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Ecosystem services and disservices provided by small rodents in arable fields: Effects of local and landscape management

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Abstract

1. In agriculture, both valuable ecosystem services and unwanted ecosystem disservices can be produced by the same organism group. For example, small rodents can provide biological control through weed seed consumption but may also act as pests, causing crop damage.

2. We studied the hypothesized causal relationships between ecosystem services (removal of weed seeds) and disservices (removal of wheat grains and crop damage) derived by small rodents (voles and mice) at multiple spatial scales. At the landscape scale, we studied the effects of landscape compositional and configurational heterogeneity on the abundance of voles and mice and their related ecosystem services and disservices along the former inner German border in east and west Germany. At the local scale, we studied how abundance and ecosystem functions are affected by management intensity (organic vs. conventional winter wheat), associated differences in crop characteristics and edge effects.

3. Linear mixed-effects models and path analysis show that voles drove ecosystem disservices, but not ecosystem services, in agricultural fields. Daily wheat seed removal by voles was influenced by increasing wheat height and was almost three times higher than weed seed removal, which was not related to local- or landscape-scale effects.

4. Abundance of voles and associated crop damage decreased with lower crop density and higher wheat height, which were associated with organic farming. Abundance of voles and crop damage were highest in conventional fields in west Germany.

5. *Synthesis and applications.* As the ecosystem disservice of wheat seed consumption by small rodents must be considered mainly during crop sowing, management before crop harvest should focus on decreasing the pest potential of voles but not mice. Our results suggest that densities of voles and their ecosystem disservices could be reduced by having fields with low crop density and high wheat height, practices associated with organic farming. Surrounding landscapes with low

compositional and configurational heterogeneity could further reduce voles' pest potential, but with probable negative effects on farmland biodiversity.

KEYWORDS

agricultural intensification, biological weed control, crop damage, ecosystem functioning, ecosystem services, edge effect, *Microtus arvalis*, organic farming, rodents, seed predation

1 | INTRODUCTION

During the past few decades, agricultural land use has further intensified. Natural and semi-natural habitats have been converted into arable land, and management intensity has increased (Foley et al., 2005). These land use changes enhance crop production, and also affect species richness, community composition, and abundance of single species (Chapin et al., 2000), which in turn change species interactions, food web structure and ecosystem functioning (Diaz et al., 2013; Tylianakis, Didham, Bascompte, & Wardle, 2008). For example, ecosystem services, such as biological pest control and pollination, suffer from the use of inorganic fertilizers, pesticides and monocultures (Kremen & Miles, 2012). Additionally, landscape fragmentation resulting in decreasing compositional and/or configurational heterogeneity (Fahrig et al., 2011) can cause regime shifts in ecosystem functioning, leading to degradation of these ecosystem functions (Crowder & Harwood, 2014; Haddad et al., 2015).

To date, most studies have focused on ecosystem functions that provide ecosystem goods and services of value to humans (de Groot, Wilson, & Boumans, 2002; Foley et al., 2005). Other functions result in "perceived or actual negative impacts on human well-being", known as ecosystem disservices (Shackleton et al., 2016). These include herbivores, pathogens and seed predators that increase production costs and negatively affect productivity in agricultural ecosystems (Zhang, Ricketts, Kremen, Carney, & Swinton, 2007). In fact, the same taxa can provide both ecosystem services and disservices (Shapiro & Báldi, 2014).

Small rodents are important seed predators (Daedlow, Westerman, Baraibar, Rouphael, & Gerowitt, 2014; Fischer & Türke, 2016) and are abundant in agricultural landscapes, where they are keystone herbivores (Cornulier et al., 2013; Fischer & Schröder, 2014). In terms of ecosystem functions, small rodents can provide both ecosystem services and disservices (Shapiro & Báldi, 2014). On the one hand they provide biocontrol by consuming weed seeds (Daedlow et al., 2014; Fischer & Türke, 2016) and plant material of (noxious) weeds (Butet & Delettre, 2011), affecting plant population growth, recruitment and population densities (Pearson, Hierro, Chiuffo, & Villarreal, 2014). On the other hand, voles in particular can become pest species, damaging crops and affecting agricultural productivity (Jacob, Manson, Barfknecht, & Fredricks, 2014). The pest potential of mice, including *Apodemus* spp., has rarely been measured in arable fields (Heroldová & Tkadlec, 2011).

When studying the complex interactions between ecosystem functions, their providers, and the resulting positive or negative

