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ARTICLE

The day after mowing: Time and type of mowing influence grassland arthropods

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Abstract

Recent losses in the abundance and diversity of arthropods have been documented in many regions and ecosystems. In grasslands, such insect declines are largely attributed to land use, including modern machinery and mowing regimes. However, the effects of different mowing techniques on arthropods remain poorly understood. Using 11 years of data from 111 agricultural grassland plots across Germany, we analyzed the influence of various grassland management variables on the abundance and abundance-accounted species richness of four arthropod orders: Araneae, Coleoptera, Hemiptera, and Orthoptera. The analysis focused on detailed mowing information, for example, days after mowing and mower type, and compared their effect with other aspects of grassland management, that is, rolling, leveling, fertilization, and grazing. We found strong negative effects of mowing on all four arthropod orders, with arthropod abundance being lowest directly after mowing and steadily increasing to three to seven times the abundance after 100 days post-mowing. Likewise, Hemiptera and Coleoptera species richness was 30% higher 100 days after mowing. Mower width showed a positive effect on Orthoptera abundance, but not on the other arthropods. Arthropod abundance and

Coleoptera species richness were lowest when a mulcher was used compared to rotary or bar mowers. In addition to mowing, intensive grazing negatively affected Orthoptera abundance but not the other orders. Mowing represents a highly disturbing and iterative stressor with negative effects on arthropod abundance and diversity, likely contributed by mowing-induced mortality and habitat alteration. While modifications of mowing techniques such as mower type or mowing height and width may help to reduce the negative impact of mowing on arthropods, our results show that mowing itself has the most substantial negative effect. Based on our results, we suggest that reduced mowing frequency, omission of mowing in parts of the grassland (refuges), or extensive grazing instead of mowing have the greatest potential to promote arthropod populations.

KEYWORDS
grassland management, grazing, insect conservation, mower, mowing width, mulcher, rolling

INTRODUCTION

The decline of insects and other arthropods, such as spiders, is a major threat to biodiversity and ecosystem functioning, and has been increasingly documented in various regions of the world (Dirzo et al., 2014; Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019; Seibold et al., 2019; Van Klink et al., 2020; Wagner, 2020). On the one hand, biodiversity is high in anthropogenic seminatural grasslands, which depend on regular interventions that inhibit shrub encroachment and forest succession (Marini et al., 2009; Pärtel et al., 2005). On the other hand, land use intensification negatively influences insect populations and is the main contributor to the loss of insect diversity, particularly affecting species found in grassland ecosystems (Dirzo et al., 2014; Sánchez-Bayo & Wyckhuys, 2019; Seibold et al., 2019). Intensified grassland management, particularly mowing, can have a strong negative impact on arthropods. For example, spatial comparisons across meadows and pastures showed the negative effects of local grassland management on arthropod abundance and diversity (Blüthgen et al., 2022; Chisté et al., 2016, 2018; Humbert, Ghazoul, Richner, et al., 2010; Humbert, Ghazoul, Sauter, et al., 2010; Proske et al., 2022; Simons et al., 2014). Compared to fertilization and grazing, mowing has a particularly strong negative impact on grassland invertebrates (Chisté et al., 2016, 2018).

Mowing causes both immediate and long-term effects on grassland arthropods. Direct impacts include high mortality (Humbert, Ghazoul, Richner, et al., 2010; Humbert, Ghazoul, Sauter, et al., 2010) and sudden disturbances that differentially affect arthropod species in relation to their escape strategies. Highly mechanized modern grassland management is particularly harmful, but mowing techniques differ in their impact. Mowers with rotating blades (rotary mowers and mulchers) are more harmful to invertebrates than mowers with horizontally moving blades (bar mowers). Blades of rotary mowers cover 5–10 times more area per stroke than bar mowers (Von Berg et al., 2023), and high rotational speeds of rotary mowers generate stronger airflow that could suck arthropods into the blades. Modified mowers that reduce the surface area of the mowing disc and prevent vertical airflow show a strongly reduced arthropod mortality (Steidle et al., 2022). Moreover, bar mowers caused lower insect mortality than rotary mowers in studies conducted by Humbert, Ghazoul, Richner, et al. (2010) and Humbert, Ghazoul, Sauter, et al. (2010), with lower mortality rates on Orthoptera (13% vs. 21%) and Lepidoptera caterpillars (20% vs. 37%). Additionally, when a conditioner was used with the rotary mower, caterpillars' mortality increased (from 37% to 69%). These higher mortality rates are likely because the conditioner compresses the grass after mowing, destroying the evaporation-inhibiting waxy layer of the grass and causing the hay to dry faster (Hecker et al., 2022; Humbert, Ghazoul, Richner, et al., 2010). Other studies showed particularly negative effects of mulching, as mulching also shreds the grass (Löbbert et al., 1994; Richner et al., 2019). Mulching resulted in a nearly 30% greater reduction in grasshopper densities than bar mowing without hay removal (Richner et al., 2019).

In addition to the functional principle (oscillating vs. rotating), other properties of the mower settings can affect grassland arthropods such as cutting height or mower width. A higher cutting height may reduce mortality in grassland animals (including amphibians and ground-nesting birds), so a minimum height of at least 8–10 cm is often recommended for conservation purposes (Humbert, Ghazoul, Sauter, et al., 2010; Oppermann et al., 2000; Van de Poel & Zehm, 2015). Mortality from tractor wheels on ground-dwelling organisms causes additional impacts, experimentally shown by Humbert, Ghazoul, Sauter, et al. (2010) with artificial caterpillar models. This raises the question of whether a wider mower is less damaging because of the lower relative area being run over by the wheels or more damaging as it limits the ability of arthropods to escape. This question has not been tested with living invertebrates (Van de Poel & Zehm, 2015).

The long-term effects of mowing include the homogenization of vegetation characteristics (Löbbert et al., 1994; Van Klink et al., 2019), altered or harsher microclimatic conditions (Gardiner & Hassall, 2009; Völkl et al., 1993), lower availability of plant resources (Völkl et al., 1993), and an increased risk of predation, for example, by predatory arthropods or bats due to the reduced cover (Arlettaz, 1996; Sonoda et al., 2013). All this can lead to additional losses in arthropods (Van Klink et al., 2019) and the homogenization of arthropod communities (Chisté et al., 2018; Gossner et al., 2016). The net impact of mowing appears to increase with the number of cuts per year (Proske et al., 2022; Watson et al., 2020). This negative effect on arthropods was found to be smaller when there was more time between the mowing and the sampling event (Simons et al., 2014), possibly because mobile arthropods can recolonize grasslands from adjacent unmown sites.

