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LETTER

Functional redundancy of weed seed predation is reduced by intensified agriculture

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Abstract

Intensified agriculture, a driver of biodiversity loss, can diminish ecosystem functions and their stability. Biodiversity can increase functional redundancy and is expected to stabilize ecosystem functions. Few studies, however, have explored how agricultural intensity affects functional redundancy and its link with ecosystem function stability. Here, within a continental-wide study, we assess how functional redundancy of seed predation is affected by agricultural intensity and landscape simplification. By combining carabid abundances with molecular gut content data, functional redundancy of seed predation was quantified for 65 weed genera across 60 fields in four European countries. Across weed genera, functional redundancy was reduced with high field management intensity and simplified crop rotations. Moreover, functional redundancy increased the spatial stability of weed seed predation at the field scale. We found that ecosystem functions are vulnerable to disturbances in intensively managed agroecosystems, providing empirical evidence of the importance of biodiversity for stable ecosystem functions across space.

KEYWORDS
arable plants, carabids, ecosystem services, hierarchical modelling of species communities

INTRODUCTION

Intensified agriculture, characterized by intensive use of new pesticides and fertilizers coupled with a simultaneous decrease in crop species diversity (Matson et al., 1997), along with landscape simplification, are two of the main drivers of biodiversity loss (Kotze & O'Hara, 2003; Outhwaite et al., 2022). These drivers can reduce biodiversity via a range of mechanisms. Increased management intensity can erode biodiversity through more frequent disturbances and reduced crop rotation diversity (Geiger et al., 2010; Tiemann et al., 2015), while landscape simplification impairs biodiversity through reduced availability of semi-natural habitat and habitat heterogeneity (Batáry et al., 2012; Weibull et al., 2003). It is also becoming evident that biodiversity loss due to agricultural intensification and landscape simplification can impede ecosystem functions. For example, in a synthesis, Dainese et al. (2019) showed that biodiversity loss as a result of reduced landscape heterogeneity led to reductions in the strength of pollination and biological pest control in agroecosystems. Moreover, in addition to these immediately observable effects, the loss of biodiversity can reduce the resilience of ecosystem functions to disturbances (Hooper et al., 2005; Isbell et al., 2018). Up to now, studies of the effects of intensified agriculture and landscape simplification on biodiversity-driven ecosystem functions have almost exclusively focused on the level of these functions (Rusch, Chaplin-Kramer, et al., 2016) and only a few have explored the effects on stability or degree of variability (Larsen & Noack, 2021; Rusch et al., 2013). Consequently, the ecological effects of functional redundancy, as the diversity of functionally equivalent species (Rosenfeld, 2002), and its role in providing stability of ecosystem functions remain poorly explored within real-world scenarios.

Functional redundancy has been proposed as one mechanism by which biodiversity can increase the stability (or reduce the variability) of ecosystem functions such as pest predation, in space and time (Biggs et al., 2020; Cardinale, 2012; Loreau & de Mazancourt, 2013). The insurance hypothesis predicts that stability arises when functionally similar species respond differently to environmental perturbations and compensate for changes in each other's contribution to functioning (Yachi & Loreau, 1999). With higher levels of functional redundancy within a functional group, for example predators of crop pests in agriculture, there is an increased likelihood that at least some species can deliver the ecosystem function (in this case predation) when other species are lost or inactivated due to a disturbance or adverse environmental conditions (de Bello et al., 2021; Thibaut & Connolly, 2013). While the relationship between functional redundancy and stability has been challenged by theoretical studies in the past (May, 1973; Pimm & Lawton, 1978), experimental studies suggest that high functional redundancy can reduce the impact of species loss on ecosystem functions (Hallett et al., 2017; Sanders et al., 2018). Furthermore, a synthesis of empirical studies shows that the correlation between functional redundancy and ecological stability and resilience is positive (Biggs et al., 2020).

Methodological difficulties in evaluating the contribution of functionally equivalent species to an ecosystem function, and thus quantifying the levels of functional redundancy, have hampered its broader use in ecology (de Bello et al., 2021). Analyses of functional redundancy have more typically used less precise proxy metrics, such as the diversity of species and traits or the relationship between species diversity and functional diversity (Laliberté et al., 2010; Pillar et al., 2013). Molecular diet analysis has been proven as a powerful tool to evaluate the contribution of functionally equivalent species and unravel specific trophic relationships within biodiverse food webs (King et al., 2008; Pompanon et al., 2012). Combining the molecular trophic data with metabolic theory (Brose et al., 2008; Brown et al., 2004), allows for the quantification of redundancy at the level of a specific ecosystem function (Feit et al., 2019).

Using this approach, we assess the functional redundancy of the ecosystem function of weed seed predation and then explore how it is affected by agricultural intensity at the field scale and by landscape simplification. Predation of weed seeds by seed predators such as carabid beetles is an ecosystem function that contributes to biological weed control (Carbonne et al., 2020; Daouti et al., 2022). Functional redundancy of weed seed predation has never been directly quantified using field data, in part due to difficulties in specifying predator seed choices in the field. Nevertheless, the considerable overlap in seed preferences between different seed feeding carabid species found in laboratory studies (Petit et al., 2014; Saska et al., 2008) and modelling approaches inferring interaction strength between carabids and seeds (Pocock et al., 2021), indicate that functional redundancy within this guild is high. Field management intensity can decrease seed predator diversity (Menalled et al., 2007; Purtauf et al., 2005) which is likely to reduce functional redundancy at the field scale and hence also the spatial stability of weed seed predation rates (Lami et al., 2020). If this is the case, fields dominated by communities of seed predators with high functional redundancy will provide insurance effects, leading to lower spatial variability (i.e., higher spatial stability), of seed predation to occur by at least some species at the field scale when others are lost.

