Land-use components, abundance of predatory arthropods, and vegetation height affect predation rates in grasslands

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Abstract

Land use is a major driver of biodiversity loss in many taxa including the mega-diverse
arthropods, but consequences for arthropod-mediated processes are still little understood.
Using a rapid ecosystem function assessment (REFA), we approximated predation by
quantifying predation attempts on artificial sentinel prey. Dummies were placed on the soil
surface of 83 managed temperate grasslands across a broad range of land-use intensities
(grazing intensity, mowing frequency, and the amount of applied fertiliser) in two regions of
Germany. Additionally, we measured vegetation height and assessed the abundance of
ground-dwelling arthropods using pitfall traps. We documented predation marks left by
arthropods, rodents, and birds. The proportion of dummies with predation marks (i.e.
predation rates) differed between regions. Vegetation height was the strongest predictor for

predation in our study but correlated only weakly with land use. Predation rates increased with increasing vegetation height, for rodents and for all predator groups combined. All three land-use components affected predation, which was most prominent for arthropod predation. Arthropod predation increased with higher grazing intensity and decreased with higher mowing frequency and higher fertilisation intensity. Also, the abundances of ground-dwelling arthropods affected predation. While predation rates generally increased with a higher abundance of carabids and decreased with higher abundance of ants, the effects of spider abundance interacted with region. Our results demonstrate that different components of land use can have counteracting effects on predation rates acting together with changes in the abundance of different predator groups and vegetation height. This suggests that land-use practices that sustain high vegetation and ground-dwelling predator abundances increase predation rates in grasslands and consequently the potential to provide ecosystem services in the form of pest control.

Keywords

Land use, mowing, grazing, fertilising, arthropods, predation, multitrophic interactions, carabids, ants

1. Introduction

Land-use change (conversion from one land-use type to another) and intensification of land use (within one land-use type), have been identified as the most important drivers of global species loss (Sala *et al.*, 2000; Maxwell *et al.*, 2016). In temperate Europe, extensively managed grasslands are habitats that harbour high plant and animal diversity (Poschlod *et al.*, 2009; Hejman *et al.*, 2013). These grasslands are largely human-made and have to be managed as meadows or pastures to prevent long-term scrub and tree encroachment and associated diversity declines (Ratajczak *et al.*, 2012). Low-intensity management implies little

or no fertilisation, and grazing at low stocking density or mowing with one or two cuts per year to make hay. During the last century, grassland management has intensified by increasing the number of cuts per year or the stocking density, with a concomitant increase in fertilisation (Statistisches Bundesamt (Destatis), 2017).

Intensification of grassland management has been documented to reduce the abundance and diversity of plants (Kleijn *et al.*, 2009; Blüthgen *et al.*, 2012; Socher *et al.*, 2012), arthropods (Haddad *et al.*, 2000; Attwood *et al.*, 2008; Simons *et al.*, 2014; Chisté *et al.*, 2016; but see also Leidinger *et al.*, 2017 for opposing effects), and multidiversity (the diversity across many different taxa; Allan *et al.*, 2014), causing a homogenization of grassland communities (Gossner *et al.*, 2016). Grassland management affects animal communities either directly, e.g. by killing or driving away individuals during mowing (Humbert *et al.*, 2010) or indirectly by trampling and soil compaction associated to livestock grazing (Helden *et al.*, 2010; van Klink *et al.*, 2015) or by inducing changes in the plant community or prey availability occurring in the grasslands (Simons *et al.*, 2014; Egorov *et al.*, 2017). Overall, land use decreases plant diversity directly and indirectly through increased competition because of higher plant biomass. Reduced plant diversity leads to a decrease in herbivore diversity and a following decrease in predator diversity. Also, land use increases plant biomass, but this effect was not leading to an increase in herbivore biomass.

Nevertheless, increasing herbivore biomass generally increases predator biomass which in turn increases predator diversity (Simons *et al.*, 2014).