Other techniques for the maintenance of grasslands, such as rolling or leveling, have not yet been investigated, but could also have negative impacts on arthropods through severe disturbance. Rolling is used to flatten the soil and leveling removes surface irregularities caused by soil animals, such as molehills (Mögel, 2020). Such procedures are assumed to compact the soil, support grass, and suppress pressure-sensitive plants. This might also affect grassland arthropods in the long term due to changes in plant composition.

The various aspects of mowing and grassland management could affect arthropod orders differently based on their respective life histories and phenology. For example, in holometabolous insect species where adults can be found in grasslands, their larvae develop not only in meadows but also below ground or in other habitats, rendering them less vulnerable to direct mowing impacts. In taxa, where adults are very mobile, such as pollinators, direct mowing mortality may also be lower, but these species may be sensitive to long-term mowing effects, such as changes in resource availability, vegetation structure, and exposition (Buri et al., 2014). Taxa that complete their entire life history above ground in grasslands, for example, many hemimetabolous insects such as Orthoptera or Auchenorrhyncha (Mühlethaler et al., 2019), seem to be more directly affected by mowing.

While experimental studies showed the effects of individual mowing techniques on arthropods (Humbert, Ghazoul, Richner, et al., 2010; Humbert, Ghazoul, Sauter, et al., 2010; Steidle et al., 2022), few studies have quantified the relative impacts of all aspects together in real-world grasslands, representing all mowing techniques that are actually applied in agricultural grasslands. To fill this gap, we use 11 years of data from 111 grassland sites of the Biodiversity Exploratories (www.biodiversity-exploratories.de) and arthropod community data including Araneae, Coleoptera, Hemiptera, and Orthoptera (Fischer et al., 2010; Vogt et al., 2019; Weisser, Gossner, et al., 2023). For these grasslands, detailed information is obtained for a broad range of mowing, rolling, leveling, grazing, and/or fertilization applications (Vogt et al., 2019). These different management regimes are typically applied simultaneously in real-world managed grasslands and are potentially confounded, unlike in experimental studies. To compare the relative importance of grassland management for arthropod abundance and diversity, it is necessary to disentangle the effects of different practices. We thus explicitly included the breadth of mowing practices in statistical models to facilitate recommendations for arthropod conservation.

We test the following hypotheses:

1. Given the evidence for negative direct and indirect mowing impacts on arthropod abundance and diversity, and because these effects are likely additive, we predict that arthropod abundance and species richness decrease with an increase in the number of cuts per year.
2. Decreases in arthropod abundance and species richness are greatest immediately after mowing and partly recover as the time between mowing and sampling increases.
3. The negative impact of bar mowers is lower than that of rotary mowers, and mowing with a mulcher has the greatest negative impact.
4. Arthropod losses decrease with greater cutting heights.
5. The wider a mower, the smaller is the negative effect on arthropods due to less area overrun by tractor wheels.
6. Intensive grazing, fertilization, rolling, leveling, and the application of a conditioner negatively affect arthropod abundance and species richness.

MATERIALS AND METHODS

Study sites

Data on land use and arthropod diversity were collected annually from 2008 to 2018 as part of the large-scale and long-term project Biodiversity Exploratories (www.biodiversity-exploratories.de), which covers three regions in Germany: (1) Swabian Alb in southwestern Germany (460–860 m above sea level [asl]), (2) Hainich-Dün in central Germany (285–550 m asl), and (3) Schorfheide-Chorin in northeastern Germany (3–140 m asl). These regions are characterized by different environmental factors, such as climate, geology, and topography, as well as varying land use regimes and intensities. The Biodiversity Exploratories contain a total of 150 grassland plots of 50 m × 50 m (50 per region) within larger management units and were randomly selected to cover different intensities of land use and to minimize other influential effects such as soil type or spatial position (Fischer et al., 2010). All three regions contain pastures, meadows, and mown pastures. For our study, we selected only meadows and mown pastures, excluding pastures, which resulted in 111 plots.

Land use characterization

Land use information (Table 1) has been collected annually using a structured questionnaire from all landowners and land users (Vogt et al., 2019, 2023). To represent varying degrees of general land use practices, we assessed (1) mowing by the number of cuts in the previous year, (2) grazing through livestock units per hectare and grazing days (livestock unit × days per hectare), and (3) quantified fertilization as kilograms of nitrogen per hectare (Blüthgen et al., 2012; Ostrowski et al., 2020). The detailed data on land use allow the assessment of the dates of the last cut, information about the mowing machines (bar mower, mulcher, or rotary mower), whether a conditioner was used, the mowing height and width, and the number of rolling and leveling events of the respective year. To test for the direct effects of mowing regimes, we counted the number of cuts conducted in the same year and plot before each arthropod sampling event. In addition, we determined the time since the last cut (days after mowing). Therefore, we only used plots that were mown before the sampling in that year. Day 0 indicates that sampling was performed on the same day directly after mowing. Missing data points for mowing height and width were replaced by the mean value for each plot from all years. The mowing width varied between 2 and 12 m, while the mowing height ranged from 3 to 15 cm. For classifying the mower type, the utilization of mower conditioner, mowing height, and width, we used the information of the last cut previous to the arthropod sampling dates, or if unavailable, we used those collected earliest in the same year for the respective plot.

Arthropod sampling

Arthropods were sampled annually using sweep nets. Sweep netting was conducted along a 150-m transect covering three adjacent plot borders of the 50 m × 50 m plot,

TABLE 1 Descriptions and details about the land use variables used in the models.

Variables	Description and unit	Median	Min	Max
Days after mowing	Time difference (days) between the date of the last cut and the sampling date. Day 0 = directly after mowing, sampling was conducted on the same day after mowing.	37	0	182
Width	Mowing width (m)	6	2	12
Height	Mowing height (cm)	7	3	15
Rolling	No. rolling events per year	0	0	2
Leveling	No. leveling events per year	1	0	3
Cuts prev. year	No. cuts per previous year	1	0	5
Cuts	No. cuts before each arthropod sampling date per respective year	1	1	3
Fertilization	Quantity of nitrogen = kg (N)/ha	50	0	433
Grazing	Livestock units per hectare and days of grazing = livestock unit × days/ha	11.67	0	1480
Conditioner	Binary: Application of a conditioner (yes/no)			
Mower	Categorical: Mower type: Bar mower, mulcher, or rotary mower			

Note: Values (median, minimum, and maximum) were calculated from the larger abundance dataset.

with a total of 60 double sweeps per site. Sampling was restricted to rain-free days with low wind speeds, and only took place after the morning dew was gone. Arthropod sampling was carried out at least twice per year, mainly in June and August, to cover the different phenological peaks of adult arthropods and, thus, as many species as possible (Seibold et al., 2019; Weisser, Gossner, et al., 2023). If sampling was incomplete for a plot, these plot-level data were excluded from the respective year.