impacts on human well-being (Shapiro & Báldi, 2014), scale dependencies of the underlying processes and components must be considered (de Groot et al., 2002). At the local scale, densities of *Apodemus sylvaticus* (Macdonald, Tattersall, Service, Firbank, & Feber, 2007; but not *Microtus arvalis*, Jacob, 2003) and seed predation rates (Diekötter, Wamser, Dörner, Wolters, & Birkhofer, 2016; Menalled, Smith, Dauer, & Fox, 2007; but see Jonason, Smith, Bengtsson, & Birkhofer, 2013) are found to be enhanced by organic farming and high vegetation cover (Figure 1a; Ouin, Paillat, Butet, & Burel, 2000). At the landscape scale, increasing naturalness raises the abundance of mice (mainly *Apodemus* spp.) and reduces the abundance of voles (mainly *Microtus* spp.; Gentili, Sigura, & Bonesi, 2014). Furthermore, percentage growth of arable land increases small mammal species richness (Fischer & Schröder, 2014; but see Silva, Hartling, & Opps, 2005), and positive effects of greater landscape compositional heterogeneity occur on seed predation rates (Figure 1a; Diekötter et al., 2016; Trichard, Alignier, Biju-Duval, & Petit, 2013; but see Schäckermann, Mandelik, Weiss, Wehrden, & Klein, 2015). Thus, local- and landscape-scale effects often interact with each other, leading to highest seed predation rates in organic fields of complex landscapes (low % arable land) and lowest seed predation rates in conventional fields of simple landscapes (Fischer, Thies, & Tscharntke, 2011a). Moreover, edge effects shape characteristics of crop and associated removal rates, with lower weed seed predation rates at the headland of agricultural fields due to low vegetation cover (Navntoft, Wratten, Kristensen, & Esbjerg, 2009) and decreasing vegetation height (Díaz, 1992). Rodent abundances also decrease with increasing distance to field margins and decreasing vegetation height (Figure 1a; Jacob, 2008; Rodriguez-Pastor, Luque-Larena, Lambin, & Mougeot, 2016; but see Delattre et al., 2009).

To investigate the opposing functional roles of small rodents in agricultural landscapes, we simultaneously studied their associated ecosystem services and disservices at two different scales. At the broad scale (Hierarchical Level A), we used the historical East–West division along the former inner German border, which offers an excellent opportunity to study marked landscape-scale effects within the same ecoregion (Fischer et al., 2011), as well as effects of management intensity (organic vs. conventional farming), and edge effects. At the fine scale (Hierarchical Level B), we tested for the effects of landscape compositional and configurational heterogeneity (measured by Shannon habitat diversity and edge length respectively), as well as local crop characteristics (density and height) on the abundance of voles and mice on weed seed removal vs. removal of wheat seeds and crop damage. We applied path analysis to answer the following overall questions:
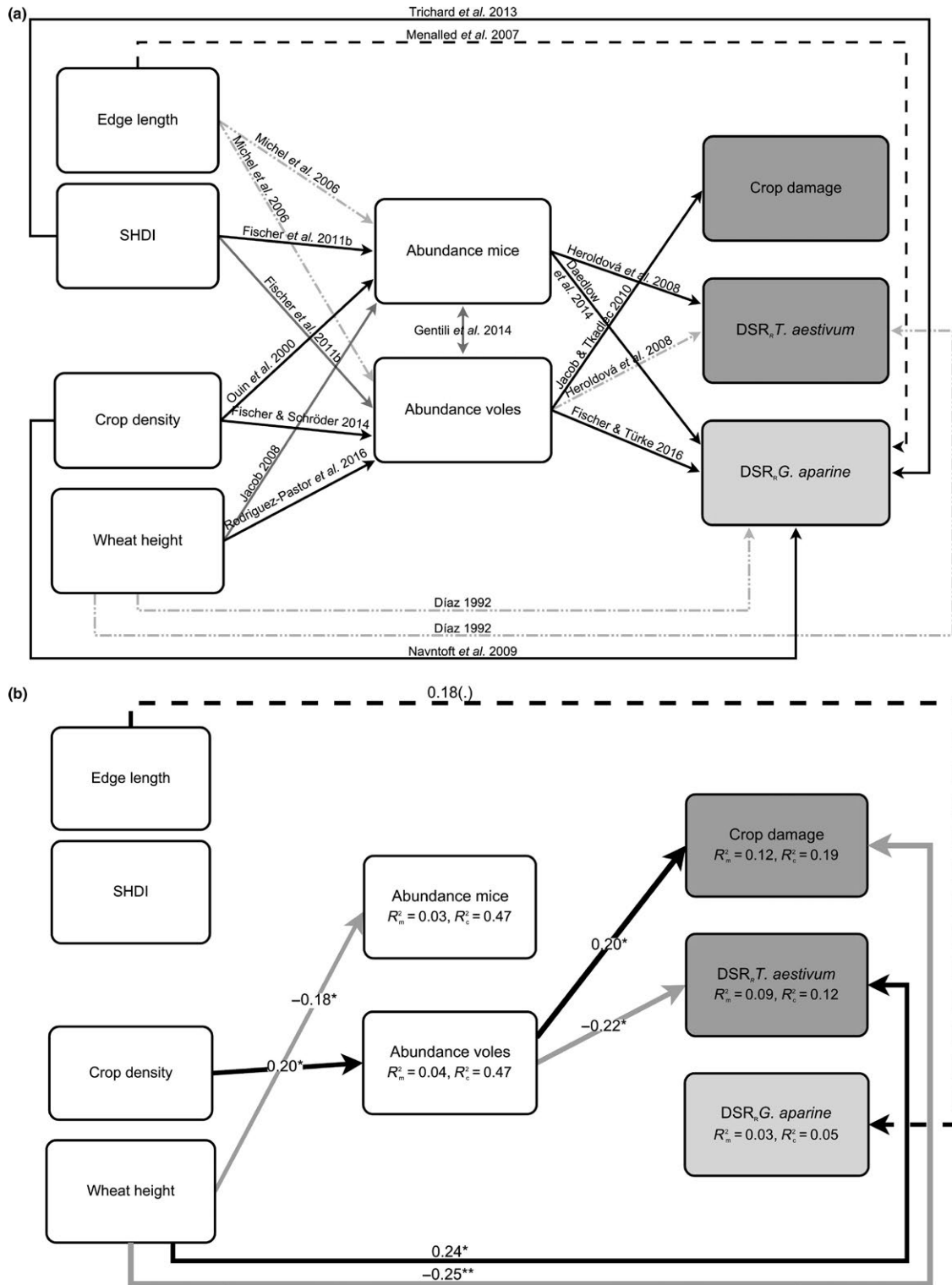
FIGURE 1 Hypothesized causal relationships among landscape variables (edge length, Shannon habitat diversity: SHDI), local characteristics of the crop (crop density, wheat height), and abundance of mice and voles, as well as their ecosystem services (daily seed removal rates of *Galium aparine*) and their ecosystem disservices (crop damage and daily seed removal rates of *Triticum aestivum*) derived from (a) literature showing hypothesized links and (b) path analysis of the data. In both graphs, arrows represent unidirectional relationships among variables. Black arrows represent positive relationships and grey arrows represent negative relationships. Solid lines indicate significant paths (*$p < .05$, **$p < .01$) and dashed lines indicate marginally significant paths ($^{(.)}p < .10$). For hypothesized links, (a) light grey dot-dash lines indicate non-significant paths. If no link between variables is shown, no reference has been found. For hypothesized causal relationships derived from the data, (b) thickness of lines has been scaled to the magnitude of the standardized regression coefficient (given above the arrows). Marginal and conditional R^2 values from component models are given for each response variable (for details see Appendix S1)