Here we use data from a standardized continental-wide study in 60 cereal fields in four European countries, to quantify functional redundancy in weed seed predation within the functional group of carabid seed predators. Molecular dietary data from 5738 field-sampled carabids that tested positive for the presence of plant DNA, were used to estimate the level of functional redundancy in predation of 65 weed genera as the exponential Shannon entropy of predation risk for each weed genus (Feit et al., 2019). With Hierarchical Modelling of Species Communities (HMSC) (Ovaskainen et al., 2017) we test how different aspects of agricultural intensity, namely field management intensity, crop rotation diversity at the field level, and landscape simplification, affect the functional redundancy of predation on each weed genus and Linear Modelling (LM), to test the relationship between functional redundancy and within-field spatial stability of weed seed predation. We hypothesize that the functional redundancy of carabid seed predator communities will be reduced by agricultural intensity at the field scale and by landscape simplification and that in turn, should result in reduced spatial stability (increased variability) of weed seed predation. To test the latter hypothesis that functional redundancy enhances the within-field spatial stability (degree of variability) of weed seed predation, functional redundancy of *Poa* predation was related to empirical field estimates of predation of the same weed *Poa annua* on seed cards. We found that agricultural intensity at the field scale but not landscape simplification reduced the functional redundancy of weed seed predation and a weak but positive relationship between functional redundancy and the spatial stability of *P. annua* predation. This demonstrates the importance of maintaining a diversity of functionally equivalent species to safeguard resilient ecosystem functioning.

METHODS

Study location and sampling design

The study was conducted in 60 cereal fields (Figure S1; Table S1) across four European countries in 2018: France (FR), Austria (AT), Czech Republic (CZ), and Sweden (SE) (i.e., 15 fields per country) to cover a landscape gradient ranging from 5% to 95% of arable land within 1 km^2 of each field. Four fields were sown with winter barley and 56 with winter wheat, while field size was 5.58 ± 3.85 ha (mean ± SD) (Table S2). In each field, sampling was carried out along four transects, each starting at another field edge, with sampling points at 4, 8, 16 and 32 m into the field (Figure S2). Collection of carabid seed predators for molecular gut content analysis, estimation of carabid activity density as well as the approximation of *P. annua* predation rates with seed cards, were conducted during two sampling sessions between May and July 2018 (for details see Figure S3).

Sampling of carabid predator activity density

In each field, the activity density of carabid seed predators was estimated using pitfall traps. At each of the four sampling points along each transect, a polypropylene pipe (7 cm diameter, 15 cm depth) was buried level with the soil surface, resulting in a total of 16 traps per field (Figure S2). A plastic cup (7 cm diameter, 7 cm depth) was placed inside each pipe and filled with approximately 100 mL of a water-salt (NaCl) solution and fragrance-free detergent to reduce surface tension. Above each trap, a cover was installed to avoid flooding (Figure S3). After 7 days, traps were emptied and carabids were counted and identified to species level following the nomenclature of Löbl and Smetana (2003).

Molecular gut content analysis

To collect carabid beetles for molecular gut content analyses (MGCA) we placed two additional pitfall traps, at each sampling point, resulting in a total of 32 traps per field for trapping alive carabid beetles (Figure S2). These traps contained wood chips to increase the surface within the trap and reduce the risk of intraguild predation (King et al., 2008) (Figure S3) and were deployed simultaneously to the pitfall traps with salt solution and setting of the *P. annua* seed cards. After 24 h, the traps containing wood chips were inactivated and alive carabids were collected for the next steps of the MGCA. Each individual was placed in a 1.5, 2 or 5 mL reaction tube (Eppendorf, Germany) depending on body size. Samples were stored in cooling boxes and on the sampling day, the beetles were stimulated to regurgitate in the laboratory as described by Wallinger et al. (2015). A total of 10,088 regurgitate samples were collected. After regurgitation, carabids were identified at the species level and released into an appropriate habitat. Regurgitates were cooled and then mixed with 205 μL lysis buffer (or 300 μL for larger carabids) of 5 μL proteinase K (20 mg/mL) and 200 μL TES-buffer. Depending on the infrastructure in each country, regurgitates were stored at −20°C to −30°C and then transported at freezing temperature to the Applied Animal Ecology laboratory at the Department of Zoology, University of Innsbruck, Austria, for further analysis.