Importantly, effects of the individual land-use components can differ in strength or even direction (Socher *et al.*, 2012; Socher *et al.*, 2013; Simons *et al.*, 2014; Gossner *et al.*, 2016).

Frequent mowing creates a homogenous sward, reduces flowering and seed set, causes high insect mortality and may lead to soil compaction, all of which may cause extinctions of rare species and favour a reduced set of disturbance-tolerant species thereby decreasing plant diversity and also decreasing plant biomass through mechanical disturbances during the

77 growing period. Grazing affects plants in a much patchier manner in space and time
78 compared to mowing (Helden *et al.*, 2010) and can increase plant diversity – by increasing
79 the number of niches for plants or preventing competitive exclusion – and decrease plant
80 biomass via recurrent disturbance of plant growth. At very high grazing densities effects on
81 species richness might become negative, as for mowing. Fertilization decreases plant
82 diversity because of a dominance of fast-growing species and increases plant biomass
83 because of growth promotion of increased nutrient input (Socher *et al.*, 2012; Socher *et al.*,
84 2013; Simons *et al.*, 2014; Gossner *et al.*, 2016). Species richness of arthropods correlates
85 positively with species richness of plants in most cases (Simons *et al.*, 2014). Often, mowing
86 has been demonstrated to have the strongest negative effects on biota (Gossner *et al.*,
87 2016).

88 Losing species is more than a conservation concern because diversity can drive ecosystem
89 functioning (Scherber *et al.*, 2010; Allan *et al.*, 2013; Meyer *et al.*, 2018). Consequently,
90 increasing land-use intensity in grasslands can affect ecosystem functions (e.g., herbivory,
91 Gossner *et al.*, 2014; seed removal and soil microbe activity, Leidinger *et al.*, 2017) as well as
92 multifunctionality (Allan *et al.*, 2015) often via a change in the functional composition of
93 animal or plant communities (Flynn *et al.*, 2009; Birkhofer *et al.*, 2015b; Simons *et al.*, 2016).

94 Because of trade-offs between some ecosystem functions or services (Raudsepp-Hearne *et al.*,
95 2010; Allan *et al.*, 2015) and because individual land-use components can show
96 contrasting effects on different functions (Leidinger *et al.*, 2017), previous results are not
97 generalizable and land-use effects on individual ecosystem functions need to be
98 investigated. One ecosystem function not studied in relation to land use in grasslands is
99 predation, however, declines in plant species richness have previously been shown to cause
100 lower rates of predation by arthropods in grasslands (Hertzog *et al.*, 2017).

101 In grasslands, ground-dwelling spiders, ants, and carabid and staphylinid beetles are
102 important generalist predators, and their potential for biocontrol has been shown in the past

(Riechert and Lockley, 1984; Kromp, 1999; Symondson *et al.*, 2002; Sanders and Platner, 2007). Vertebrates such as small mammals and birds are also important predators in grasslands affecting the insect populations (Bock *et al.*, 1992). While there have been a number of studies on how grassland management intensity and the individual land-use components grazing, mowing and fertilization affect the predator community (Grandchamp *et al.*, 2005; Simons *et al.*, 2014; Birkhofer *et al.*, 2015b; Gossner *et al.*, 2016), little is known on how management affects predation rates. Previous studies have shown that especially arthropod abundances decrease with land-use intensification, which is partly mediated by a change in vegetation structure (Simons *et al.*, 2014). Thus, we expect a strong negative effect of land-use intensity on predation rates.

Here we investigate the effect of land-use intensity on predation rates using grasslands differing in management intensity in two regions of Germany as a model system. We approximated predation rates employing a sentinel prey method (Lövei and Ferrante, 2017) by assessing bite marks left in dummy caterpillars by various groups of predators (Meyer *et al.*, 2017) in response to land use (including its components mowing, grazing, and fertilising), vegetation height, and the abundance of different predatory arthropod groups. We hypothesised that 1) predation rates decline with higher land-use intensity. Further, we asked 2) whether the land-use components grazing, mowing and fertilisation differ in their effect on predation rates, and 3) whether predation rates are linked to vegetation height and abundance of different groups of predatory arthropods.