1. How do abundances of small rodents and their ecosystem functions respond to the interacting effects of management intensity, landscape compositional and configurational heterogeneity in east and west German croplands?

2. What management actions facilitate biological weed control by small rodents, without promoting their disservices of damaging crops?

2 | MATERIALS AND METHODS

2.1 | Study area and environmental variables

We selected nine pairs of organic and conventional winter wheat fields in east Germany (Thuringia, around the city of Mühlhausen, 51°13′N, 10°27′E) and west Germany (Lower Saxony, around the city of Göttingen, 51°32′N, 9°56′E) respectively (n_{total} = 2 regions × 9 field pairs = 36 study sites). In the East, availability of organic farms was limited; therefore, we selected four villages with two organic-conventional pairs and one village with one organic-conventional pair. In the West, three villages were selected in each case. Straight line distance between paired organic and conventional fields was ($M \pm SE$) 2.8 ± 1.0 km in the East and 0.5 ± 0.1 km in the West. We studied edge effects on small rodents' abundances and ecosystem functions by collecting data at three transects, which were placed

at the field edges (behind the first wheat row), field interiors (15 m from field edge) and field centres (100 ± 10 m from field edge in East and 54 ± 5 m in West; Figure 2). Positions of the centre sites were adapted to the field size, and were placed in the centre of the smaller field of a field pair, while using the same distance for the larger field (cf. Batáry et al., 2017).

