, they probably underestimate attack probabilities from some predator groups. For a more complete picture of pest suppression services in bioenergy crops, a variety of methods will need to be used including real herbivores from different feeding guilds and/or that are economically relevant pests for a given crop. Future work will also need to examine differences in pest abundance and herbivory rates.

While attack rates in this study varied at fine scales and were context dependent, our findings in general illustrate the divergent effects bioenergy adoption could have on trophic interactions, and in particular pest suppression, in future agricultural landscapes. Importantly, these

patterns would also manifest at landscape scales and affect more than bioenergy crops themselves, as field-scale communities aggregate to determine landscape-scale species pools of natural enemies available to colonize or spill over into other crop fields (Haan et al., 2020, 2021; Landis et al., 2000; Tschardt et al., 2012). We could gain more insight from future work at landscape scales, although this may be challenging as most candidate bioenergy crops have not yet been widely deployed.

AUTHOR CONTRIBUTIONS

Nathan L. Haan and Douglas A. Landis conceived ideas and designed the study; Nathan L. Haan collected and analyzed data and wrote the initial manuscript draft. Nathan L. Haan and Douglas A. Landis edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data from this study can be found at: <https://doi.org/10.5281/zenodo.7733893>.

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REFERENCES

Bartoń, K. (2022). MuMIn: Multi-Model Inference. R package version 1.47.1.

- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Baum, S., Bolte, A., & Weih, M. (2012). Short rotation coppice (SRC) plantations provide additional habitats for vascular plant species in agricultural mosaic landscapes. *BioEnergy Research*, 5(3), 573–583. <https://doi.org/10.1007/s12155-012-9195-1>
- Casler, M. D., Vogel, K. P., Lee, D. K., Mitchell, R. B., Adler, P. R., Sulc, R. M., Johnson, K. D., Kallenbach, R. L., Boe, A. R., & Mathison, R. D. (2018). 30 years of progress toward increased biomass yield of switchgrass and big bluestem. *Crop Science*, 58(3), 1242–1254.
- Crowder, D. W., Northfield, T. D., Strand, M. R., & Snyder, W. E. (2010). Organic agriculture promotes evenness and natural pest control. *Nature*, 466(7302), 109–112. <https://doi.org/10.1038/nature09183>
- Donnison, C., Holland, R. A., Harris, Z. M., Eigenbrod, F., & Taylor, G. (2021). Land-use change from food to energy: Meta-analysis unravels effects of bioenergy on biodiversity and cultural ecosystem services. *Environmental Research Letters*, 16(11), 113005. <https://doi.org/10.1088/1748-9326/ac22be>
- Ferrante, M., Barone, G., & Lövei, G. L. (2017). The carabid *Pterostichus melanarius* uses chemical cues for opportunistic predation and saprophagy but not for finding healthy prey. *BioControl*, 62(6), 741–747. <https://doi.org/10.1007/s10526-017-9829-5>
- Ferrante, M., Lövei, G. L., Magagnoli, S., Minarcikova, L., Tomescu, E. L., Burgio, G., Cagan, L., & Ichim, M. C. (2019). Predation pressure in maize across Europe and in Argentina: An inter-continental comparison. *Insect Science*, 26(3), 545–554.
- Haan, N. L., Iuliano, B., Gratton, C., & Landis, D. A. (2021). Designing agricultural landscapes for arthropod-based ecosystem services in North America. *Advances in Ecological Research*, 64, 191–250. <https://doi.org/10.1016/bs.aecr.2021.01.003>
- Haan, N. L., Zhang, Y., & Landis, D. A. (2020). Predicting landscape configuration effects on agricultural pest suppression. *Trends in Ecology & Evolution*, 35(2), 175–186. <https://doi.org/10.1016/j.tree.2019.10.003>
- Haddad, N. M., Crutsinger, G. M., Gross, K., Haarstad, J., Knops, J. M. H., & Tilman, D. (2009). Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters*, 12(10), 1029–1039. <https://doi.org/10.1111/j.1461-0248.2009.01356.x>
- Hertzog, L. R., Ebeling, A., Weisser, W. W., & Meyer, S. T. (2017). Plant diversity increases predation by ground-dwelling invertebrate predators. *Ecosphere*, 8(11), e01990. <https://doi.org/10.1002/ecs2.1990>
- Howe, A., Lövei, G. L., & Nachman, G. (2009). Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. *Entomologia Experimentalis et Applicata*, 131(3), 325–329. <https://doi.org/10.1111/j.1570-7458.2009.00860.x>
- Immerzeel, D. J., Verweij, P. A., van der Hilst, F., & Faaij, A. P. C. (2014). Biodiversity impacts of bioenergy crop production: A state-of-the-art review. *GCB Bioenergy*, 6(3), 183–209. <https://doi.org/10.1111/gcbb.12067>
- IPCC (Intergovernmental Panel on Climate Change). (2018). Special report: Global warming of 1.5 C. Retrieved December 22, 2022, from <https://www.ipcc.ch/sr15/>
- Landis, D. A., Gardiner, M. M., van der Werf, W., & Swinton, S. M. (2008). Increasing corn for biofuel production reduces bio-control services in agricultural landscapes. *Proceedings of the*