Molecular gut content analysis was performed in two steps. First, all regurgitate samples of the 10,088 collected carabid individuals were tested for the presence of plant DNA with a general plant primer pair using diagnostic multiplex PCRs, following the methodology described by Wallinger et al. (2015) and Frei et al. (2019). During this step, 5738 samples out of 10,088 collected that tested positive for the presence of plant DNA, were selected for additional high-throughput sequencing (HTS) to identify the weed genera that had been consumed. The internal transcribed spacer 2 (ITS2) nuclear marker region was targeted with a modified version of the reverse plant primer Uni-plantR (Moorhouse-Gann et al., 2018), cut by two bases at the 5′ end, resulting in the sequence

(5′-CGHYTGAYYTGRGGTCDC-3′), and a modified forward primer UniPlantF2 (Guenay-Greunke et al., 2021), extended by two bases at the 5′ end, the final sequence being (5′-AGGGCACGYCTGYBTGG-3′). Libraries were prepared with a custom-made unique-dual indexing approach, combined with nested tagging (Kitson et al., 2019) to allow for simultaneous sequencing of a larger number of samples. Libraries were prepared in the laboratories of Sinsoma (Innsbruck, Austria) and sequenced at the Vienna BioCenter Core Facilities VBCF (Vienna, Austria).

The final plant-DNA data set is based on reads with a length of at least 190 bp and a reference database match of 99% identity or higher. All sequences coding for organisms other than plants were removed. Reads were summarized at species, genus or family level, and a final cut-off was set at *total reads per batch* $\times 10^{-5}$ as a minimum number of reads per taxon to remain in the dataset. In the majority of the 63 sample batches, the negative controls did not contain sequence reads, but if they did, the corresponding taxon was removed from the entire batch. The resulting plant reads were evaluated for plausibility by a botanist and summarized into aggregated taxa. For the next step of the analysis, data derived by HTS was pooled to weed genus detections per individual carabid species and field. Detections were grouped for 65 weed genera that had at least 10 detections within the carabid guts and that were present in the fields during separate seedbank surveys (for details see Appendix S1). Weed genera that were not present in the fields and had less than 10 detections, were grouped into one category (‘other’). We pooled detections for both sampling sessions and weed genus level to increase the number of detected interactions per predator and thereby increase the strength of our analysis. For details on sample preparation, selection, library preparation for HTS and bioinformatics sequence processing, see Appendix S1. Based on these data, we calculated the feeding probability of each weed genus for each carabid species in each field based on the total number of weed genera consumed in each field.

Functional redundancy of weed seed predation

Functional redundancy of the predation of each weed genus in each field for both sampling sessions was estimated following the methodology developed by Feit et al. (2019), expressed as the exponential Shannon entropy of each carabid species-specific predation pressure R_{ij} on each weed genus:

$$e^{H_j'} = \exp\left(- \sum R_{i,j} \times \ln\left(R_{i,j}\right)\right)$$

The species-specific predation pressure $R_{i,j}$ was calculated as a function of each carabid species' i feeding probability p_{ij} on a specific weed seed genus j in each sampled field, its metabolic rate I_i, as an approximation of a species consumption rate, and its activity density A_i as estimated from the pitfall traps:

$$R_{i,j} = p_{i,j} \times A_i \times I_i$$

The feeding probability $p_{i,j}$, was derived from the presence–absence HTS data. According to metabolic theory, the metabolic rate I_i scales as a function of body mass, and consumers' feeding rates follow the same relationship (Brown et al., 2004). Therefore, feeding rates were approximated as each species' metabolic rate (Brose et al., 2008):

$$I_i = 0.544 \times M_i^{3/4}$$

where 0.544 is a normalization constant for carabid species (Ehnes et al., 2011) and M_i is the average dry body mass (mg) of each carabid species i. Dry body mass was approximated as a function of each carabid species body length (Jarošík, 1989). Species-specific average body length (mm) retrieved from Lindroth (1985).

Predation rate estimates of *Poa annua*

To estimate predation rates by carabid seed predators, seed cards were deployed on the soil surface (Daedlow et al., 2014; Westerman et al., 2003). Each card had 50 seeds of the weed *Poa annua*, a species selected because of its wide geographical distribution and high level of attractiveness to several spring breeding carabids (Saska et al., 2008). Seeds were glued to a 95 × 40 mm card of sandpaper (grain size 60) and enclosed in a mesh cage ($1\,\text{cm}^2$ wire mesh) to exclude vertebrate predators (Figure S3). One seed card was placed at each of the four sampling points on each transect, resulting in a total of 16 seed cards per field (Figure S2). The seed cards were collected after 7 days of exposure to predation. Seed predation of *P. annua* was estimated as the proportion of seeds removed from each seed card to the number of offered seeds.

Agricultural intensity and landscape simplification variables

Two aspects of agricultural intensity and two aspects of landscape simplification were quantified for each field: field management intensity, approximated by the number of field visits by the farmer to conduct operations, from the crop sown (including soil preparation) until harvest, crop rotation diversity, calculated as the Shannon diversity index of the crops sown in the same field during the previous 5 years ($\text{SCDI} = 1 - \sum_{i=1}^{n} p_i \ln p_i$), landscape simplification, approximated as the proportion of semi-natural habitat surrounding each field (pSNH), and the length (m) of the interface between crops and semi-natural habitat (iSNH).

Field management and crop rotation data were collected by sending questionnaires to the farmers managing the selected fields (Table S3). Number of field visits was selected as a proxy of each field's management intensity since it represents each field's frequency of disturbance, and previous analysis has shown that the same metric has an impact on carabid species abundance and diversity (Carbonne et al., 2022). The field operations that were performed during the field visits were pre-sowing soil preparations, pesticide applications (including insecticides, herbicides and fungicides), fertilizer applications, mechanical weed control, and harvest. If several operations were performed during the same visit (e.g. application of both herbicides and fungicides), these were considered as one field visit. Field visits were positively correlated with the number of all pesticides used (Spearman correlation: $r=0.83$, $p<0.001$). For details on the contribution of each operation on the field visits, see Figure S4 and Table S4. Field management intensity represented a gradient from 4 to 18 field visits (10±4; mean±SD; Table S2). The Shannon diversity index (SCDI) was considered an appropriate metric to describe crop rotation diversity since carabid species abundance and diversity can increase with higher diversity of crops sown in rotation (Eyre et al., 2012; O'Rourke et al., 2008). Crop rotation diversity ranged from 1 to 2.61 (2.08±0.35; Table S2).