Management intensity was lower in organic fields, which receives no applications of pesticides, growth regulators and synthetic fertilizers, compared to conventional fields, which receive 3.9 ± 0.2 and 5.0 ± 0.3 pesticide applications/year and 193.1 ± 4.7 and 164.7 ± 18.6 kg nitrogen/ha ($M \pm SE$) in east and west Germany respectively. We characterized the local properties of the crop by counting the number of wheat shoots (hereafter referred to as crop density) and measuring wheat height at three 25 × 25 cm plots, selected at each transect respectively (Figure 2). From each 25 × 25 cm plot, crop density was extrapolated to 1 m² and mean values per transect were calculated. Characterization of the crop took place in June 2014 simultaneously to rodent trapping. Crop density was higher in the East compared to the West and in conventional compared to organically managed fields, whereas wheat height did not differ between regions, but was higher in organic compared to conventionally managed fields (Table 1). Furthermore, crop density was lower at the field edges (478 ± 23 shoots/m²) compared to the interior (619 ± 32) and centre (566 ± 29; linear mixed-effects model:
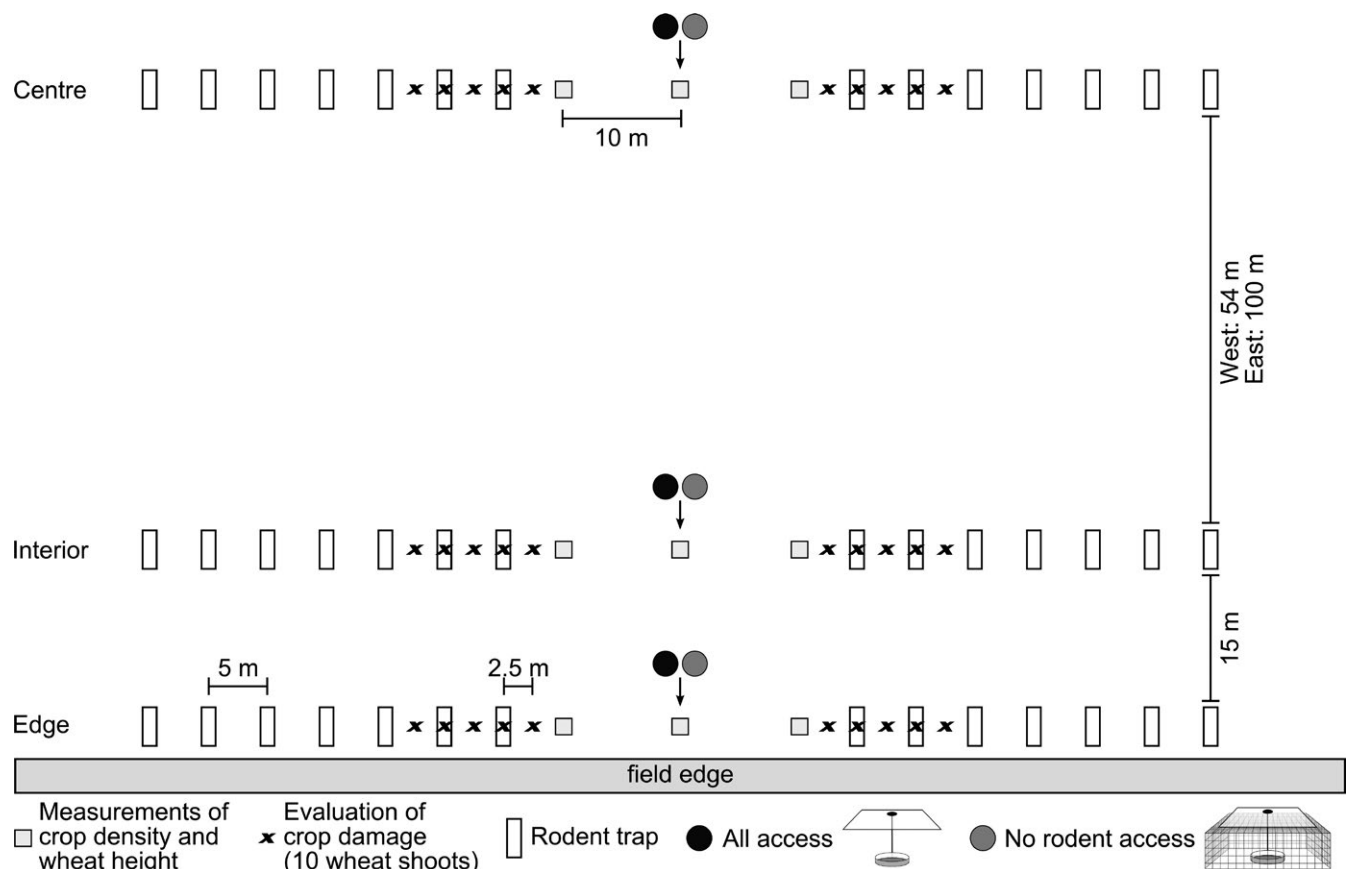

FIGURE 2 Sampling design including seed removal treatments, Ugglan traps for small rodents, sampling points of crop damage, crop density and wheat height in the winter wheat fields

F_{88} = 7.78, p < .001), whereas wheat height did not differ between transects (edge: 92 ± 3 cm, interior: 96 ± 2, centre: 96 ± 3; F_{88} = 0.95, p = .39).

Regional differences in landscape compositional heterogeneity were measured by calculating the Shannon habitat diversity index (SHDI: from the amount of cereal, oilseed rape, grassland, maize and other crops) in a radius of 500 m around the field interior using official digital topographical maps (ATKIS DTK 50) and the Geographical Information System (GIS) ArcGIS 10.2 (1999–2012 ESRI Inc.). Differences in landscape configurational heterogeneity were measured by mean field size and edge length in a 500 m radius. Field size was an order of magnitude lower in the West compared to the East, whereas edge length and SHDI showed reverse patterns. There was no difference in landscape variables between management types (Table 1).

2.2 | Small rodent sampling

We evaluated small rodent abundance by using a capture–mark–recapture approach. In total 42 Ugglan multiple capture live traps (240 × 60 × 90 mm; Grahnab, Gnosjo, Sweden) were used per study site, with 14 traps per transect spaced 5 m apart (Figure 2). Rodent trapping was conducted following Fischer, Thies, and Tscharntke (2011b) for three consecutive trap nights per study site. To identify recaptures, we marked individuals trapped for the first time by fur-clipping. Trapping was carried out between mid-May and mid-July 2014 over nine consecutive weeks. Two field pairs were sampled per week and data collection switched each week between East and West, to avoid bias due to changes of population densities within the sampling period. Total small rodent abundance per study site did not change over the course of the nine sampling weeks (one-way ANOVA: F_8 = 1.94, p = .09). We calculated the relative abundance of

mice (*Apodemus agrarius*, *A. flavicollis* and *A. sylvaticus*) and voles (*M. arvalis*, *M. agrestis* and *Myodes glareolus*) as the total number of individuals excluding recaptures (c.f. Michel, Burel, & Butet, 2006). We did not use mark–recapture analysis to estimate abundance and density of mice and voles, as we did not mark animals individually and as the recapture rate per study site and transect was quite low (M ± SE; mice = 12 ± 2%, voles = 15 ± 2%), leading to a possible overestimation of the actual population (Krebs, 2014). We focused our analyses on species that were either granivorous–insectivorous (*Apodemus* spp.) feeding among others on cereal grains (Heroldová, Tkadlec, Bryja, & Zejda, 2008), herbivorous (*Microtus* spp.) or omnivorous feeding on mixed food (*M. glareolus*; Butet & Delettre, 2011). Insectivorous small mammals caught by accident, such as shrews (*Sorex araneus* and *Crocidura leucodon*), were excluded from further analysis.