All specimens were sorted to order level and adults of Araneae, Coleoptera, Hemiptera (only Heteroptera and Auchenorrhyncha), and Orthoptera were identified to the species level. Few adults (1.1%) that could not be determined at the species level were excluded (Seibold et al., 2019). We used two different datasets for our analyses on arthropods: a species-level dataset for species richness analyses (Weisser, Gossner, et al., 2023), and an order-level dataset for abundance analyses (Staab et al., 2023). The reason for this differentiation is that the order-level dataset contained more observations and included larval stages, except for Coleoptera, in which larvae were not representatively sampled with sweep netting. For the species-level dataset, we included two samples per year, with the earliest date on 21 April and the latest on 23 August (Julian days 148–272) from 2008 to 2018. For the order-level dataset, sampling dates ranged from 6 May to 8 November (Julian days 126–312).

Data analysis

All statistical analyses were performed using R Statistical Software version 4.3.2 (R Core Team, 2022). Two separate generalized linear mixed-effects models were performed for each of the four arthropod orders, with abundance and species richness as response variables. In every model, mowing and grassland management were accounted for by the following fixed effects (predictor variables; for all land use variables summarized, see Table 1): days after mowing, mower type (categorial: bar mower, mulcher, or rotary mower), conditioner application (binary variable), mowing height (in centimeters), mowing width (in meters), rolling (in counts per year), leveling (in counts per year), and number of cuts before arthropod sampling. Further, we characterized the general land use intensity per site and year with the number of cuts (previous year), fertilization (in kilograms of nitrogen per hectare per actual year), and grazing (livestock unit × days per hectare per actual year) as fixed effects. Fertilization and grazing were square-root-transformed to optimally meet the assumption of linear models. Finally, we included the Julian day (i.e., the day of the year) of the different sampling dates, and to account for possible nonlinear phenology, we also included the quadratic Julian day as fixed effects. To account for variation linked to weather, we further included the average daily aboveground temperature (in degrees Celsius, measured 200 cm above ground, from weather stations on each plot or, for some missing data, interpolated data from the German Weather Service) as a variable. In addition, the square-root-transformed precipitation (in mm, RADOLAN product of the German Weather Service) of the previous day was included, as sweep netting does not take place on rainy days (Wöllauer et al., 2023). All numerical fixed effects were scaled to mean = 0 and SD = 1 before the analyses. Due to the spatially and temporally nested design of the sampling, plot nested within region and year were included as crossed random slopes. For abundance models, we fitted four negative binomial models as a result of overdispersion, whereas we assumed Poisson errors for species richness models. To account for the remaining overdispersion, we added an observation-level random effect to the Coleoptera abundance model. We used the glmmTMB package for all models (Brooks et al., 2017).

To determine the true effects on species richness, it is important to consider potential abundance-related relationships based on the "More Individuals Hypothesis" (Srivastava & Lawton, 1998). For comparison, we computed a model with the scaled and log-transformed abundance (log + 1, because we have zeros in our data) of each order as a covariate and a model without this variable. Because species richness and abundance were strongly correlated and the models fitted better when abundance was included (based on difference in Akaike information criterion between models: Araneae = 1126.36, Coleoptera = 1234.18, Hemiptera = 1083.29, Orthoptera = 453.51), we focused on models that were accounted for abundance in our main analysis. Therefore, in the following, we will refer to the abundance-accounted species richness as species richness and the uncorrected species richness as raw species richness, unless specified in more detail. We further analyzed the inverse Simpson index using the vegan package (Oksanen et al., 2022) as a measure of diversity that accounts for species abundance (Appendix S1: Methods and Table S4). We always report marginal effect sizes and test for significance with type II sums of squares in the package car (Fox & Weisberg, 2019). For the categorical fixed effect "mower," we performed a "Tukey" post hoc test and calculated pairwise contrasts using the "glht" function of the multcomp package (Hothorn et al., 2008). Model fit and dispersion were assessed using the DHARMa package (Hartig, 2022) and variance inflation factor (VIF) was assessed using the performance package (Lüdecke et al., 2021). VIFs were always smaller than 4, indicating that there was no serious collinearity between the linear fixed effects. Model predictions and 95% CIs were obtained using the sjPlot package (Lüdecke, 2023). To mitigate type I errors, we used the Benjamini–Hochberg false discovery rate (FDR) correction to obtain adjusted *p* values for the four tests (per arthropod order) performed (Benjamini & Hochberg, 1995). We report the original *p* values, but restrict the results and discussion to the significant values adjusted for FDR.

RESULTS

A total of 162,399 individuals (including juveniles) were collected in 1516 samples from the 111 plots surveyed during the 11 years in the three regions of Germany. The overall numbers of individuals per arthropod order were as follows: Araneae: 24,760; Coleoptera: 22,525; Hemiptera (only Heteroptera and Auchenorrhnycha): 109,958; and Orthoptera: 5156. The total number of identified adult individuals for the species-level dataset was 86,415 from 1217 samples (110 plots), including 105 Araneae, 453 Coleoptera, 244 Hemiptera (only Heteroptera and Auchenorrhnycha), and 21 Orthoptera species.

As a general pattern, days after mowing had the strongest effect on arthropods, affecting both their abundance and raw species richness, as well as partly species richness when accounting for abundance. Also, mower type and mowing width influenced arthropods, but differently depending on the order. The variables grazing and rolling showed little significant effects. In comparison, fertilization, conditioner use, number of cuts, leveling, and mowing height showed no effects. However, when omitting the variable days after mowing, the abundance of all four orders decreased with an increasing number of cuts (Appendix S1: Table S6, Figure S8).

Mowing impact on arthropod abundance

We found a strong and significant increase in abundance with days after mowing for all four orders. Araneae and Hemiptera abundance was more than three times higher on plots that had not been mown for 100 days compared with meadows where sampling took place on the same day the grassland was mown (day 0). The abundance of Coleoptera was more than five times higher, and that of Orthoptera more than seven times higher, on day 100 after mowing (Table 2, Figure 1). Additionally, we tested for an interaction between days after mowing and the number of cuts (Appendix S1: Methods and Table S5). Coleoptera abundance increased strongly on meadows that were only mown once compared with meadows that were mown three times (Appendix S1: Figure S7).

The type of mower also had a significant effect on abundance. Hemiptera and Araneae abundance was higher in meadows that were mown with a rotary mower or bar mower than in meadows that were managed with a mulcher (Table 2, Figure 2). For Coleoptera and

TABLE 2 Summary statistics (estimate, SE, *z* value, and *p* value) of the negative binomial models with the abundance of Araneae, Coleoptera, Hemiptera, and Orthoptera as response variables.