To quantify landscape simplification variables, circles of 1 km^2 were created centred in each field using ArcGIS 10.6. We selected this spatial scale since it is a relevant scale to detect the landscape response of carabid communities in agricultural systems (Rusch, Binet, et al., 2016). In the software CHLOE 4.0 (Boussard & Baudry, 2017) a rasterized map was produced with a pixel size of 2 m. The rasterized map was based on the Corine Land Cover (CLC) classification with geometrical accuracy of ca. 100 m and available national databases for each country (Table S5). With additional field surveys, we validated the annual crops grown during the sampling season in 1 km radius around each field. The map was used to calculate the proportion of semi-natural habitat (pSNH) and the length (m) of the interface between crops and semi-natural habitat (iSNH). These two landscape variables were selected to represent both compositional and configurational landscape heterogeneity since it has been shown that carabid species abundance and diversity depend on both the amount and configuration of habitat (Chaplin-Kramer et al., 2011; Martin et al., 2019). The proportion of semi-natural habitat (pSNH) surrounding each field ranged from 0.01 to 0.74 (0.28±0.18; Table S2) while iSNH ranged between 266 and 13,064 m (4596±2899; Table S2). For details on landscape analysis and habitat types see Table S6 in Appendix S1.

Statistical analysis

To examine the effects of agricultural intensity and landscape simplification on the redundancy of predation of each weed genus, Hierarchical Modelling of Species Communities (HMSC) (Ovaskainen et al., 2017) was adopted. This approach relates community responses to environmental covariates while accounting for random effects related to sampling design. Two matrices were built for the analysis, each with every sampled field on individual rows. In the columns, one matrix included estimations of functional redundancy for each weed genus, and the other included the aspects of agricultural intensity and landscape simplification: field management intensity (number of field visits), SCDI (Shannon diversity index of the crops sown in the same field during the previous 5 years), iSNH and pSNH representing landscape heterogeneity, and Country. One model was fitted with the matrix containing the redundancy of each weed genus in each field as the response variable, using a log-normal link function. The matrix of the explanatory variables consisted of the aspects characterizing agricultural intensity, landscape simplification and country was included as a random effect to account for similar management and landscape characteristics within each country. The unavailability of management data for two fields in Sweden meant that these fields were excluded. Therefore, data from 58 fields were used in the analysis. The selected variables of agricultural intensity and landscape simplification had low or no correlation with each other (Table S7). Functional redundancy, agricultural intensity and landscape simplification variables were scaled and standardized, by subtracting each value from its mean and dividing it by its standard deviation, prior to fitting them to the model (Ovaskainen & Abrego, 2020). To make predictions across all fields which are not conflated with weed diversity, redundancy values were scaled by dividing them by the number of genera for which functional redundancy was estimated in each field. The fitted model was then used to predict functional redundancy of seed predation for all weed genera, by summing the corresponding predicted redundancy of predation for individual weed genera. The model was fitted to the data with the HMSC-R package (Tikhonov et al., 2020). The model was run with two Markov chains for 1,500,000 iterations, of which the first 500,000 were discarded as transient. Model convergence was assessed by inspecting the trace plots of β estimates and the width of credible intervals of model estimates. Trace plots revealed no convergence problems for any weed genus. Comparisons across environmental covariates were made by examining the overlap between 84% credible intervals (CI) of posterior median estimates. This interval width was used because it approaches an $\alpha=0.05$ error rate, while comparisons with 95% intervals are excessively conservative (MacGregor-Fors & Payton, 2013). Non-overlapping CIs indicated significant differences at $\alpha \sim 0.05$ (MacGregor-Fors & Payton, 2013). The explanatory power of the model was evaluated using R^2 (Tikhonov et al., 2020). All analyses including the calculation of redundancy for each weed genus, and statistical analysis were conducted in R (version 4.1.3; R Core Team, 2022).

To test the relationship between functional redundancy and spatial variability of predation estimates of *P. annua*, the coefficient of spatial variation (CV) of predation rates of *P. annua* was calculated as the standard deviation of the proportion of seeds removed from the seed cards across the 16 sampling points for both sampling occasions within a field, divided by the mean seed removal for each field. Spatial variability analysis, based on our sampling design, was supported by a lack of spatial autocorrelation among estimates of seed card predation (Moran's $I = -0.00055$, $p = 0.20$). To meet parametric assumptions, spatial variation (CV) of *P. annua* predation was log-transformed. To evaluate the relationship between spatial variability in *P. annua* predation rates, and functional redundancy a linear model was used, with the log-transformed CV of *P. annua* predation as a response variable and redundancy of *Poa* genus predation (calculated at the field level) as a predictor.

RESULTS

Overall, DNA of 201 different weed genera representing 40 plant families was detected in 5738 regurgitate samples from 32 carabid species that had plant DNA detected in their regurgitates (Figures S5–S7).