2. Methods

2.1. Study sites and grassland land use

The study was conducted in two regions of Germany within the Biodiversity Exploratory project (www.biodiversity-exploratories.de; Fischer *et al.*, 2010): (1) The biosphere reserve Schorfheide-Chorin in north-east Germany (3–140m a.s.l., 53°02'N 13°83'E, annual mean

precipitation 500–600mm, mean temperature 8–8.5°C); (2) The biosphere reserve Schwäbische Alb in south-west Germany (460–860m a.s.l., 48°43'N 9°37'E, 700–1000mm, 6–7°C). In total 83 (Schorfheide: 40, Schwäbische Alb: 43) grasslands of different types of land use (meadows 29, pastures grazed by different kinds of livestock, i.e. cattle, sheep or horses 22, or mown pastures that are both mown and grazed 32) were included in the study. Of the 83 grasslands, 34 were not fertilised, while on the remaining 49 grasslands fertiliser was applied in different amounts. Plots (50m × 50m) were located within larger grasslands of homogeneous land use and selected based on a stratified random sampling of a total of >1000 candidate plots, considering soil types (consistency and constancy), slope (<20%) and spatial distance among plots (>200m between the outer edges of two plots). Studied plots covered the complete range of grassland land-use intensities in the regions. For details see Fischer *et al.* (2010).

2.2. Land-use information

Land use was quantified in the grasslands based on the intensity of three land-use components: (1) grazing intensity, (2) mowing frequency, and (3) fertilisation. Management practices on the grasslands were assessed annually by standardised interviews with the land-owners, gaining information on fertilisation, grazing and mowing (Blüthgen *et al.*, 2012). Briefly, fertilisation intensity was calculated as the total amount of nitrogen (kg) applied per hectare and year, in the form of chemical fertiliser, manure or slurry. For grazing, information on livestock type, number of livestock units and the duration of grazing periods were combined as a measure of grazing intensity. Mowing intensity was included as the number of cuts per year. All measures were standardised to a common scale by dividing the value of each plot by the regional average of the respective land-use component. Land-use components were integrated into the land-use intensity measure LUI by averaging the three measures (Blüthgen *et al.*, 2012). To quantify long-term land-use intensity a mean LUI for the

years 2006–2015 was used as an explanatory variable. Also for the individual land-use components, the long-term average for the years 2006–2015 was used. To quantify recent land-use intensity, the LUI for the year of the predation measurements (2015) was used. For those plots that had been cut in 2015 before the measurements the number of days since the last cut was calculated as an additional explanatory variable. In all plots in the region Alb, the height of the vegetation was measured by measuring the highest point of the vegetation from the ground on each of the four sides of each plot (Supplementary Fig. 1).

2.3. Quantifying predation

In June (Schwäbische Alb) and July (Schorfheide) 2015, predation was measured in the 83 grasslands described above. To quantify predation we used a sentinel prey method (Lövei and Ferrante, 2017) with artificial caterpillars as prey as suggested for the Rapid Ecosystem Function Assessment (REFA; Meyer *et al.*, 2015; Meyer *et al.*, 2017). In the centre of larger grasslands of homogenous land-use intensity plots of 50m x 50m were marked. Along the edge of each plot, 16 artificial caterpillars (dummies) made from green plasticine (Noris Club 8421-5; STAEDTLER Mars Deutschland GmbH, Nuernberg, Germany) were exposed on the ground for 72 hours (Supplementary Fig. 1; four dummies along each edge at 7.5m, 17.5m, 32.5m and 42.5m from the corners). Marks left by animals interacting with the dummies during this period were investigated in the laboratory under a dissecting microscope. Marks were attributed to four different groups of animals: (1) arthropods: mandibular, cheliceral and stylet marks; (2) mammals: tooth marks left by small rodents; (3) birds: beak marks; and (4) slugs: radula marks (Low *et al.*, 2014; Hertzog *et al.*, 2017; Meyer *et al.*, 2017). As slugs are opportunistic scavengers and not predators, only marks by arthropods, mammals, and birds were considered indicative of predation attempts. Predation was quantified using presence-absence of marks on caterpillars (binary coding: 1=predation mark, 0= no

predation mark) for total predation and for each predator group separately (Hertzog *et al.*, 2017; Leidinger *et al.*, 2017; Meyer *et al.*, 2017).