2.3 | Ecosystem functions: Seed removal and crop damage

A seed removal experiment was conducted twice, at the end of May and at the beginning of June 2014. We used organic wheat grains (*Triticum aestivum* L.) (Alnatura Produktions- und Handels GmbH), as well as seeds of *Galium aparine* L. (Appels Wilde Samen GmbH), a harmful weed in cereal stands, which can cause high yield loss (Gehring & Thyssen, 2011). *Galium aparine* was selected based on the plant surveys during the preceding field season in 2013, where it occurred in almost all study fields and showed the highest average % cover among the weeds (Batáry et al., 2017). Ten seeds of *G. aparine* and *T. aestivum* were exposed consecutively per study site to predators for 4 days during the first run and for 2 days during the second run, due to high wheat removal rates during the first run. We offered the seeds in a Petri dish (55 mm diameter, 14.2 mm height), which was buried flush with the soil surface and covered by a plastic roof to

TABLE 1 Variables characterizing study sites (n = 36) in agricultural systems in east and west Germany (region) with organic and conventional management (M ± SE) in 2014. Parameter estimates with standard error (SE) and levels of significance from linear mixed-effects models are given to test for effects of region, management and their interaction

	East		West		Estimate ± SE		
Parameter	Organic	Conventional	Organic	Conventional	Region W[a]	Management O[b]	Region: management
Mean field size (ha)	22.79 ± 3.80	19.31 ± 3.02	3.50 ± 0.62	3.60 ± 0.52	**−1.47 ± 0.23*****	0.14 ± 0.10	−0.18 ± 0.15
Edge length (km)	13.47 ± 0.70	13.52 ± 0.98	20.06 ± 1.08	20.04 ± 1.08	**6.28 ± 1.62****	−0.06 ± 0.96	0.07 ± 1.36
SHDI	1.02 ± 0.05	0.95 ± 0.07	1.23 ± 0.06	1.34 ± 0.05	**0.39 ± 0.09****	0.07 ± 0.08	−0.19 ± 0.12
Crop density (shoots/m²)	574.62 ± 31.01	669.43 ± 33.84	405.73 ± 21.82	567.90 ± 28.72	**−101.53 ± 42.26***	**−94.81 ± 40.78***	−67.36 ± 57.67
Wheat height (cm)	108.46 ± 3.64	88.40 ± 1.47	95.49 ± 2.31	86.91 ± 1.61	−1.87 ± 5.03	**20.06 ± 2.88*****	**−11.48 ± 4.07****

Bold values indicate those predictor variables which significantly affect response variables at p < .05.
SHDI, Shannon habitat diversity index; W, region West; O, management organic; ":" indicates two-way interaction.
*p < .05, **p < .01, ***p < .001.
[a]Region East was the reference category.
[b]Management conventional was the reference category.

protect seeds from rainfall. In order to measure the seed removal only by rodents, one treatment allowed access to all animals ("all access") and one treatment excluded rodents by using a 210 × 210 × 60 mm (l × w × h) cage with a mesh size of 12.7 mm ('no rodent access') allowing access only to invertebrates. Treatments were used simultaneously, and were placed next to each other at each transect (Figure 2). After each run, we counted remaining seeds and inspected them for further seed damage. First, seed removal by rodents (SR_R) was calculated following Fox, Reberg-Horton, Orr, Moorman, and Frank (2013), with $SR_R = (SR_{NRA} - SR_{AA})/SR_{NRA}$, where SR_{NRA} is the number of seeds remaining in the 'no rodent access' treatment, and SR_{AA} is the number of seeds remaining in the 'all access' treatment. Thereby the fraction of seed removal by invertebrates was assumed to be equal in the 'all access' and 'no rodent access' treatment. In case SR_{AA} exceeded SR_{NRA} by more than 5:4, the data point was removed from the analysis (Fox et al., 2013); in all other cases, SR_R was set to 0% (Saska, van der Werf, de Vries, & Westerman, 2008). The daily seed removal rate by rodents (DSR_R in %) was then calculated accounting for the different exposure times of the first and second run, following Mittelbach and Gross (1984) by assuming an exponential decline with $DSR_R = 100 \times (1 - (1 - SR_R)^{1/t})$ [%], using the previously calculated SR_R at the end of the exposure time, and the exposure time t in days. We calculated mean values of both runs to be in accordance with the temporal resolution of the other environmental variables (c.f. Fischer et al., 2011a).

We evaluated crop damage by rodents by checking 100 tillers per transect for feeding traces following Heroldová and Tkadlec (2011). At 10 sampling points per transect spaced 2.5 m apart, 10 randomly selected wheat shoots were inspected for rodent crop damage. We recorded the total number of cut shoots per transect (Figure 2). We assessed rodent damage approximately 2 weeks prior to the intended date of wheat harvest during the first half of July.