The mean redundancy of predation across all weed genera was 1.78 ± 0.52 (mean ± SD) and ranged from 1.00 to 3.18 (Table S8). The highest mean redundancy of predation was found for the genera *Lolium* 3.18 ± 1.33 and *Poa* 3.13 ± 1.34 (Table S8). The overall proportion of variation explained (R^2) by the HMSC model, was 31.7%. From the two aspects of agricultural intensity, field management intensity explained the largest portion of variation in redundancy, accounting for 35.3 ± 14.5% of the total variance (Figure 1; Table S9). A similar amount of variation was explained by the two variables representing landscape simplification combined. Proportion of semi-natural habitat (pSNH) accounted for 14 ± 6.2% and length of the interface between crop and semi-natural habitat (iSNH) for 14.5 ± 7.1% (Figure 1; Table S9). Crop rotation diversity accounted for 15.7 ± 7% of the total

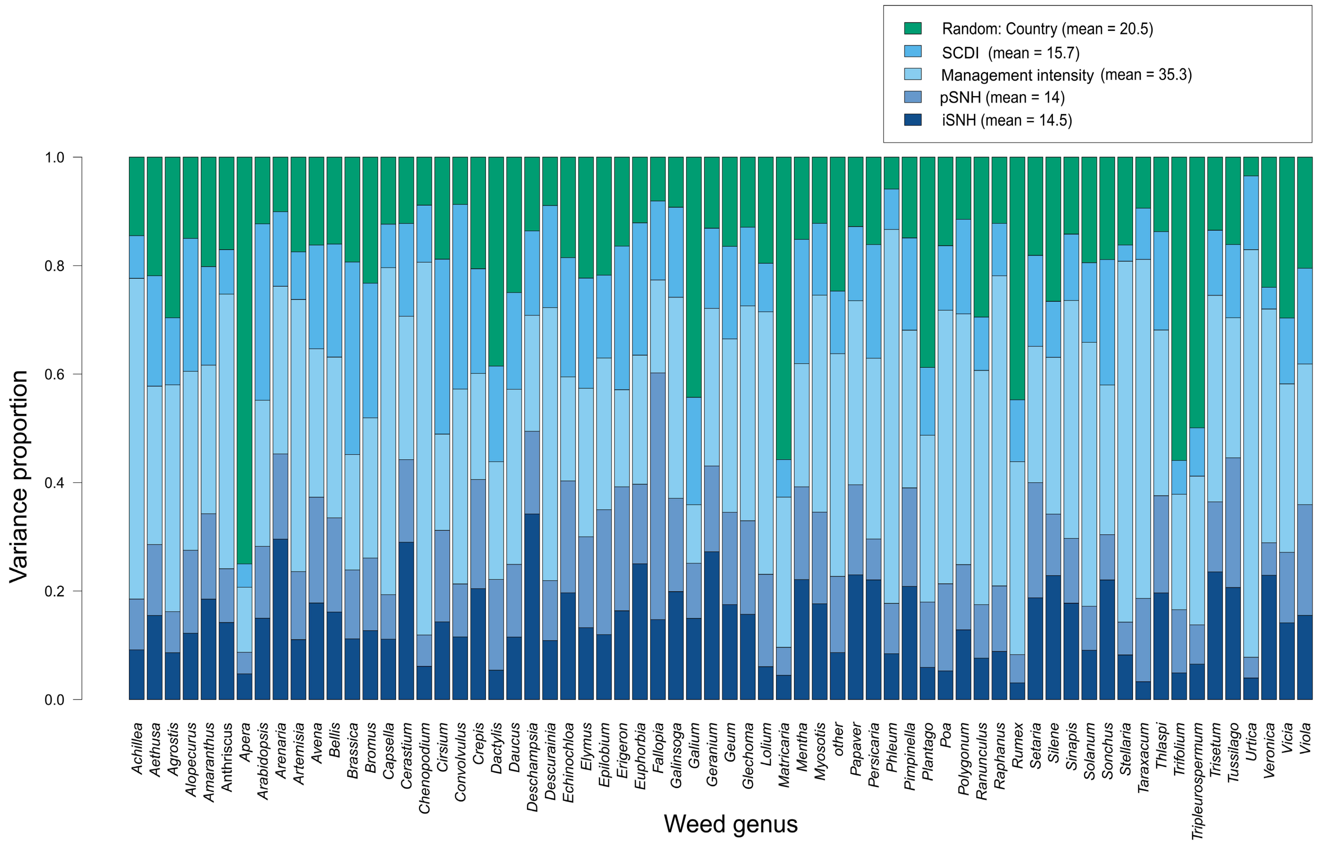

FIGURE 1 Relative proportion of variance in predation redundancy across 65 selected weed genera attributed to the aspects of agricultural intensity and landscape simplification: field management intensity (number of field visits), crop rotation diversity (SCDI), proportion of semi-natural habitat (pSNH) and length in meters of the interface between crop and semi-natural habitat (iSNH), and the country-level random effect. The variance attributed to the fixed effects is indicated in shades of blue, and the variance attributed to the random effect is indicated in green. Each bar represents a weed genus. The results are drawn from the HMSC log-normal model fitted to the functional redundancy of seed predation.