Variables	Estimate	SE	*z*	*p*
Araneae				
Days after mowing	0.349	0.051	6.869	<0.001
Temperature	0.278	0.043	6.465	<0.001
Precipitation	−0.070	0.031	−2.286	0.022
Mulcher—Rotary mower*	−1.174	0.265	−4.428	<0.001
Bar mower—Mulcher*	1.431	0.497	2.879	0.010
Coleoptera				
Days after mowing	0.528	0.069	7.697	<0.001
Julian day	3.055	0.457	6.691	<0.001
Julian day^2	−3.480	0.461	−7.557	<0.001
Temperature	0.188	0.057	3.315	0.001
Hemiptera				
Days after mowing	0.350	0.050	6.953	<0.001
Julian day	2.911	0.325	8.965	<0.001
Julian day^2	−2.885	0.326	−8.860	<0.001
Rolling	0.090	0.035	2.594	0.009
Temperature	0.398	0.040	9.865	<0.001
Precipitation	−0.086	0.029	−2.978	0.003
Mulcher—Rotary mower*	−0.892	0.245	−3.639	0.001
Bar mower—Mulcher*	1.491	0.465	3.207	0.003
Orthoptera				
Days after mowing	0.607	0.095	6.424	<0.001
Width	0.192	0.076	2.546	0.011
Julian day	5.032	0.876	5.748	<0.001
Julian day^2	−6.595	0.932	−7.075	<0.001
Grazing	−0.164	0.061	−2.678	0.007

Note: Sample size = 1516. *p* values were obtained from type II sums of squares and, for mower types, by Tukey's post hoc tests. Only significant variables (after false discovery rate correction) are shown here. Full summary statistics are provided in Appendix S1: Table S1. Asterisk (*) indicates the results of pairwise contrasts (Tukey).

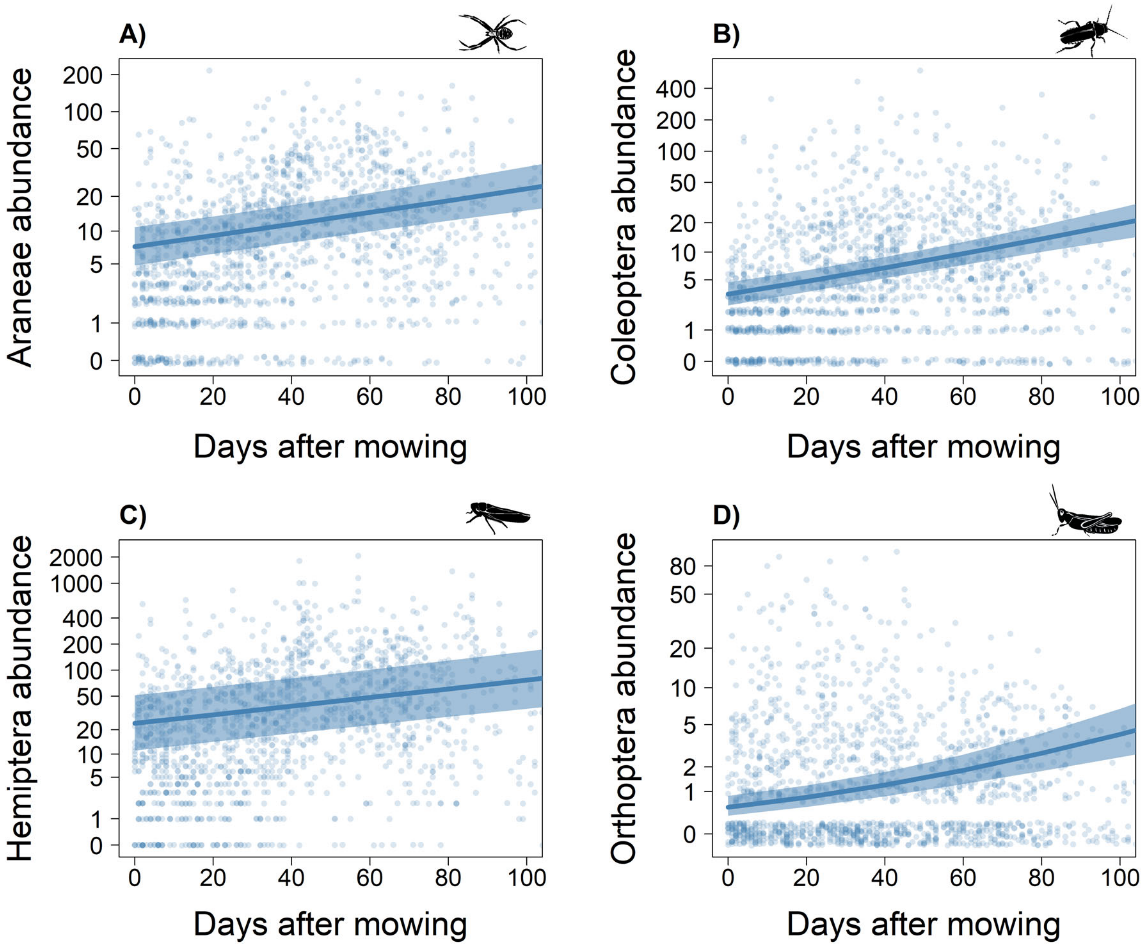

FIGURE 1 Abundance of (A) Araneae, (B) Coleoptera, (C) Hemiptera, and (D) Orthoptera (negative binominal models) increases with the number of days between mowing and the respective sampling date (days after mowing). Sample size = 1516. Points display raw count values, and solid lines (solid = significant after false discovery rate correction) show model predictions accounting for all other covariates (shaded area indicates 95% CIs). For visualization, *y*-axes were log(x + 1) transformed. All arthropod icons are illustrated by Johanna L. Berger.

Orthoptera, we found no significant effect relating to the mower type. However, the utilization of mowers across our study plots was very imbalanced; rotary mowers were used most frequently across all years and regions, comprising 98% of the observations (with mulcher at 1.5% and bar mower at only 0.4%).

Mowing width showed a positive effect on Orthopteran abundance (Table 2, Figure 3). Grazing intensity negatively affected Orthoptera abundance (Table 2, Appendix S1: Figure S3). When rolling was conducted more frequently, Hemiptera abundance increased (Table 2, Appendix S1: Figure S1).

Mowing impact on arthropod species richness

The diversity of arthropods showed similar relationships with management practices as abundances (Appendix S1: Table S3, Figure S5), given that species richness and abundance were strongly correlated in each of the arthropod orders (Table 3). Hence, we focused on the true diversity effects by accounting for log abundance in the models. After this correction, days after mowing affected the species richness of Hemiptera and Coleoptera positively, with species numbers being about 30% higher 100 days after mowing compared with day 0; Orthoptera species richness showed only a positive tendency (Table 3, Figure 4). In comparison, raw species richness models and Simpson diversity models (Appendix S1) showed stronger effects concerning days after mowing, that is, all orders responded positively for raw species richness (Appendix S1: Table S3, Figure S5), but not all for Simpson diversity (Appendix S1: Table S4, Figure S6).