2.4 | Statistical analysis

We used linear mixed-effects models (lme function; Pinheiro & Bates, 2000) with maximum likelihood implemented in the R package *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2016) to test for landscape- and local-scale effects for the Hierarchical Level A (see Figure S1 in supporting information), as well as edge effects on the abundance of mice and voles, DSR_R of *G. aparine* and *T. aestivum*, and crop damage. The full models contained region (East vs. West), management intensity (organic vs. conventional) and edge effects (transect: edge, interior, centre), and their two-way interactions. With respect to the spatial autocorrelation of our study design, village (*n* = 11) and pair nested in village (*n* = 18) were included as random effects to model the independence of errors (Pinheiro & Bates, 2000). To achieve a normal error distribution and/or to avoid heteroscedasticity, abundance of mice and voles were square-root transformed, DSR_R of *G. aparine* and *T. aestivum* were arcsine square-root transformed, crop damage was log(x + 1) transformed. An automatic backward stepwise model selection by Akaike's information criterion (AIC; Pinheiro & Bates, 2000) implemented by the 'stepAIC' function in the R package *MASS* (version

7.3–45; Venables & Ripley, 2002) was used for model simplification. Parameter estimates and standard errors, *t*- and *p*-values were derived from summary tables. Contrasts between different transects were investigated by re-ordering factor levels.

The hypothesized causal relationships (Figure 1a) between abundance of mice (*Apodemus* spp.), voles (*Microtus* spp.), their ecosystem functions (DSR_R of *G. aparine* and *T. aestivum*, crop damage), and landscape- and local-scale effects for the Hierarchical Level B were investigated using path analysis (see Figure S1). At the landscape scale, non-correlated (Spearman rank correlation r_s < 0.7; Dormann et al., 2013) variables included were edge length and SHDI, and at the local scale, crop density and wheat height (see Table S1). We applied structural equation models (SEM) involving random effects implemented in the R package *piecewiseSEM* (Lefcheck, 2016). Model structure was adapted to the linear mixed-effects models described above, using the same parameter transformations and random effect structure. From the global SEM, which contained all possible paths, least significant variables were removed applying a manual backward model selection based on AIC until a minimal SEM was reached. Standardized path coefficients, and marginal and conditional R^2 values for component models, as well as Fisher's *C* statistic, and associated *p*-value were extracted (for path analysis details, see Appendix S1). For all analyses, R version 3.3.1 (R Core Team, 2016) was used. *M* and *SE* are given in the text.

3 | RESULTS

In total, 1700 rodents feeding at least partly on seeds were trapped in 4536 trap nights. Mean rodent abundance was 47.22 ± 4.93 individuals/field (= 126 trap nights; mice: 13.08 ± 1.81, voles: 34.14 ± 5.08), which totals 239 rodents/ha (calculated for a 20 m buffer around trapping lines). *Microtus arvalis* was the most abundant species (1181 individuals = 69%), followed by *A. agrarius* (217 individuals = 13%), *A. sylvaticus* (216 individuals = 13%), *A. flavicollis*, *M. agrestis* and *M. glareolus* with 86 individuals in total (1%–2% respectively). Daily seed removal rates by rodents were with 24.33 ± 2.50% almost three times lower for *G. aparine* than for *T. aestivum* with 65.21 ± 3.48%. Mean crop damage was 5.47 ± 0.96 cut shoots/100 tillers.

Results for the Hierarchical Level A showed no main effects of region, management intensity and transect position on the abundance of mice and voles (Figure 3a,b), or on ecosystem services measured by seed removal of *G. aparine* (Table 2, Figure 3c). Ecosystem disservices in terms of DSR_R of *T. aestivum* were (marginally) higher in the field interior (72.32 ± 5.48%) compared to the centre (56.87 ± 6.84%, Figure 3d). Abundance of voles and crop damage were highest in conventional fields in the West (vole abundance: 21.19 ± 2.89 individuals, Figure 3b; crop damage: 11.96 ± 3.36 cut shoots, Figure 3e; interaction region:management). Crop damage was lower in the East (2.89 ± 0.44 cut shoots/100 tillers) compared to the West (8.06 ± 1.81, Table 2).

The path analysis (Fisher's C_{36} = 16.23, *p* = 1.00) for the Hierarchical Level B confirmed the minor importance of detailed

landscape variables (SHDI, edge length) for the abundance of voles and mice, DSR_R of *G. aparine* and *T. aestivum*, and crop damage. At the local scale, piecewise SEMs showed that dense crops increased the number of voles and thereby crop damage, but decreased DSR_R of *T. aestivum*. Wheat height had a direct negative effect on the number of mice and crop damage, as well as a positive effect on DSR_R of *T. aestivum*. At the landscape scale, only one effect was observed: edge length (marginally) increased DSR_R of *G. aparine* (Figure 1b).

