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RESEARCH ARTICLE

Linking macrodetritivore distribution to desiccation resistance in small forest fragments embedded in agricultural landscapes in Europe

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Abstract

Purpose Most of the agricultural landscape in Europe, and elsewhere, consists of mosaics with scattered fragments of semi-natural habitat like small forest fragments. Mutual interactions between forest fragments and agricultural areas influence ecosystem processes such as nutrient cycling, a process strongly mediated by the macrodetritivore community, which is however, poorly studied. We investigated macrodetritivore distribution patterns at local and landscape-level and used a key functional trait (desiccation resistance) to gain mechanistic insights of the putative drivers.
Methods Macrodetritivores were sampled in forest edges-centres of 224 European forest fragments across 14 landscapes opposing in land use intensity. We used a multilevel analysis of variance to assess the relative contribution of different spatial scales in explaining activity-density and Shannon-diversity of woodlice and millipedes, together with a model-based analysis of the multivariate activity-density data testing the effect on species composition. Secondly, we tested if desiccation resistance of macrodetritivores varied across communities at different spatial scales using linear mixed effect models.
Results Forest edge-centre and landscape use intensity determined activity-density and community composition of macrodetritivores in forest fragments, while fragment characteristics like size and continuity were relatively unimportant. Forest edges and higher

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Data accessibility All data is available in the smallFOREST geodatabase. Access to this database can be achieved after contacting the smallFOREST geodatabase management committee (http://www.u-picardie.fr/smallforest/uk/).

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intensity landscapes supported higher activity-density of macrodetritivores and determined species composition. Forest edges sustained woodlouse communities dominated by more drought tolerant species.

Conclusions Landscape use intensity and forest edges are main drivers in macrodetritivore distribution in forest fragments with desiccation resistance a good predictor of macrodetritivore distribution. Key functional traits can help us to predict changes in community structure in changing landscapes.

Keywords Forest edges · Landscape use intensity · Litter dwelling soil fauna · Millipedes · Nutrient cycling · Woodlice

Introduction

Currently, a large share of the European landscapes consists of small forest fragments embedded in an agricultural matrix varying in landscape use intensity (Honnay et al. 2005). The often sharp boundaries between small forest fragments and agricultural fields causes mutual influences on communities and ecosystems, like spill-over effects of organisms and nutrients altering ecosystem processes (for an overview see e.g., Tscharntke et al. (2012)). Litter breakdown is an important ecosystem process in both small forest fragments and agricultural landscapes, cause of its implications on, respectively, tree and crop growth. A fast recycling of nutrients is facilitated by a quick breakdown of litter and enhances plant growth (Belovsky and Slade 2000) a process that is strongly mediated by soil invertebrate communities (de Vries et al. 2013).

In forests, macro-arthropod detritivores are amongst the largest representatives of this soil invertebrate community. They fragment dead organic material on the forest floor (Anderson 1988; Grelle et al. 2000) and their activity significantly increases nitrogen mineralisation (David 2014). Woodlice and millipedes are important taxa in this context, as they are amongst the most important litter dwelling macrodetritivores, at least in terms of their biomass (Jeffery et al. 2010), but poorly studied in a landscape context (David and Handa 2010). These taxa can be extremely abundant and perform a critical first step in the breakdown of organic matter in almost every terrestrial ecosystem (Hättenschwiler et al. 2005). The distribution of woodlouse and millipede communities varies at different spatial scales. Landscape characteristics like land cover heterogeneity or land use intensity affect woodlouse and millipede distribution (Dauber et al. 2005; Báldi 2008). Their distribution patterns vary, within landscapes, between forest fragments differing in size, age or dominating tree species (Dekoninck et al. 2005; Topp et al. 2006; Tajovský et al. 2012; De Smedt et al. 2016). Within forest fragments, there are large differences in

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macrodetritivore distribution between forest edges and forest interiors (Riutta et al. 2012; Bogyó et al. 2015; De Smedt et al. 2016). These environmental aspects affect distribution patterns at different spatial scales, but it is unclear whether local or regional drivers predominate (Wolters 2001; Dauber et al. 2005; David and Handa 2010; Martins da Silva et al. 2015). Therefore, we studied distribution of macrodetritivores at three diverse spatial scales focussing on some important drivers acting at these scales based on the abovementioned references: (1) landscape scale, comparing forest fragments that occur in landscapes differing in land use intensity; (2) fragment scale, comparing forest fragments with different size and continuity; and (3) within-fragment scale comparing forest edges and interiors within the same forest fragment.