For abundance-accounted species richness, mower type had a significant effect on Coleoptera, with species richness being higher in meadows mown by bar and rotary mowers compared with mulched meadows (Table 3,

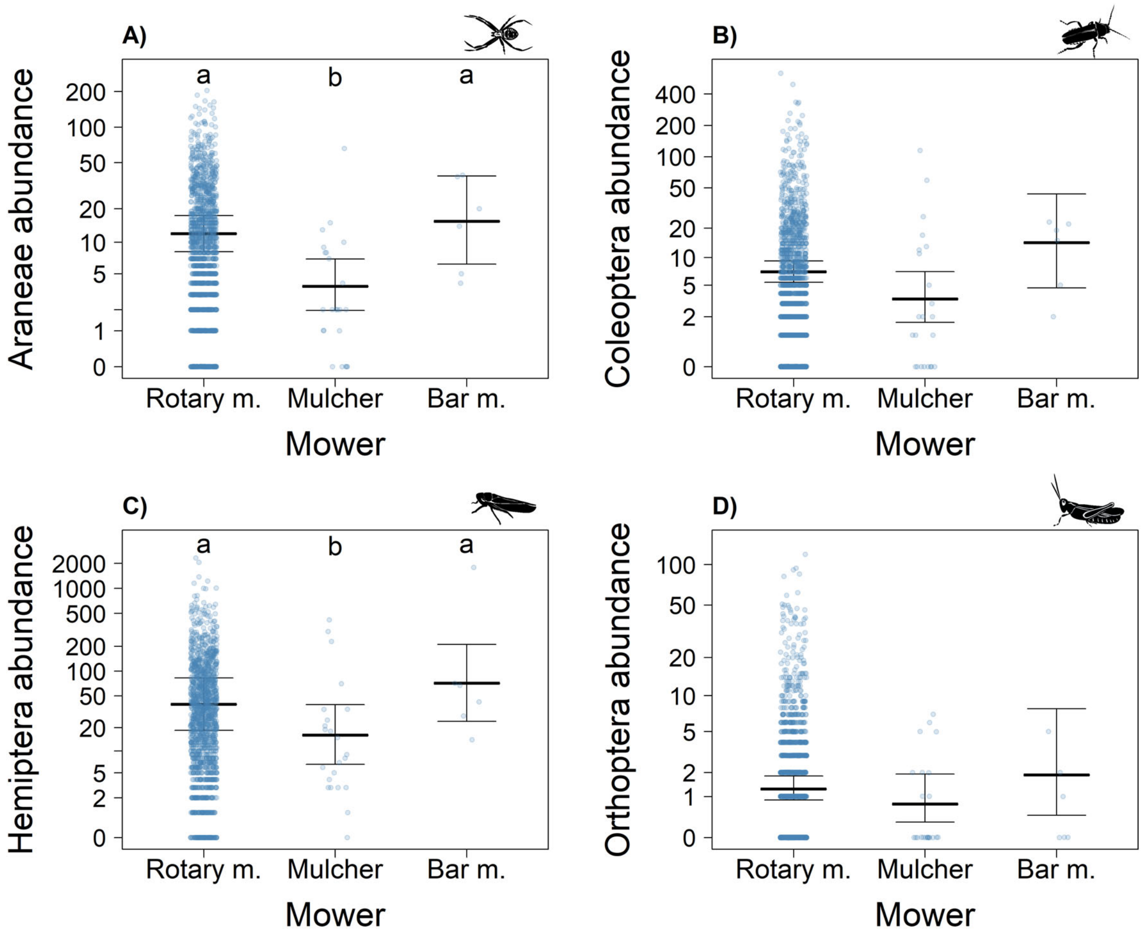

FIGURE 2 Differences in the expected mean abundance of (A) Araneae, (B) Coleoptera, (C) Hemiptera, and (D) Orthoptera in grasslands treated with different mowing machines: rotary mower ($n = 1487$), mulcher ($n = 23$), and bar mower ($n = 6$). Sample size = 1516. Black horizontal lines and error bars show the means and 95% CIs of estimates from models accounting for all covariates, and points display raw values. Lowercase letters indicate significant differences. For visualization, y-axes were $\log(x + 1)$ transformed. Bar m., Bar mower; Rotary m., Rotary mower. All arthropod icons are illustrated by Johanna L. Berger.

Figure S4). Furthermore, rolling affected Hemiptera species richness negatively (Table 3, Appendix S1: Figure S2).

DISCUSSION

This 11-year observational study across 111 real-world grasslands showed strong mowing effects. Overall, the results largely confirmed hypotheses regarding temporal recovery and mower type. Arthropod abundance was lowest immediately after mowing, but gradually recovered over time and reached three to seven times higher levels 100 days after the last mowing. While days after mowing affected raw species richness of all orders, abundance-accounted species richness of Hemiptera and Coleoptera was 30% higher than immediately after mowing. Among the various machines used, the mulcher had the most harmful effect on arthropods. Other grassland management variables had limited effects. Only Hemiptera were affected by rolling, where abundance was positive but species richness was negative. Orthoptera abundance benefited significantly from wider mowers, but none of the other three arthropod orders did. Fertilization had no significant effects on arthropods, while intensive grazing only affected Orthoptera abundance negatively.

Arthropod abundance and species richness increase with days after mowing

Mortality, together with emigration, is the most important reason for the direct reduction of arthropods after mowing, according to a few experimental studies (Humbert, Ghazoul, Sauter, et al., 2010; Steidle et al., 2022; Thorbek & Bilde, 2004). Supporting these findings, our investigation in real-world grasslands revealed significantly fewer arthropods on meadows