4 | DISCUSSION

4.1 | Rodent abundance and crop damage

Although rodent densities of 240 individuals/ha in our study are relatively low compared to peak densities of more than 1000 individuals/ha (reviewed in Jacob et al., 2014), we still found a direct positive relationship between abundances of voles (but not mice) and crop damage at the ripening stage just before the wheat harvest. This could cause an estimated financial loss of *c.* 3.5% of farmers' income at mean values of 5% cut wheat shoots (Jacob et al., 2014). From an economic perspective, it is therefore important to control voles using rodenticides (Jacob & Tkadlec, 2010), although such measures often negatively impact non-target raptors (Lemus et al., 2011). From an ecological perspective, environmentally friendly rodent pest management via habitat management would be more appropriate and may also enhance biological control by their predators (Crowder & Harwood, 2014). Our study shows that interacting local- and landscape-scale effects influence the abundance of voles and their ecosystem disservices, with highest abundances and crop damage in conventional fields in Western Germany. In general, common voles, the predominant species in our study, primarily occur in grassland habitats, field margins and clover fields, and spill over into crop fields when the carrying capacity of the primary habitats is reached (reviewed in Jacob et al., 2014). Higher habitat connectivity in the West due to lower field size, higher edge length and higher habitat diversity may facilitate spillover of voles into secondary habitats. In association with high vegetation cover, which is a key factor driving densities of voles (Fischer & Schröder, 2014; Ouin et al., 2000), higher habitat connectivity in the West may have led to higher crop damage relative to the East. Furthermore, path analysis showed that crop damage decreased with increasing wheat height related to organic farming. This negative relationship between wheat height and crop damage may be related to rodents' harvesting behaviour. As mice are climbing and cutting down the culm (Heroldová & Tkadlec, 2011), higher wheat culms may lower the feeding rates and thereby crop damage, even though we did not find links between abundance of mice and ecosystem disservices. Organic farming can contribute
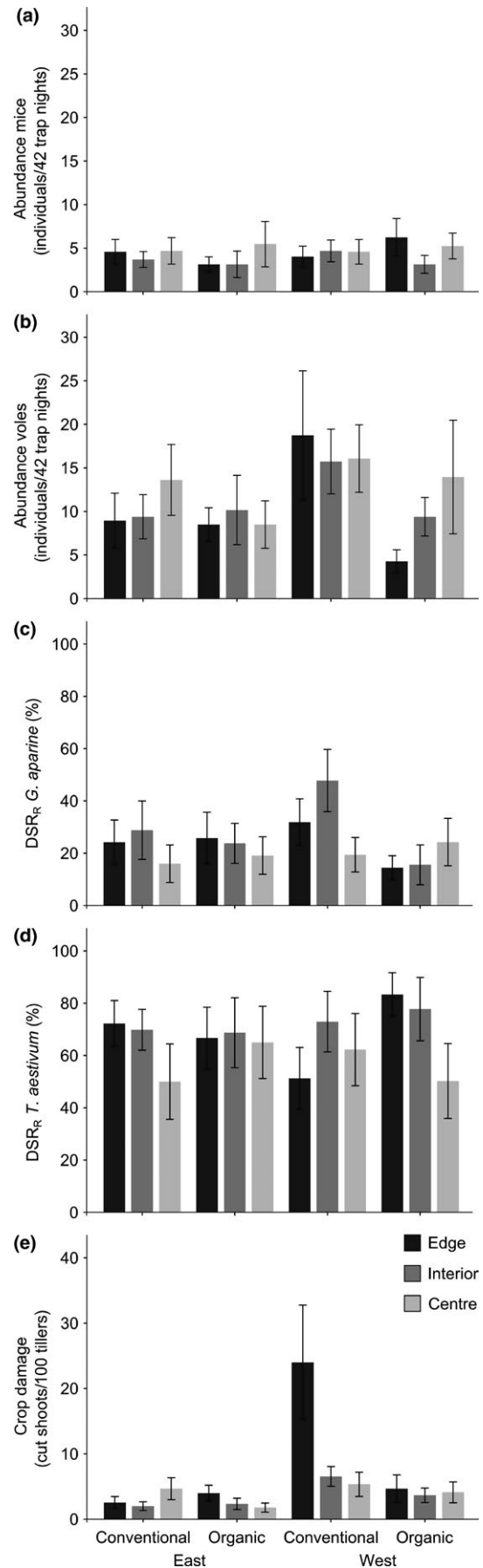

FIGURE 3 Bar plots representing abundance of (a) mice, (b) voles; daily seed removal rate by rodents (DSR_R) of (c) *Galium aparine* and (d) *Triticum aestivum*, and (e) crop damage in agricultural systems in east and west Germany with organic and conventional management at the different transects ($M \pm SE$; $n = 36$)

TABLE 2 Results of linear mixed-effects models, after an automatic backward stepwise model selection, showing effects of the landscape and local scale for the Hierarchical Level A, as well as edge effects on abundance of mice and voles, daily seed removal rates by rodents (DSR$_R$) of *Galium aparine* and *Triticum aestivum* and crop damage

Parameter	Abundance mice		Abundance voles		DSR$_R$ *G. aparine*		DSR$_R$ *T. aestivum*		Crop damage	
	Estimate ± *SE*	*t*-value	Estimate ± *SE*	*t*-value	Estimate ± *SE*	*t*-value	Estimate ± *SE*	*t*-value	Estimate ± *SE*	*t*-value
(Intercept)	**1.94 ± 0.17**	**11.48*****	**3.08 ± 0.50**	**6.15*****	**0.40 ± 0.08**	**5.30*****	**1.08 ± 0.10**	**11.01*****	**1.09 ± 0.18**	**6.22*****
Region W[a]	—	—	0.70 ± 0.69	1.01	0.18 ± 0.17	1.65	—	—	**0.89 ± 0.254**	**3.57****
Management O[b]	—	—	−0.28 ± 0.32	−0.89	0.01 ± 0.10	0.07	—	—	−0.06 ± 0.24	−0.27
Transect	—	—	—	—	—	—	—	—	—	—
Edge – Centre	—	—	—	—	—	—	0.18 ± 0.13	1.42	—	—
Edge – Interior	—	—	—	—	—	—	−0.07 ± 0.13	−0.54	—	—
Interior – Centre	—	—	—	—	—	—	**0.25 ± 0.13**	**1.96**[(.)]	—	—
Region : Management	—	—	**−0.83 ± 0.45**	**−1.84**[(.)]	−0.22 ± 0.14	−1.57	—	—	**−0.62 ± 0.33**	**−1.87**[(.)]
Region : Transect	—	—	—	—	—	—	—	—	—	—
Management : Transect	—	—	—	—	—	—	—	—	—	—