Besides describing the observed patterns of macrodetritivore distribution, we want to understand the underlying mechanisms. An analysis of the differences in functional traits across spatial scales provides a valuable way forward, as functional traits are being widely used in ecology to study the causes and potential ecosystem consequences of changes in communities (McGill et al. 2006; Suding et al. 2006). These causes and consequences could be explained through the functional trait composition of communities. We could use functional traits of species to gain mechanistic insights in how environments select species in different habitats. If a species possesses the "right" traits, meaning that it has characteristics that enhances its fitness under certain environmental conditions, it will be selected through the environmental filter. If the species has the "wrong" traits it will not occur in the community or at lower abundance. For this reason, we could use community trait composition to get insights in potential environmental drivers on the species community structure. These insights could then be tested in lab experiments. Macrodetritivores show strong responses to changes in soil moisture levels which has been proposed a key factor in their distribution (David and Handa 2010; Hornung 2011; Purse et al. 2012). We therefore want to use desiccation resistance of the species to study how community changes could be shaped by changes in soil moisture and temperature of habitats (Dias et al. 2013) within forest fragments (Chen et al. 1995; Gehlhausen et al. 2000), but also between forest fragments and landscapes (Bindlish et al. 2008).

Accordingly, besides describing community patterns across different spatial scales, we want to understand macrodetritivore patterns in small forest fragments using community weighted desiccation resistance of the species. Significant trait-patterns could therefore indicate drivers of macrodetritivore biodiversity in these landscapes and give insights about the potential effects on ecosystem functioning.

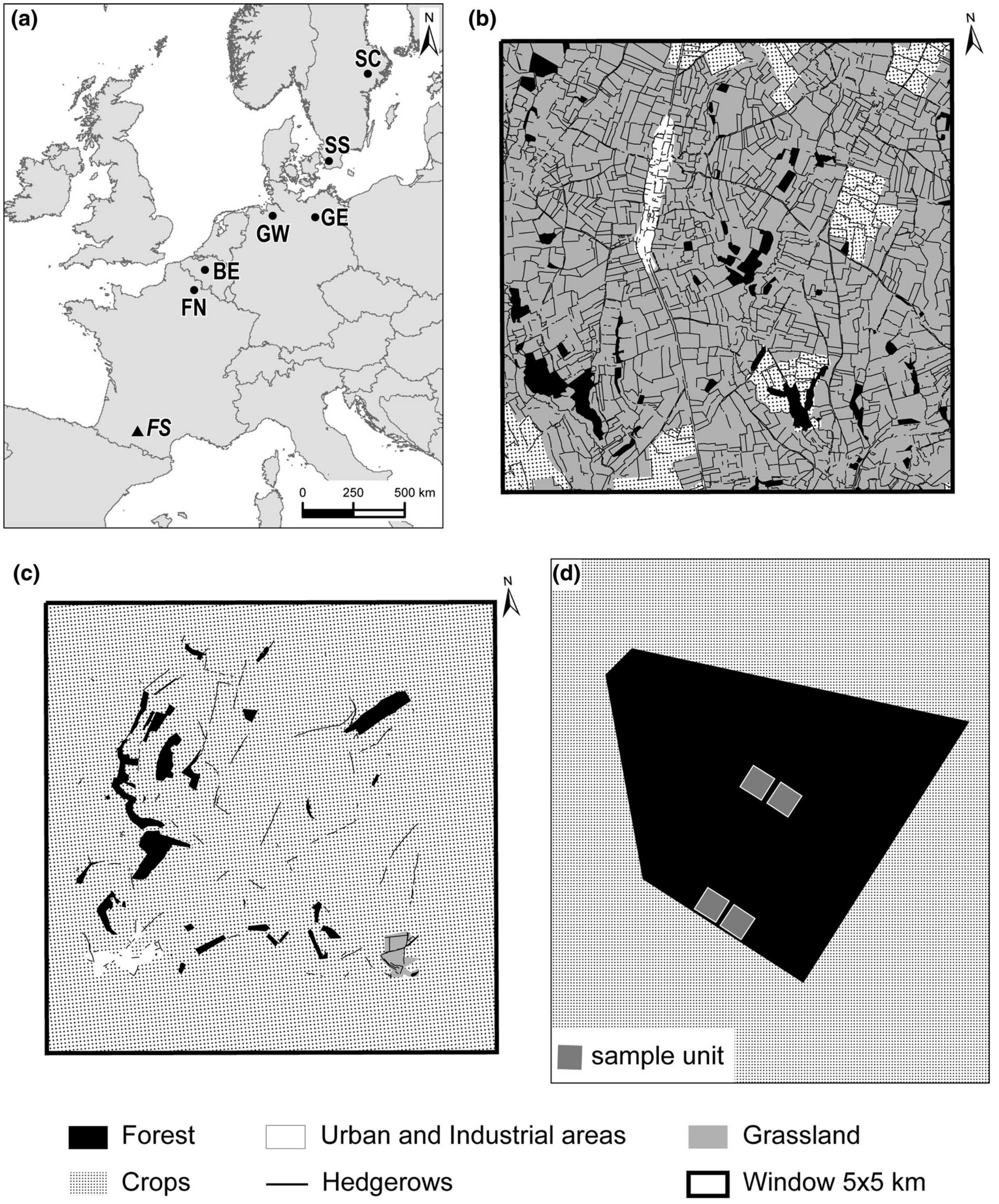
We intend to investigate the following hypotheses (1) macrodetritivore distribution differs at different spatial scales across Europe; (i) between landscapes, (ii) forest fragments and (iii) locations within forest fragments; (2) community weighted mean macrodetritivore desiccation resistance, which will help us to understand how the environment at different spatial scales influences community structure.