2.4. Abundance of predatory arthropods and activity of ants

Simultaneously with the assessment of predation rates, we used pitfall traps to assess the abundance (in the form of activity densities) of ground-dwelling arthropod predators (ground beetles, spiders, rove beetles, ants) and quantified the activity of ants attracted to baiting stations. A combination of both methods is proposed to assess ant abundance (Gotelli *et al.*, 2011).

Per plot 12 pitfall traps were installed together with the dummy caterpillars. Three pitfall traps were placed at each of the four sides of the 50m x 50m plot between the sites where dummies were exposed (Supplementary Fig. 1). The traps were placed along the edges of the plots at 12.5m, 25m and 37.5m from the corners (5 m distance to the dummy caterpillars). Plastic cups with a diameter of 7cm were put into the soil and filled with a solution of water, salt and soap (200g salt, 1ml liquid soap per litre of water). The content of traps was collected three days after the installation together with the dummies.

Per plot 16 bait stations for ants were placed along the edges of the plots at the same locations as the dummies (four stations on each side at 7.5m, 17.5m, 32.5m and 42.5m from the corners; Supplementary Fig. 1). Bait stations were installed and monitored for one hour either before installing the dummies (on the day of placing the dummies in the field) or after having collected the dummies (on the day they were collected). Four bait stations were placed on each side at 7.5m, 17.5m, 32.5m and 42.5m from the corners (Supplementary Fig. 1). As baiting station, we used Petri dishes (90mm diameter) with a round filter paper and placed five types of baits made from an artificial diet (based on whey protein, caseinate, egg powder, sucrose, and water, gelled with agar) on each filter paper. Each type of bait contained different protein to carbohydrate ratios (1:1, 1:2.5, 1:5, 1:7.5 and 1:10

206 protein:carbohydrate) to attract all ants feeding on different food sources. We counted all
207 ants at these baiting stations 30 minutes and 60 minutes after placing them in the field and
208 summed the number of all ants feeding on agar cubes for both measurements and all
209 nutrient ratios to obtain one value for ant activity per baiting station.

210

211 2.5. Statistical analysis

212 Predation was analysed based on the 0/1 response of all individual dummies in a generalised
213 linear mixed effect model (GLMM) with binomially distributed data. The proportion of
214 dummies with bite marks was analysed as response variable for each predator group
215 (arthropods, rodents, and birds) separately and for all three predator groups jointly. For
216 each type of predation marks, a series of models were fitted including different explanatory
217 variables, because not all explanatory variables were available for all plots sampled. A first
218 set of models was based only on data from the region Alb with only vegetation height as an
219 explanatory variable (*glmer(cbind(Pred1, Pred0) ~ VegetationHeight + (1|Plot/Side),*
220 *family="binomial")*).

221 Second, models were estimated based on data of all plots that had been already cut in 2015
222 before the measurements. These models contained region, days since last cutting, and their
223 interaction as explanatory variables (*glmer(cbind(Pred1, Pred0) ~ Region*DaysSinceLastCut +*
224 *(1|Plot/Side), family="binomial")*).