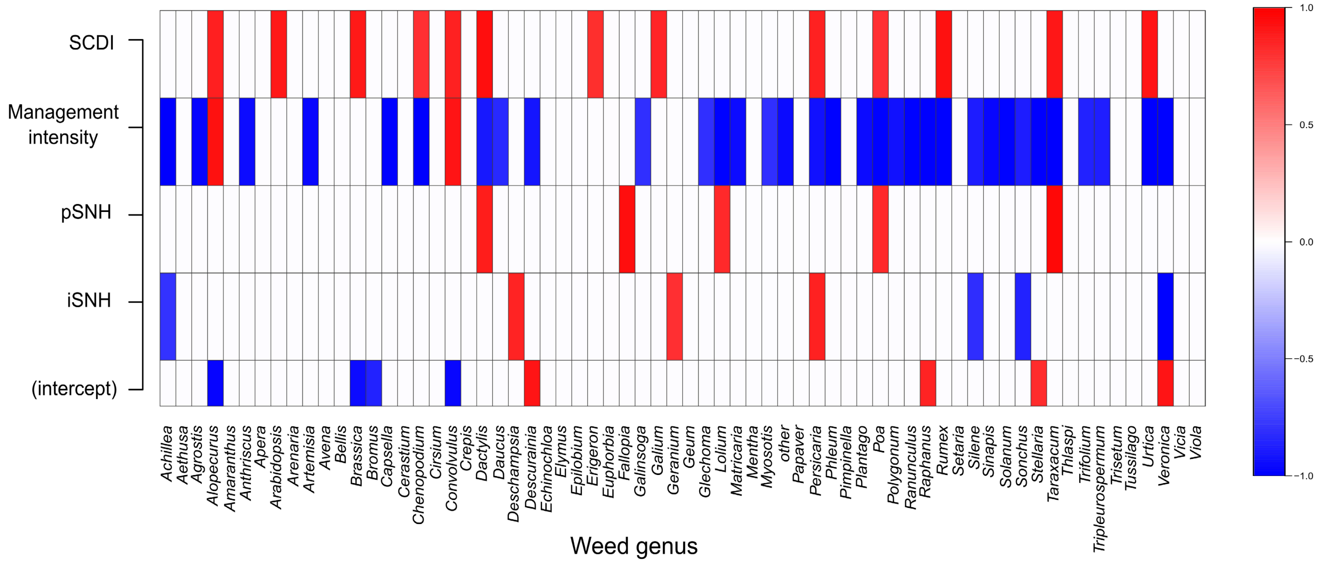

FIGURE 2 Heatmaps of the effects (β estimates) of variables representing agricultural intensity and landscape simplification: crop rotation diversity (SCDI), field management intensity (number of field visits), proportion of semi-natural habitat (pSNH), and length in meters of the interface between crop and semi-natural habitat (iSNH), on the functional redundancy of predation for 65 selected weed genera. The represented responses for each weed genus have received high statistical support (posterior probability >95%) of being positive (red) or negative (blue).

variance (Figure 1; Table S9), while the random effect Country accounted for 20.5±13% (Figure 1; Table S9).

Overall, the model revealed a negative effect of field management intensity on the functional redundancy of seed predation across different weed genera (Figures 2 and 3a). For 32 of the 65 selected weed genera, field management intensity had a negative effect on the redundancy of seed predation (Figure 2), while for two (*Alopecurus* and *Convolvulus*) it had a positive effect (Figure 2). Functional redundancy of predation was increased in diversified crop rotations (Figure 3b) with a positive effect on 13 weed genera (Figure 2) and no effect on the remaining weed genera (Figure 2). The two different variables reflecting landscape heterogeneity, iSNH and pSNH, combined had a positive effect on the redundancy of predation for in total eight weed genera, while iSNH had a negative effect on four weed genera (*Achillea*, *Silene*, *Sonchus* and *Veronica*; Figure 2). Overall, across the weed genera, proportion of semi-natural habitat (Figure 3c) and iSNH had no effect on the redundancy of predation (Figure 3d).

Spatial variability of in-field estimates of *P. annua* seed predation (coefficient of variation of predation across sampling points) ranged from 0.48 to 3.68 (1.36±0.62) and decreased with increasing redundancy of *Poa* predation (estimate = − 0.10±0.03, $t = -2.69$, $p = 0.009$, Adjusted $R^2 = 0.1$; Figure 4).

DISCUSSION

Functional redundancy in seed predation of 65 weed genera was estimated using data from a standardized continental-wide experiment in 60 European cereal fields across four European countries. Using molecular gut content data combined with metabolic theory and estimates of activity density, we showed that overall functional redundancy of weed seed predation was reduced by intensive agricultural management but not landscape simplification. Specifically, greater field management intensity but also simplified crop rotations were negatively correlated with the functional redundancy of weed seed predation across most weed genera. The observed reduction in functional redundancy by intensified agriculture is consistent with the notion that increasing land-use intensity will impede ecosystem functions, for example through the simplification of landscape structure and frequent pesticide use (Dainese et al., 2019; Gagic et al., 2021). For example, a reduction of functional redundancy in aphid predation has been linked to decreasing landscape heterogeneity surrounding the crop field (Feit et al., 2019). The study presented here shows that functional redundancy is positively but weakly related to the in-field spatial stability of weed seed predation. This provides support for the expectation that functional redundancy contributes to the resilience of ecosystem functions (Biggs et al., 2020; Martin et al., 2019).