Methods

Study area and selected forest fragments

The study was carried out in seven regions across the temperate forest biome of Western Europe, along a latitudinal gradient spanning more than 2000 km (Fig. 1a). In every region, we selected two 5-km × 5-km landscape windows: one higher land use intensity landscape and one lower land use intensity landscape ($n = 14$ windows). Higher land use intensity landscapes are characterised by an intensive cultivation matrix with larger proportion of open fields and isolated forest fragments, more often found in flat areas with fertile soils allowing agricultural intensification (see e.g., Fig 1b, Table 1). Lower land use intensity landscapes are characterised by smaller crop fields and a larger percentage of pastures with scattered forest fragments more or less connected by hedgerows or other linear forest elements, more often found in areas with a more complex topography and low soil fertility (see e.g., Fig 1c, Table 1). We expect these landscapes to be more permeable for species to move across the landscape.

We selected forest fragments dominated by temperate deciduous forest stands for further sampling. Purely coniferous plantations and recently afforested lands (< 12 years of afforestation) were excluded. We calculated size and forest continuity of all fragments using a digitized 1:25,000 map and historical maps (from the 18th, 19th, 20th centuries), respectively,



within a geographic information system environment (ArcGis® v.10.2, ESRI). Fragment temporal continuity was quantified by a weighted average of different stand ages (based on stand area). The forest fragments occurring in a given landscape window were evenly distributed among the following categories (the ranges

◀**Fig. 1** Study area and experimental set-up. **a** Study area with all regions sampled for woodlice and millipedes; FS: southern France, FN: northern France, BE: Belgium, GW: western Germany, GE: eastern Germany, SS: southern Sweden and SC: central Sweden. All regions represented by a dot are incorporated in the trait study as well. **b** lower land use intensity landscape window (5 km × 5 km) of northern France. **c** higher land use intensity landscape window (5 km x 5 km) of northern France. **d** Zoom in of a sampled forest with two pitfall-trap setups (5 m from each other) in the forest interior and two setups (5 m from each other) in the southern edge. All traps were set up parallel to the forest edge

of the continuity and surface variables defining the categories varied between regions): small-recent, small-old, big-recent and big-old. This was done to be sure to have a wide range of surfaces and continuity within each window. Four fragments per category and per window were retained for field sampling: hence, 16 fragments per window and 224 fragments across Europe were selected. We used the actual forest size and continuity numbers to make these factors comparable across the study for analysis. Forest size ranged from 0.08 to 44.12 ha with a median of 1.39 ha. Forest continuity ranged from 12 years to 269 years with a median of 51 years.