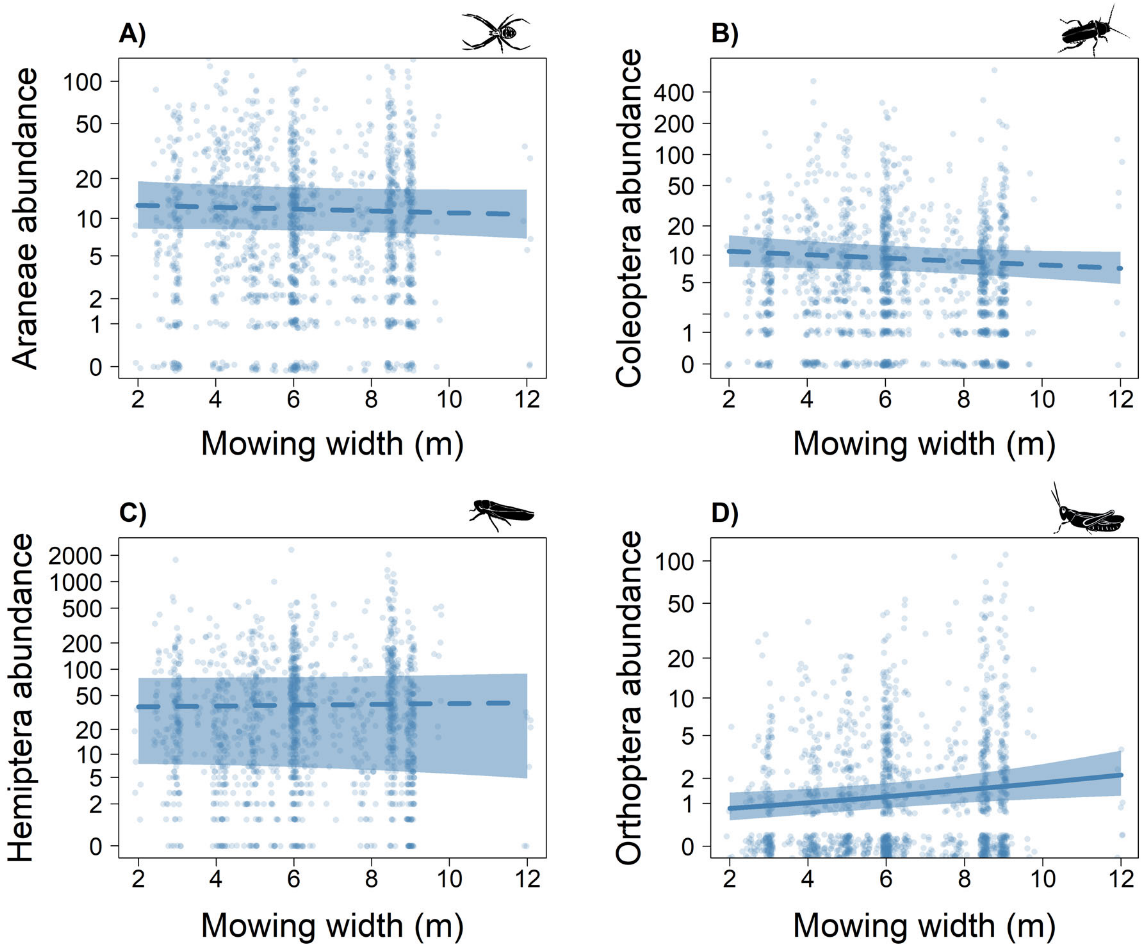

FIGURE 3 Abundance of (A) Araneae, (B) Coleoptera, (C) Hemiptera, and (D) Orthoptera (negative binomial models) responding differently to mowing width (in meters). Sample size = 1516. Points display raw count values, and lines (dashed = nonsignificant, solid = significant after false discovery rate correction) show model predictions accounting for all other covariates (shaded area indicates 95% CIs). For visualization, y-axes were $\log(x + 1)$ transformed. All arthropod icons are illustrated by Johanna L. Berger.

immediately after mowing, unlike meadows where the mowing event occurred further in the past. In agreement with our findings, both Heteroptera (Tribe Stenodemini) and Orthoptera populations (*Chorthippus mollis*) were found to be reduced after mowing in other European studies (Bockwinkel, 1988; Thorens, 1993). Additionally, Lafage and Pétillon (2014) showed a negative response in the abundance of ground beetles (Carabidae) and Araneae after mowing, but respective cutting dates modulated the responses. In fact, we found a strong constant increase in abundance along days after mowing for all four studied orders. Analysis of the interaction between days after mowing and number of cuts showed that the negative effect of mowing was additive for Coleoptera, with higher abundance increases on once-mown than frequently-mown meadows. The other three orders showed no differences. However, when the variable days after mowing was omitted, the negative effect of the number of cuts on arthropod abundance emerged, showing the strong direct effect of the mowing event itself. Our results indicate a direct negative impact of mowing due to mortality or displacement of arthropods, followed by an increasing abundance with time after mowing. Such "recovery" may partly mirror additional hatching of larvae after (or because of) mowing, for example, from eggs in the soil due to the altered warmer microclimate once vegetation is shorter, or even resulting from the reproduction of survivors. More likely, however, this increase indicates a recolonization of individuals that emigrated from mowing, or colonization of new individuals from surrounding habitats or unmown grasslands. Such colonization depends on the availability and connectivity of source habitat in the surrounding landscape, but also on species characteristics such as mobility (Collinge, 2000). For example, grassland species that disperse poorly showed stronger temporal declines at sites surrounded by a high cover of arable fields compared with strong dispersers (Seibold et al., 2019).

TABLE 3 Summary statistics (estimate, SE, *z* value, and *p* value) of the four abundance-accounted models with the species richness of Araneae, Coleoptera, Hemiptera, and Orthoptera (generalized mixed models) as response variables.

Variables	Estimate	SE	*z*	*p*
Araneae				
Abundance	0.890	0.026	33.686	<0.001
Coleoptera				
Abundance	0.714	0.017	42.225	<0.001
Days after mowing	0.076	0.028	2.751	0.006
Julian day	−0.870	0.354	−2.457	0.014
Julian day^2	0.812	0.353	2.303	0.021
Mulcher—Rotary mower*	−0.522	0.162	−3.224	0.003
Bar mower—Mulcher*	0.659	0.230	2.871	0.011
Hemiptera				
Abundance	0.616	0.018	33.475	<0.001
Days after mowing	0.072	0.019	3.717	<0.001
Julian day	1.462	0.279	5.235	<0.001
Julian day^2	−1.432	0.276	−5.191	<0.001
Rolling	−0.049	0.014	−3.481	<0.001
Orthoptera				
Abundance	0.710	0.030	23.441	<0.001
Julian day	3.865	1.019	3.792	<0.001
Julian day^2	−3.415	0.990	−3.451	0.001

Note: Sample size = 1217. *p* values were obtained from type II sums of squares and, for mower types, by Tukey's post hoc tests. Only significant variables (after false discovery rate correction) are shown here. Full summary statistics are provided in Appendix S1: Table S2. Asterisk (*) indicates the results of pairwise contrasts (Tukey).

Moreover, intensively managed grasslands harbor a greater proportion of species with high dispersal ability (Simons et al., 2016). As a result, the recovery rate of species populations after mowing may depend on species characteristics, but this needs to be further investigated.

To disentangle the effect of mowing on arthropod species richness from the effects of mowing on individual numbers, we accounted for differences in abundance in the models. Abundance was always positively correlated with species richness, supporting our assumption based on the "More Individuals Hypothesis," which states that higher abundance due to a higher resource availability allows for a greater number of species (Srivastava & Lawton, 1998). Accordingly, the more individuals are killed by mowing, the greater the likelihood that the population size will be reduced to the point where the species cannot reproduce locally and will be lost from the grassland. The effects of days after mowing on abundance-accounted species richness were smaller than in models with raw species richness, indicating that mowing directly reduces the abundance of grassland-dwelling arthropods and thus diversity. However, the mowing impacts of the abundance-accounted models showed that effects are not only driven by abundance but also influence arthropod diversity including less abundant species.