Even though agricultural intensity affected the redundancy of predation overall, there was some variation in effects between weed genera. While for most of the weed genera, at least one aspect representing agricultural intensity or landscape simplification, led to reduced functional redundancy in predation, for 24 genera we observed no effects and field management intensity increased the functional redundancy for two. For instance, increased field management intensity and increased landscape heterogeneity were found to have a negative effect on the functional redundancy of predation on *Sonchus* and *Veronika*, two common weed genera. In

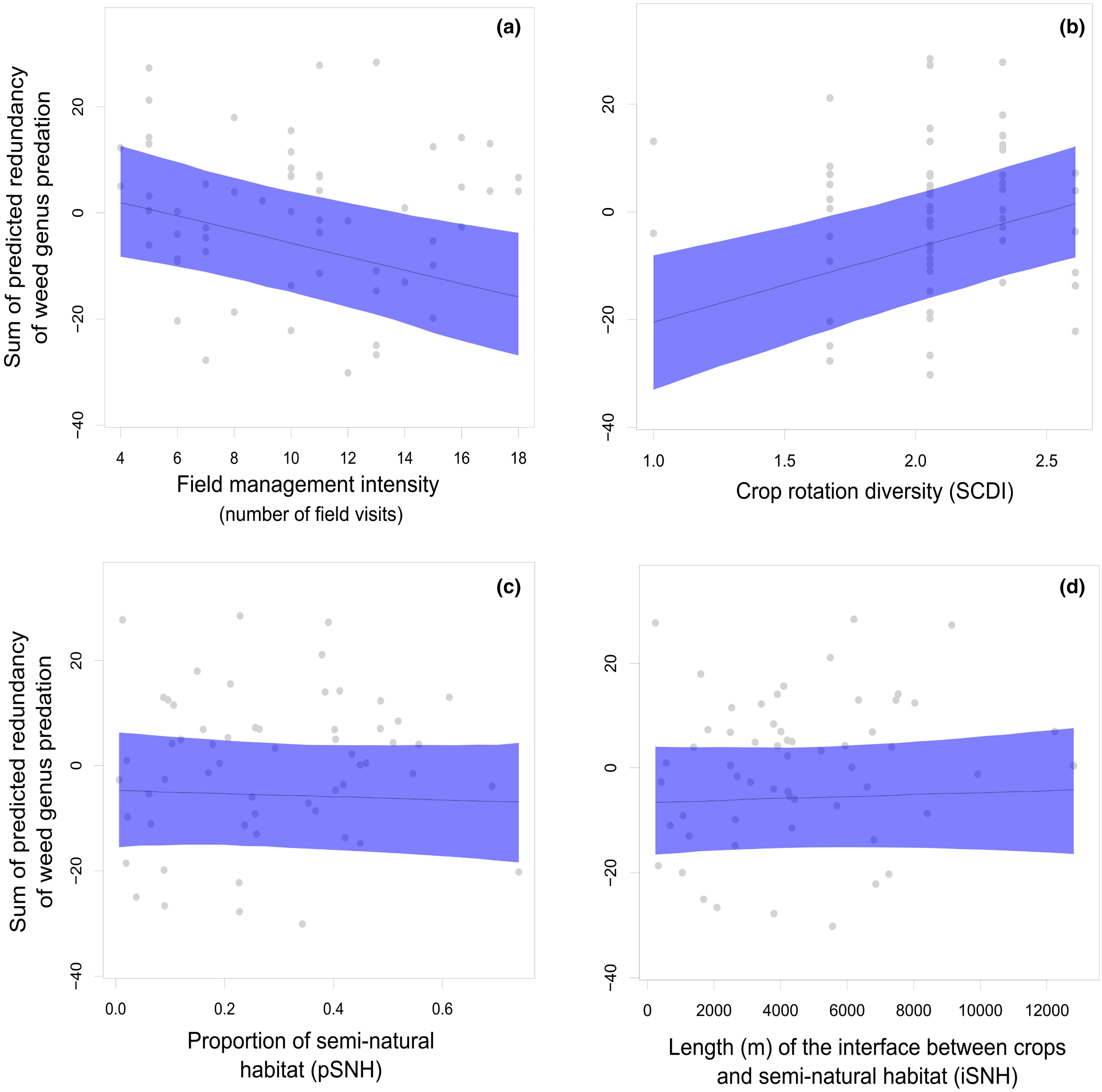

FIGURE 3 Variation in sum of redundancy of predation for 65 selected weed genera in 58 cereal fields across Europe (grey dots) in relation to (a) field management intensity (number of field visits), (b) crop rotation diversity (SCDI), and variables representing landscape simplification (c) the proportion of semi-natural habitat (pSNH) and (d) the length (m) of the interface between crops and semi-natural habitat (iSNH). Variation predicted from Hierarchical Modelling of Species Communities and shown the posterior mean (black solid line) and 84% credible intervals (blue shaded area). Increased field management intensity and reduced crop rotation diversity had a negative effect on the redundancy of predation. No effect was observed for the two variables representing landscape simplification.

contrast, for the genus *Alopecurus*, which thrives in intensively managed fields and can cause substantial yield losses (Lutman et al., 2013; Varah et al., 2020), field management intensity had a positive effect on the functional redundancy of the predation of its seeds. Given that *Alopecurus* is abundant in agricultural fields despite the intensive measures of control (Moss, 2017), seed availability of *Alopecurus* is probably higher in intensively managed fields (Comont et al., 2019) and this may in turn lead to seed predation by a higher diversity of predators. For *Lolium*, however, another problematic weed genus (Lemerle et al., 1995), increased field management intensity reduced the functional redundancy of its predation. Since *Lolium* seems to develop different morpho-physiological seed traits in response to management type and intensity (Maity et al., 2021), seed traits in addition to seed availability can potentially drive the diversity of species predating on weed seeds.