- National Academy of Sciences of the United States of America, 105(51), 20552–20557. <https://doi.org/10.1073/pnas.0804951106>
- Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, 45(1), 175–201. <https://doi.org/10.1146/annurev.ento.45.1.175>
- Lark, T. J., Hendricks, N. P., Smith, A., Pates, N., Spawn-Lee, S. A., Bougie, M., Booth, E. G., Kucharik, C. J., & Gibbs, H. K. (2022). Environmental outcomes of the US renewable fuel standard. *Proceedings of the National Academy of Sciences of the United States of America*, 119(9), e2101084119.
- Lark, T. J., Spawn, S. A., Bougie, M., & Gibbs, H. K. (2020). Cropland expansion in the United States produces marginal yields at high costs to wildlife. *Nature Communications*, 11(1), 4295. <https://doi.org/10.1038/s41467-020-18,045-z>
- Letourneau, D. K., Armbrrecht, I., Rivera, B. S., Lerma, J. M., Carmona, E. J., Daza, M. C., Escobar, S., Galindo, V., Gutiérrez, C., López, S. D., Mejía, J. L., Rangel, A. M. A., Rangel, J. H., Rivera, L., Saavedra, C. A., Torres, A. M., & Trujillo, A. R. (2011). Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications*, 21(1), 9–21.
- Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *BioScience*, 56(4), 311–323. [https://doi.org/10.1641/0006-3568\(2006\)56\[311:TEVOE SJ\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[311:TEVOE SJ]2.0.CO;2)
- Lövei, G. L., & Ferrante, M. (2017). A review of the sentinel prey method as a way of quantifying invertebrate predation under field conditions. *Insect Science*, 24(4), 528–542.
- Low, P. A., Sam, K., McArthur, C., Posa, M. R. C., & Hochuli, D. F. (2014). Determining predator identity from attack marks left in model caterpillars: Guidelines for best practice. *Entomologia Experimentalis et Applicata*, 152(2), 120–126. <https://doi.org/10.1111/eea.12207>
- Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., Hassan, D. A., Albrecht, M., Andersson, G. K. S., Asís, J. D., Aviron, S., Balzan, M. V., ... Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, 22(7), 1083–1094. <https://doi.org/10.1111/ele.13265>
- McCalmont, J. P., Hastings, A., McNamara, N. P., Richter, G. M., Robson, P., Donnison, I. S., & Clifton-Brown, J. (2017). Environmental costs and benefits of growing Miscanthus for bioenergy in the UK. *GCB Bioenergy*, 9(3), 489–507. <https://doi.org/10.1111/gcbb.12294>
- McLaughlin, S. B., & Kszos, L. A. (2005). Development of switchgrass (*Panicum virgatum*) as a bioenergy feedstock in the United States. *Biomass and Bioenergy*, 28(6), 515–535. <https://doi.org/10.1016/j.biombioe.2004.05.006>
- Meehan, T. D., Werling, B. P., Landis, D. A., & Gratton, C. (2011). Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proceedings of the National Academy of Sciences of the United States of America*, 108(28), 11500–11505. <https://doi.org/10.1073/pnas.1100751108>
- Moore, C. E., von Haden, A. C., Burnham, M. B., Kantola, I. B., Gibson, C. D., Blakely, B. J., Dracup, E. C., Masters, M. D., Yang, W. H., DeLucia, E. H., & Bernacchi, C. J. (2021). Ecosystem-scale biogeochemical fluxes from three bioenergy crop candidates: How energy sorghum compares to maize and miscanthus. *GCB Bioenergy*, 13(3), 445–458. <https://doi.org/10.1111/gcbb.12788>
- Muneret, L., Mitchell, M., Seufert, V., Aviron, S., Djoudi, E. A., Pétilion, J., Plantegenest, M., Thiéry, D., & Rusch, A. (2018). Evidence that organic farming promotes pest control. *Nature Sustainability*, 1(7), 361–368. <https://doi.org/10.1038/s41893-018-0102-4>
- Nimalrathna, T. S., Solina, I. D., Mon, A. M., Pomoim, N., Bhadra, S., Zvereva, E. L., Sam, K., & Nakamura, A. (2023). Estimating predation pressure in ecological studies: Controlling bias imposed by using sentinel plasticine prey. *Entomologia Experimentalis et Applicata*, 171(1), 56–67. <https://doi.org/10.1111/eea.13249>
- Núñez-Regueiro, M. M., Siddiqui, S. F., & Fletcher, R. J. (2021). Effects of bioenergy on biodiversity arising from land-use change and crop type. *Conservation Biology*, 35(1), 77–87. <https://doi.org/10.1111/cobi.13452>
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., ... Weedon, J. (2022). vegan: Community Ecology Package. R package version 2.6-4.
- Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, 100(910), 65–75.
- Robertson, G. P., Hamilton, S. K., Barham, B. L., Dale, B. E., Izaurre, R. C., Jackson, R. D., Landis, D. A., Swinton, S. M., Thelen, K. D., & Tiedje, J. M. (2017). Cellulosic biofuel contributions to a sustainable energy future: Choices and outcomes. *Science*, 356(6345), eaal2324. <https://doi.org/10.1126/science.aal2324>
- Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., Barrio, I. C., Basset, Y., Boesing, A. L., Bonebrake, T. C., Cameron, E. K., Dáttilo, W., Donoso, D. A., Drozd, P., Gray, C. L., Hik, D. S., Hill, S. J., Hopkins, T., Huang, S., ... Slade, E. M. (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, 356(6339), 742–744. <https://doi.org/10.1126/science.aaj1631>
- Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D., Roscher, C., Weigelt, A., Allan, E., Beßler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L. W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., ... Tscharnkte, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, 468(7323), 7323. <https://doi.org/10.1038/nature09492>
- Tilman, D., Hill, J., & Lehman, C. (2006). Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science*, 314(5805), 1598–1600. <https://doi.org/10.1126/science.1133306>
- Tscharnkte, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, 8(8), 857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>
- Tscharnkte, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes—eight hypotheses. *Biological Reviews*, 87(3), 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>