225 Third, models based on all plots for which data from pitfall traps and ant baiting were
226 available were tested that contained as explanatory variables region, the abundance of
227 Staphylinidae, Carabidae, Arachnida (Araneae and Opiliones), and Formicidae (each taxon as
228 separate variable), the ant activity at the baits, land-use intensity (LUI) in 2015, the long-
229 term average LUI (2006-2015), and all two-way interactions between region and each other
230 explanatory variable respectively (*glmer(cbind(Pred1, Pred0) ~ Region +*
231 *log(Staphylinidae+1)* Region + log(Carabidae+1)* Region + log(Arachnida+1)* Region +*

$\log(\text{Formicidae}+1) * \text{Region} + \log(\text{AntActivity}+1) * \text{Region} + \log(\text{LUI2015}+1) * \text{Region} +$
 $\text{LUIlong} * \text{Region} + (1 | \text{Plot/Side}), \text{family} = "binomial")$). To account for the hierarchical
 sampling design, all models included a random effect for the side of the plot (north, east,
 west, and south) nested in the identity of each plot. Minimum adequate (i.e. most
 parsimonious) models were derived by step-wise models simplification starting with the
 most complex model as described below.

To test for the effect of individual land-use components, the minimum adequate models
 estimated in step 3 were tested for the inclusion of the individual land-use components
 (long-term average of grazing, mowing, fertilising, and their interactions with region). All
 models were fitted using the function *glmer* from the package *lme4* (Bates *et al.*, 2015) in R
 version 3.3.0 (R Development Core Team, 2014). All explanatory variables were tested in the
 order stated in the text and given in Tables 1-3. The significance of the fixed effects was
 established by removing these from the model and comparing the log likelihood of the
 resulting simpler models via chi-square tests using the function *drop1*. Significance levels for
 the terms retained in the minimum adequate models were established using the function
mixed from the *afex* package (Singmann *et al.*, 2017).

Models estimated the probability of an individual dummy to show at least one mark of the
 tested group of predators after exposure of three days. For simplicity, we will refer to this in
 the following as “predation rates”. Values are rates because they are a probability per unit
 time, i.e. the three days of exposure in the field.

3. Results

Overall, 1278 dummies could be recovered from 83 plots after exposure in the field and be
 analysed for predation marks. Most dummies (982, 76.8%) showed a mark of at least one of
 the four types. Arthropods were most important, with marks observed on 649 (50.8%) of the
 dummies, followed by slugs (429, 33.6%), and rodents (228, 17.8%). Predation marks by

birds were very scarce and only observed on 11 (0.9%) of the dummies. Due to this low number, they were not analysed separately for effects of the different explanatory variables (Table 1) and are not shown separately in the main figures (Fig. 1-3). However, marks by birds were included in the total number of marks for all predator groups (arthropods, rodents, and birds). Excluding marks by slugs, 808 dummies (63.2%) showed marks by at least one of the three predator groups.

Vegetation height had significant effects on predation rates by rodents ($\text{Chi}^2_1=13.43$; $p<0.001$) and all predator groups combined ($\text{Chi}^2_1=6.136$; $p=0.013$) but not arthropods ($\text{Chi}^2_1=0.054$; $p=0.816$; Fig. 1). Predation rates by rodents and by all predator groups combined increased with higher vegetation height. However, for those plots that had been cut already in 2015 before the measurements of predation rates, the number of days since the last cut did not show significant effects on the predation rates by any group (Table 1).

Predation rates differed significantly between the two regions investigated (Table 2, Fig. 2). Predation rates by arthropods and by all predators combined were higher in the region Schorfheide, while predation rates by rodents did not differ between regions (Table 2, Fig. 2).

The abundance of various groups of predatory arthropods affected predation rates significantly (Table 2, Fig. 2). Predation rates by all predators combined mirrored the patterns of predation rates by arthropods alone. Both predation rates increased with higher abundance of Carabidae and decreased with higher ant activity on the plots (Table 2, Fig. 2). For the abundance of Arachnida (Aranea and Opiliones combined), there was a significant interaction with region. Predation rates increased with higher abundance of Arachnida in the Schorfheide but decreased with higher abundance of Arachnida in the Alb.