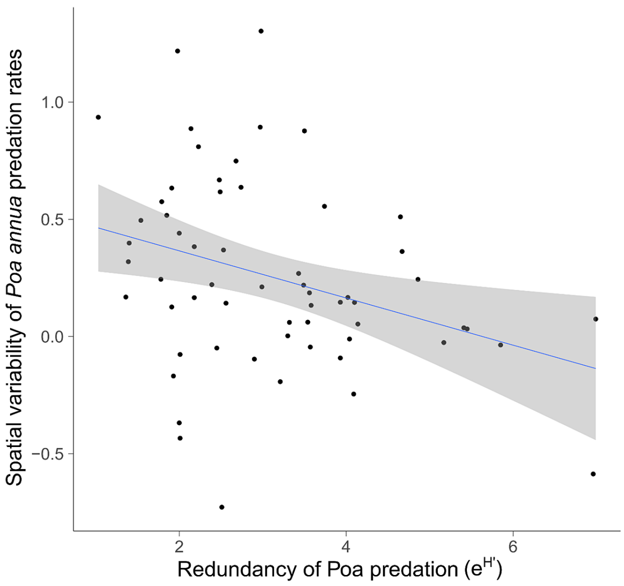

FIGURE 4 Relationship between spatial variability (CV) of *Poa annua* predation estimates and redundancy of *Poa* predation for 60 fields across Europe. Spatial variability of predation estimates decreased with increasing level of redundancy of *Poa* predation. Spatial variability of weed seed predation was log-transformed. The figure shows the partial residuals (black dots), prediction line (blue line), and 95% confidence intervals (grey shaded area).

To test whether the metric of functional redundancy relates to stability in weed seed predation, we explored the correlation between functional redundancy in predation of *Poa* spp. seeds with the spatial variability of seed card predation rates of *P. annua*. We found a weak but negative relationship between the spatial variability of *P. annua* predation with functional redundancy of *Poa* predation. This indicates that higher functional redundancy can reduce spatial variability of seed predation and thus lead to more reliable weed suppression over space. Previous work has demonstrated that the diversity of small carabid species, can decrease spatial variability in weed seed predation (Lami et al., 2020). Similarly, in host-parasitoid networks, high functional redundancy has been reported to increase the spatial stability of community-level parasitism rates (Peralta et al., 2014). Our results are also consistent with theoretical expectations that increasing species diversity should increase the spatial stability of ecosystem functioning (Naeem & Li, 1997; Weigelt et al., 2008). Nevertheless, since the stability of ecosystem functions is essential both in time and space in order to persist through disturbances (Loreau & de Mazancourt, 2013; MacArthur, 1955), additional work is needed to ascertain whether the metric of functional redundancy can also predict the temporal stability of ecosystem functioning. Since carabid species are active from early spring until autumn (Knapp et al., 2019; Thiele, 2012), temporal replication can also strengthen estimations of functional redundancy, especially for weed genera shedding seeds later in summer or appearing on the soil surface after soil cultivation. Ideally, other variables within the redundancy metric such as body mass could be measured at the individual level as well.

To conclude, it was shown that agricultural intensity in the form of increased field management intensity and reduced crop rotation diversity reduced the functional redundancy of weed seed predation. A negative but weak correlation between redundancy of *Poa* predation and spatial variability in *P. annua* predation estimates suggests that decline in functional redundancy can potentially lead to less reliable weed seed predation across space. High functional redundancy however in itself, is not enough to provide resilience of ecosystem functions against disturbances (Elmqvist et al., 2003) such as climatic variability (Feit et al., 2021) or land-use change from natural to agricultural habitat (Cariveau et al., 2013). To ensure resilient ecosystem functions, functionally similar species also need to respond differently to disturbances. Response traits, such as feeding and movement response diversity (de Castro-Arrazola et al., 2023), could provide valuable insights into functions resilience to specific types of disturbance such as soil cultivation and pesticide applications. Therefore, field management approaches that increase species functional diversity and thus increase functional redundancy are likely to safeguard ecosystem functions as long as there is high response diversity within their community.

AUTHOR CONTRIBUTIONS

DAB, MJ, PS, WW, RB, MT and SP conceived the experimental study and with contributions from ED, BC, HV and VN designed the study. ED, BC, HV, VN, JS, PS and CW carried out fieldwork and processed the samples with additional support from VN and CW that processed and digitized the molecular data. ED performed the analyses with the support of MJ, SV and BF. ED interpreted the results and wrote the first version of the manuscript supported by MJ, BF and RB. All authors contributed to the interpretation of results and contributed substantially to further revisions.

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CONFLICT OF INTEREST STATEMENT

All co-authors declare no conflict of interest.

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DATA AVAILABILITY STATEMENT

The data and code to generate the figures presented in this study are freely accessible in Dryad Digital Repository: doi: 10.5061/dryad.dfn2z357r.

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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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