- Tudge, S. J., Purvis, A., & De Palma, A. (2021). The impacts of biofuel crops on local biodiversity: A global synthesis. *Biodiversity and Conservation*, 30(11), 2863–2883. <https://doi.org/10.1007/s10531-021-02232-5>
- Vanbeveren, S. P. P., & Ceulemans, R. (2019). Biodiversity in short-rotation coppice. *Renewable and Sustainable Energy Reviews*, 111, 34–43. <https://doi.org/10.1016/j.rser.2019.05.012>
- Werling, B. P., Dickson, T. L., Isaacs, R., Gaines, H., Gratton, C., Gross, K. L., Liere, H., Malmstrom, C. M., Meehan, T. D., Ruan, L., Robertson, B. A., Robertson, G. P., Schmidt, T. M., Schrottenboer, A. C., Teal, T. K., Wilson, J. K., & Landis, D. A. (2014). Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, 111(4), 1652–1657. <https://doi.org/10.1073/pnas.1309492111>
- Werling, B. P., Meehan, T. D., Gratton, C., & Landis, D. A. (2011). Influence of habitat and landscape perenniality on insect natural enemies in three candidate biofuel crops. *Biological Control*, 59(2), 304–312. <https://doi.org/10.1016/j.biocontrol.2011.06.014>

- Zvereva, E. L., & Kozlov, M. V. (2022). Predation risk estimated on live and artificial insect prey follows different patterns. *Ecology*, e3943. <https://doi.org/10.1002/ecy.3943>

SUPPORTING INFORMATION

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

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