Bold values indicate those predictor variables which significantly affect response variables at $p < .10$.
W, region West; O, management organic; ":" indicates two-way interaction.
[a]Region East was the reference category.
[b]Management conventional was the reference category.
Parameter estimates with standard error (*SE*), *t*-values and levels of significance ([(.)]$p < .1$, **$p < .01$, ***$p < .001$).

to the conservation of farmland biodiversity by stabilizing food web structure (Tylianakis et al., 2008), in addition to benefits through reduced pest potential under low crop densities and high crop heights.

4.2 | Weed and wheat seed removal

In our study, the potential of small rodents to provide ecosystem services in terms of weed seed removal was three times lower than their potential for ecosystem disservices, i.e. their feeding rate on wheat seeds. In general rodents prefer nutrient-rich over nutrient-poor seeds (Fischer & Türke, 2016; Wang & Yang, 2014). Higher wheat removal rates may therefore be explained by the 6.1% oil content of *T. aestivum*, which is two times higher than in *G. aparine* (oil content: 3.1%; Royal Botanic Gardens Kew, 2015). The ecosystem disservice of *T. aestivum* seed removal was negatively related to abundances of voles, which is most likely explained by their food preferences. *Microtus* spp. are herbivorous and mainly feed on vegetative parts of plants and only to a lesser extent on seeds (Butet & Delettre, 2011), which may also explain the non-existent relationship with *G. aparine* seed removal. However, even if wheat removal rates by rodents outweighed removal of weed seeds, in the field, seed feeding rates are complemented by arthropods (Baraibar, Daedlow, de Mol, & Gerowitt, 2012; but see Meiss, le Lagadec, Munier-Jolain, Waldhardt, & Petit, 2010), which accounted for about 30% daily seed removal of *G. aparine*, resulting in a total of 50% daily seed removal (Friederike Riesch, unpublished data). As overall weed seed removal was much higher than in other studies (22% in 2 days: Fischer et al., 2011a; 33% in 18 days:

Baraibar et al., 2012), environmental factors favouring weed control by vertebrates as well as invertebrates must be identified to develop management practices (Menalled, Liebman, & Renner, 2006).

From farmers' perspectives wheat seed removal by rodents is only relevant during times of wheat seeding in autumn (Menalled et al., 2006), when vole populations are at yearly peak densities (Jacob et al., 2014). Therefore, management of seed removal rates before the crop harvest should primarily focus on the increase of weed seed predation by small rodents. However, our study showed that biological weed control of *G. aparine* was not related to densities of mice and voles or local crop characteristics. At the landscape scale, only landscape configurational heterogeneity increased weed seed removal, possibly by the higher availability of microsites for seed predators (Orrock, Levey, Danielson, & Damschen, 2006). To understand management and landscape-scale effects on ecosystem services and disservices provided by small rodents as a whole, future studies must include linkages between biological control and habitats for natural enemies, as well as their dispersal potential and interaction with climate change (Crowder & Harwood, 2014). Finally, to develop management options for sustainable crop management, all stages of the crop production process and weed recruitment must be considered, including seed production, pre-dispersal seed loss, herbivory and adult mortality (Nathan & Muller-Landau, 2000). Additional management considerations should include seed predation rates of weed species with varying nutrient content and seed size (Wang & Yang, 2014) and of grains around the sowing time of winter crops (Menalled et al., 2006).

5 | CONCLUSIONS

Promoting ecosystem services, but not ecosystem disservices, requires information on the causal relationships between major ecosystem processes at multiple spatial scales (Crowder & Harwood, 2014; Zhang et al., 2007). We found that ecosystem disservices of crop damage and wheat seed removal were mainly influenced by crop characteristics, whereas ecosystem services of biological weed control were not influenced by these local-scale effects. Landscape-scale and edge effects were of minor importance for rodent abundances, as well as their ecosystem functions. Voles, but not mice, were the main providers of ecosystem disservices, but not services. Therefore, farmers require options to control vole densities by managing wheat height and crop density. In summary, management options before the crop harvest should reduce densities of voles, and associated crop damage, by organically managed fields with low crop density and high wheat height, embedded in a landscape with low compositional and configurational heterogeneity. Although surrounding landscapes with low compositional and configurational heterogeneity may reduce voles' pest potential, this probably negatively affects farmland biodiversity.

AUTHORS' CONTRIBUTIONS

C.F., T.T. and P.B. developed the conception and design; C.G., K.K., F.R. and P.B. collected data; C.F. analysed and interpreted data with substantial input from P.B.; and C.F. wrote the paper. All authors contributed critically to the draft and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.fj63q (Fischer et al., 2017).

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