The index of land-use intensity (LUI) had no significant effect on the predation rates of any group, neither when calculated for 2015 alone nor as the long-term average of land use (Table 2, Fig. 3). When analysing the effects of the different components of long-term land

use individually, however, significant effects on the predation rates by arthropods emerged (Table 3). Predation rates by arthropods increased with higher grazing intensity and decreased with higher mowing frequency (Table 3, Fig. 3). Also, there was a statistical trend for predation rates by arthropods to decrease with higher fertilising intensity (Table 3, Fig. 3). Interestingly, observed effects for predation rates by rodents were opposite to patterns observed for arthropods. Predation rates by rodents decreased with higher grazing intensity, and there was a trend for higher predation rates by rodents with higher mowing frequency (Table 3, Fig. 3). For predation rates by all predators combined, the effect of grazing intensity was significant and resembled patterns for predation rates by arthropods alone (Table 3, Fig.3).

4. Discussion

We found that predation rates increased with increasing vegetation height and that all three land-use components affected predation. Effects were most prominent for arthropod predation, which increased with higher grazing intensity and decreased with higher mowing frequency and higher fertilisation intensity. When combining the different land-use components into a single index of land-use intensity, their counteracting effects on predation rates neutralised each other so that no relationship between predation rates and the overall land-use index was found. Also, the abundances of ground-dwelling arthropods affected predation. Predation rates increased with a higher abundance of carabids and decreased with higher activity of ants. The abundance of spiders interacted with region and showed a positive effect on arthropod predation in the region Schorfheide and a negative effect in the region Alb.

4.1. Comparison of observed predation rates to published predation rates

Predation rates of slightly more than 63% for true predators only (excluding slugs) documented in this study were high compared to those found in other grasslands, using also proportions of dummy caterpillars showing marks (20% in grasslands in South Brazil (Leidinger *et al.*, 2017), between 15% and 22% in the grassland plots of the Jena Experiment in central Germany (Hertzog *et al.*, 2017)). As Solovyeva (2015) showed that the number of marks in dummies scaled linearly with exposure time and all these rates have been observed for an exposure of a maximum of 24 hours, roughly three times higher predation rates with three times longer exposure times in our study seem reasonable.

4.2. Comparison to other published effects of land use on predation

While rates of predation have been investigated in response to various drivers (e.g., distance to the forest edge: Koh and Menge, 2006; plant diversity: Hertzog *et al.*, 2017; geographic latitude and altitude: Roslin *et al.*, 2017), we are aware of only one study of effects of land-use intensity on predation rates in grasslands. This study (Leidinger *et al.*, 2017) conducted in South Brazil found as only land-use effect an increase in predation rate when grasslands were mown (in contrast to the negative effects of mowing in the present study). This difference is likely explained by (1) lower mowing intensities in Brazil compared to Germany and (2) the strong negative effects of burning excess biomass on consumer communities and predation rates, which is the common alternative management practice replacing mowing in Brazil.

4.3. Potential mechanisms for effects of the land-use intensity and land-use components

Grassland management can affect predation rates by changing the predator community or by affecting prey populations or the vegetation context in which the predator-prey interactions play out. Some potential mechanisms have been tested in this study by including respective explanatory variables in the models testing for land-use effects.

Unfortunately, formally testing for indirect effects of land-use intensity or land-use components on predation rates via changes in these variables, as could be done with a structural equation modelling approach, was not possible with the available data due to a large number of explanatory variables and given constraints in the level of replication. Therefore, the discussion about the underlying causes of the documented changes in predation rates remains restricted to potential mechanisms.

4.3.1. Effects via changes in predator community

Increasing arthropod and total predation with higher carabid abundance in our study indicates that carabids are important predators in the studied grasslands. Lower predation with higher ant activity was surprising given that ants are important predators in grasslands (Sanders and Platner, 2007) and have been previously observed to attack dummies leaving clearly visible marks (pers. observ.). The negative effect of ant activity on predation in this study could be due to a negative correlation between ant activity and abundance of other predatory arthropods (Supplementary Fig. 2, Supplementary Table 1) either directly caused by interference or driven by contrasting habitat preferences (Sanders and Platner, 2007).

Also, Arachnida abundance was a significant predictor of observed predation, but the direction of this effect depended on the region studied indicating potential interactions with vegetation structure (see below).