We found a negative effect of mowing on Coleoptera and Hemiptera species richness that was not explained by reduced abundance, while the other arthropod orders were not significantly affected. The negative effects of intensive mowing on Coleoptera and Hemiptera species richness have also been shown in other studies (Chisté et al., 2018; Proske et al., 2022; Unterweger et al., 2017). The inconsistent effects on species richness across the four arthropod orders (effects on Coleoptera and Hemiptera, but not on Araneae and Orthoptera) could partly reflect differences in traits, such as mobility (Collinge, 2000) or differences in developmental and overwintering characteristics that may make arthropods more or less vulnerable depending on phenology (Heimer & Nentwig, 1991; Ingrisch & Köhler, 1998; Mühlethaler et al., 2019; Rheinheimer & Hassler, 2013, 2018). In addition, Araneae as predators and Orthoptera as herbivorous or omnivorous generalists exhibit more generalistic feeding behavior, making them more likely to inhabit previously mown meadows than the more specialized Coleoptera and Hemiptera. Among the Hemiptera, Auchenorrhyncha are particularly sensitive to mowing date, which is likely related to their high host plant specificity (about 40% are monophagous; see Chisté et al., 2018). Because these species are less flexible in finding a new host after disturbance, these specialists may be particularly vulnerable to mowing, and freshly mown meadows are unsuitable habitats for them (Mühlethaler et al., 2019).

Types of mowing and grassland management techniques influence arthropods

Rotating mowing techniques, such as mulchers and rotary mowers, clearly cause higher mortality rates than bar mowers (Humbert, Ghazoul, Richner, et al., 2010; Humbert, Ghazoul, Sauter, et al., 2010; Richner et al., 2019), which highlights the importance of mower choice for more insect-friendly grassland management (Steidle et al., 2022). However, due to their efficiency and robustness, rotary mowers are the most widespread in Germany, and thus dominate our dataset of representative agricultural grasslands (98% rotary mower). Our results suggest that mulchers are more destructive than

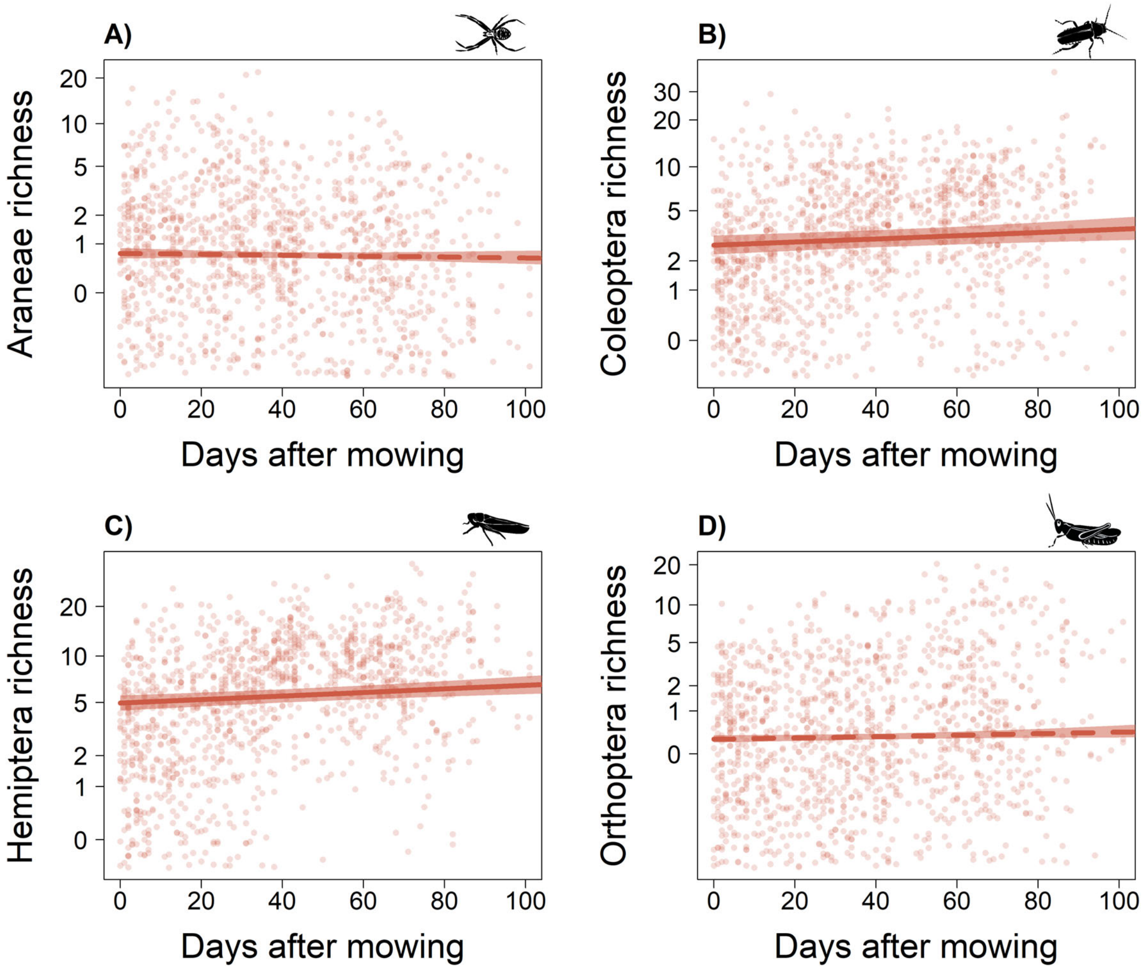

FIGURE 4 Abundance-accounted species richness of (A) Araneae, (B) Coleoptera, (C) Hemiptera, and (D) Orthoptera (generalized mixed models, except Coleoptera: Negative binomial model) in response to the number of days between mowing and the respective sampling dates (days after mowing). Sample size = 1217. Points display raw count values, and lines (dashed = nonsignificant, solid = significant after false discovery rate correction) show model predictions accounting for all other covariates (shaded area marks 95% CIs). For visualization, *y*-axes were log(x + 1) transformed. All arthropod icons are illustrated by Johanna L. Berger.

bar and rotary mowers. Mulchers had the strongest negative impact on Araneae and Hemiptera abundance, as well as on the species richness of Coleoptera. Because the mulcher crushes and shreds the cut grass, it is plausible that this technique causes high mortality among grassland-dwelling arthropods. Indeed, our finding that mulching is more harmful to arthropods than mowing is supported by the few studies on this topic (Löbbert et al., 1994; Richner et al., 2019). In addition to direct mortality, mulching also leads to a higher nutrient input and changes in microclimate from the cut grass left on the meadow. Mulching can therefore reduce plant species richness and diversity and alter plant composition compared with mowing with biomass removal (Gaisler et al., 2019). This may affect arthropods differently depending on their microhabitat preferences, life cycle, predator–prey relationships, and adaptability. For instance, changes in plant species composition can be particularly relevant for mono- and oligophagous species, many of which are Hemiptera or Coleoptera (Mühlethaler et al., 2019; Rheinheimer & Hassler, 2013).