Changes in predator abundance due to land use could be a straightforward explanation for effects on predation rates. Such mechanisms, where the abundance of consumers drives the process rate, are called mass effects (e.g., herbivore abundance driving herbivory rates: Ebeling *et al.*, 2014). Mass effects have not been documented for land-use effects on predation in grasslands, but for dung removal, whereby in grasslands of higher land-use intensity, a reduced dung beetle biomass was associated with reduced rates of dung removal (Frank *et al.*, 2017). A change in predator abundance could be an explanation for the

observed negative effects of mowing frequency on arthropod predation because many arthropod individuals are being killed during mowing (Chisté *et al.*, 2016). In contrast, no or even slightly positive effects of mowing on predation by rodents might indicate that these can escape into their underground burrows during mowing.

Besides simple mass effects changes in the composition of the predator community can affect predation rates because of predator-predator interactions, e.g. intra-guild predation. For the carabid beetles identified in this study as an important group of arthropod predators, Birkhofer *et al.* (2015a) demonstrated that frequent cutting led to a higher abundance of predaceous and omnivorous ground beetles but a lower abundance of herbivorous species. The resulting turnover in the arthropod community would contradict the patterns in predation rates found here pointing at additional mechanisms beyond mass effects.

Effects of land use beyond those driven by predator abundance could be driven by predator diversity. Higher predator diversity can increase predation rates and strengthen prey suppression (Snyder *et al.*, 2006). Reduced predation at higher land-use intensity would be consistent with a negative total effect of land-use intensity on predator diversity (Simons *et al.*, 2014). However, the effects of predator diversity on predation rates can range from strongly positive over neutral to strongly negative, depending on the prevalence of four broad functional categories: substitutable, nonlinear due to predator species interference, nonlinear due to intraguild predation, and nonlinear due to predator species synergism (Finke and Denno, 2005; Schmitz, 2007). A combination of these opposing interactions might contribute to the neutral relationship between predation and overall land-use intensity in the study. Further, the outcome of these interactions might also depend on the environmental context (Sanders *et al.*, 2008), as also evidenced in our study. The interaction of Arachnida abundance and region indicates either regional differences between predator community compositions or can indicate seasonal shifts in the predator community as one region was investigated in June and one in July. Both differences in predator communities

might cause a shift from synergistic interactions (prey species use or spatial complementarity) between Arachnida and other arthropod predator groups in the region Schorfheide to antagonistic interactions (competition or intra-guild predation) in the region Alb.

4.3.2. Effects via changes in vegetation

One vegetation parameter that is affected by land use is grassland vegetation height. Vegetation height was a strong driver for rodent predation in our study likely because of shelter and hiding places offered by higher vegetation. In contrast, neither shelter nor microclimate seems to be as important for arthropod predators as we observed no effect of vegetation height on arthropod predation rates. Effects of land-use components beyond effects driven by vegetation height could be driven by plant diversity and structural diversity of vegetation (Helden *et al.*, 2010). Higher grassland plant species richness has previously been demonstrated to increase predation rates (Hertzog *et al.*, 2017). This would be a consistent explanation for land-use effects on predation rates documented here, as species richness of plants decreased in the studied grasslands with higher land-use intensity (Blüthgen *et al.*, 2012), especially with more frequent mowing (Socher *et al.*, 2012). Finally, land-use effects on predation may also be mediated by changes in vegetation structural complexity, which can increase with plant height and diversity. However, these vegetation parameters can also vary and affect consumer behaviour independently from each other (Randlkofer *et al.*, 2009). Structural complexity can cause changes in predation directly and indirectly by affecting prey and predator behaviour, movement, and hunting efficiency (Brose, 2003; Sanders *et al.*, 2008; Diehl *et al.*, 2013) potentially disrupting the predator-prey interaction as has been demonstrated for parasitoids (Obermaier *et al.*, 2008). Higher predation rates at higher structural richness could be caused by reduced intra-guild predation (Finke and Denno, 2002), changes in temperature and humidity conditions