To date, the effects of mowing width on living arthropods have not been studied systematically. However, our results showed an increase in Orthopteran abundance with mowing width, supporting the recommendation of Humbert, Ghazoul, Sauter, et al. (2010) that reducing the run-over area using wider machines decreases the damage to arthropods by tractor wheels. Another advantage of wider machines is the reduced working time in the meadow. However, orders other than Orthoptera were not influenced by mowing width in our study. A possible explanation could be different traits, such as body size and shape, or escape strategies. Orthopterans are likely more sensitive to a smaller mowing width and increased run-over area because of their larger body size (Humbert, Ghazoul, Sauter, et al., 2010; Oppermann et al., 2000).

In contrast, it could be hypothesized that lighter individuals such as Coleoptera or Hemiptera may be sucked into rotating mowers more easily, but might be less affected by the run-over area due to their smaller body size. Moreover, Orthoptera by being more mobile may be better capable of escaping from wider machines than other arthropods. Also, distinct escape strategies could be affected differently by mowing width: Orthoptera mostly jump, while Coleoptera and Araneae drop to escape from predators (Humphreys & Ruxton, 2019). Our results leave room for speculation and highlight the need for further experimental research (Weisser, Blüthgen, et al., 2023) on the various characteristics of arthropods and their escape behavior in the presence of mechanical disturbances such as mowers.

We found no significant effects of the use of a conditioner on arthropods. However, other studies have already proven the negative impact of conditioner use, but also that subsequent harvesting (tedding, raking, baling) strongly reduces insect densities and may therefore be a reason for not finding differences between all mowing techniques (Hecker et al., 2022; Humbert, Ghazoul, Richner, et al., 2010). To date, no studies have been conducted on other grassland management techniques such as rolling or leveling. Leveling removes the unevenness of the surface and is probably less invasive than rolling as it is not supposed to compress the soil as rolling does (Mögel, 2020). Hemiptera abundance responded positively to rolling in our study. One explanation could be that the abundance of some generalist species has increased in rolling-treated meadows, due to a wider niche and their ability to be more resilient, dispersing, and having lower habitat requirements (McKinney & Lockwood, 1999). In addition, rolling could benefit some species by reducing succession and creating more open ground patches. In the case of Auchenorrhyncha, some generalists have been shown to benefit more from intensive land use while being more abundant than specialists (Chisté et al., 2018). Such winners in our study sites are *Macrosteles cristatus*, *Macrosteles laevis*, *Psammotettix alienus*, and *Psammotettix confinis* (Chisté et al., 2018), which are very common and mostly mobile pioneer species that benefit from disturbed sites (Mühlethaler et al., 2019). At the same time, the species richness of Hemiptera was strongly reduced by rolling. This may be because hemipterans, with many feeding specialists, could be negatively affected indirectly because rolling possibly displaces many plants that are sensitive to soil compaction.

Our study found no negative effects of fertilization on arthropods and indicates that grazing can be detrimental to Orthoptera abundance, but only when it is intensive. A meta-analysis has found that high grazing intensity reduces arthropod abundance and species richness, very likely induced by lower plant coverage and changes in habitat properties (Wang & Tang, 2019), while responses to grazing intensity varied among arthropod taxa. However, Chisté et al. (2016, 2018) found that grazing had the least negative impact on Orthoptera compared with mowing and fertilization. Grazing, if not too intensive, is generally a less disruptive type of grassland management than mowing while creating greater habitat heterogeneity for arthropods (Bucher et al., 2016; Weiss et al., 2013).

CONCLUSION

Our unique long-term arthropod survey, covering more than 100 plots across three regions of Germany, consistently shows that the abundance and raw species richness, and to some extent the abundance-accounted species richness, of grassland arthropods are reduced after mowing. The study's findings indicate a gradual recovery of arthropods after mowing, suggesting that carefully planned mowing regimes, especially reduced mowing frequency, could mitigate the negative effects of mowing on biodiversity. Although each mowing event is detrimental due to arthropod mortality or emigration and may mask other technical aspects, we also suggest that the impact of technical aspects should be further investigated. Rotational mowing techniques, in particular mulchers, are the most harmful. However, compared with the more insect-friendly bar mowers, rotary mowers and mulchers are much more commonly used. In conclusion, we recommend for arthropod-friendly management: the use of bar mowers (Humbert, Ghazoul, Richner, et al., 2010; Humbert, Ghazoul, Sauter, et al., 2010; Van de Poel & Zehm, 2015), the development of less damaging rotary mowers or mulchers (Steidle et al., 2022), and, most importantly, solutions through management change, such as reduced mowing, partial mowing (creation of refuges), and extensive grazing instead of mowing.

AUTHOR CONTRIBUTIONS

Johanna L. Berger, Michael Staab, and Nico Blüthgen conceived the ideas. Nadja K. Simons, Konstans Wells, Martin M. Gossner, Juliane Vogt, Andreas Hemp, Wolfgang W. Weisser, Sebastian Seibold, and Rafael Achury collected and managed the data. Johanna L. Berger analyzed the data with the support of Michael Staab and Nico Blüthgen. Johanna L. Berger wrote the manuscript and appendices, with oversight from all other authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

This work is based on raw data available in the Biodiversity Exploratories Information System as follows: arthropod species (accession no. 21969) Weisser, Gossner, et al. (2023) at https://www.bexis.uni-jena.de/ddm/data/Showdata/21969; arthropod orders (accession no. 31488) from Staab et al. (2023) at https://www.bexis.uni-jena.de/ddm/data/Showdata/31488; sampling dates (accession no. 17018) from Gossner and Weisser (2023) at https://www.bexis.uni-jena.de/ddm/data/Showdata/17018. Public climate data can be accessed via the Biodiversity Exploratories Information System climate data tool at https://www.bexis.uni-jena.de/tcd/PublicClimateData/Index; to query these public climate data, select "export," all grassland plots (AEG, HEG, SEG), and the parameters "Ta_200" for mean air temperature and "precipation_radolan" for precipitation (note: these data are not spatially aggregated by default and are aggregated by day for the years 2008–2018). Detailed land use data are available in the Biodiversity Data Journal from Vogt et al., 2019 at https://doi.org/10.3897/BDJ.7.e36387.

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SUPPORTING INFORMATION

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

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