affecting predator activity (Heck and Crowder, 1991), or reduced foraging efficiencies of top predators, such as birds, reducing predation pressure on arthropod predators (Thompson *et al.*, 2016). However, we observed no effect of vegetation height on arthropod predation rates despite previous records of increased prey suppression in structurally more complex vegetation due to reduced intra-guild predation (Finke and Denno, 2002). This might be explainable by habitat homogenization under intensified land use because fertilisation and frequent mowing typically favour fast-growing, yet structurally simple, plant species such as grasses (Zechmeister *et al.*, 2003). On the other hand, increased habitat heterogeneity in grazed fields can increase the abundance of predators. For example, increased carabid abundance with increased grazing intensity has been shown by Grandchamp *et al.* (2005). Resulting increased predation rates via mass effects (see above) could be an explanation for the observed positive effects of grazing intensity on arthropod predation.

4.4. Conclusions

Effects of land-use intensity extend beyond changes in vegetation and cascade up to higher trophic levels affecting not only consumer community composition but also the consumer dependent ecosystem functions, as documented here for predation rates. Importantly, individual land-use components showed counteracting effects (positive for grazing, negative for mowing and fertilising) so that an overall index of land-use intensity did not show any significant effects. This emphasises the importance to evaluate the individual components of management to enable a mechanistic understanding of land-use effects. Likewise, different groups of predatory arthropods may show antagonistic effects (i.e. positive for carabid beetle and negative for ant abundance in our study). Future studies should investigate how the different mechanisms proposed here interact to control predation rates in grasslands of differing land-use intensity. Irrespective of these mechanisms the current study demonstrates a potential contribution of extensively managed grasslands, especially

grasslands used as pastures, to pest-control in agricultural landscapes by increasing populations of natural enemies.

Authors' Contributions

STM, MMG, and HF conceived the study. LH conducted field work and identified arthropods. STM evaluated dummy caterpillars for bite marks. STM led the writing of the manuscript with input from all co-authors.

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Figure legends

Fig. 1: Effects of vegetation height on predation rates by (A) arthropods, (B) rodents, (C) all predators (arthropods, rodents, and birds) after three days of exposure. Predation rates were quantified as the proportion of artificial caterpillars (dummies made from green plasticine) that showed marks of predation attempts by the respective groups. Size of points scales with the number of dummies in each of 40 equal sized bins along the x-axes used to calculate proportions of dummies with marks for visualisation purposes. Lines illustrate significant effects of vegetation height on predation rates in statistical models ($p < 0.05$; Table 1).

Fig. 2: Effects of two regions and the presence of different predatory arthropod groups on predation rates by (upper row) arthropods, (middle row) rodents, (bottom row) all predators (arthropods, rodents, and birds). Predation rates were quantified as the proportion of artificial caterpillars (dummies made from green plasticine) that showed marks of predation attempts by the respective groups. Size of points scales with the number of dummies in each of 40 equal sized bins along the x-axes used to calculate proportions of dummies with marks for visualisation purposes. Solid lines illustrate significant effects on predation rates in statistical models ($p < 0.05$; Table 1). Dashed lines illustrate statistical trends ($0.1 < p > 0.05$; Table 1). In case of significant interactions between explanatory variables and region, grasslands from the Alb are shown as squares and grasslands from the Schorfheide as diamonds with separate lines for the predictions from the model.

Fig. 3: Effects of the intensity of different land-use components (grazing, mowing, fertilising) on predation rates by (upper row) arthropods, (middle row) rodents, (bottom row) all predators (arthropods, rodents, and birds). Predation rates were quantified as the proportion of artificial caterpillars (dummies made from green plasticine) that showed marks

487 of predation attempts by the respective groups. Size of points scales with the number of
488 dummies in each of 40 equal sized bins along the x-axes used to calculate proportions of
489 dummies with marks for visualisation purposes. Solid lines illustrate significant effects on
490 predation rates in statistical models ($p < 0.05$; Table 1). Dashed lines illustrate statistical
491 trends ($0.1 < p > 0.05$; Table 1).

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