Macrodetritivore sampling

Woodlice and millipedes were sampled using pitfall traps (Ø 10 cm, depth 11 cm). We are aware that pitfall traps are a composite measure of activity and abundance of organisms (see e.g., Woodcock 2004), and we will therefore talk about "activity-density" instead of abundance. Species composition has also been reported as not being reflected by pitfall traps (Topping and Sunderland 1992), but for a functional approach we assume that activity is more important than abundance. The pitfall traps contained about 200 ml of ethylene glycol and water (1/1 mixture). A drop of detergent reduced water surface tension. Traps were covered with aluminium roofs, leaving a gap of about 3 cm for arthropods to enter. We sampled in the centre of each forest fragment as well as at the south-facing edge to quantify the within forest community variation, that is, we have two sample points for each forest fragment for a total of 448 sample points. One sample point consisted of two sample units spaced five meters from each other resulting in four sample units per forest fragment (Fig. 1d and Online resource 1, appendix 1). If the south-facing edge was not suitable e.g., bordered by a ditch, road or other physical barrier (38% of the edges), we used the eastern (16% of the edges), western (18%) or northern edge (4%). Macrodetritivores were sampled twice between April and August 2013. To make data

Table 1 Characteristics of the windows in the different regions according to landscape use intensity (LUI)

Region	LUI	% Forest	% Crops	% Pasture	Hedgerows (m/ha)
Sweden (central)	Lower	79.7	16.9	1.1	5.5
	Higher	31.2	46.1	0.0	2.8
Sweden (southern)	Lower	7.4	92.5	0.1	30.4
	Higher	7.2	76.4	3.8	15.9
Germany (eastern)	Lower	4.5	78.9	14.9	22.9
	Higher	7.7	90.3	0.5	20.1
Germany (western)	Lower	25.3	29.6	41.6	42.7
	Higher	11.7	56.0	30.3	23.2
Belgium	Lower	6.1	59.1	11.4	18.4
	Higher	6.4	57.1	13.3	15.7
France (northern)	Lower	6.0	9.1	83.5	132.0
	Higher	5.8	92.1	0.9	8.2
France (southern)	Lower	23.8	24.8	25.0	48.4
	Higher	14.1	83.9	0.0	48.0
Total	Lower	21.8 ± 27.0	44.4 ± 32.5	25.4 ± 29.4	42.9 ± 41.9
	Higher	12.0 ± 9.0	71.7 ± 18.5	7.0 ± 11.3	19.1 ± 14.5

Percentage of forest cover, annual crops, pastures and the amount of hedgerows per hectare. Total represent the average value across windows ± 1* standard deviation comparable among regions, variation in phenology across the latitudinal gradient was accounted for by starting the field sampling campaigns at Growing Degree Hours values of ca. 10,000 and 20,000 (based on data of local weather stations in 2008 and 2009), respectively. Traps were open for fourteen consecutive days. All individuals were identified to the species level.

Desiccation resistance

An existing trait database from the Netherlands (Berg et al. unpublished data) was complemented with trait data measured on living individuals of a few species not available in the database (Online resource 1, appendix 2). The woodlouse species pool of southern France was very different from the other regions and trait data of most species was not available in the existing data base (Berg et al. unpublished data), therefore we excluded the southern France region from the trait analysis. Due to the lack of traits for some millipede species in the database, the trait-based part of the present study focusses only on woodlouse species.

Desiccation resistance, a measure for the capacity of the species to withstand dry conditions, was calculated by exposing specimens to 85% relative humidity (for details see Dias et al. 2013). The average survival time (h) under constant relative humidity was used as an estimate of *desiccation resistance* (h) (Moretti et al. 2016). Desiccation resistance is also strongly linked to other functional traits influencing water conservation mechanism like species body length, body mass and water loss rate (see Dias et al. 2013; Broly et al. 2015; Online resource 1, appendix 3). *Desiccation resistance* was measured on 5-35 adult specimens per species. We are aware that measuring desiccation resistance on adult individuals will overestimate true desiccation resistance of the species and community. There is a positive relationship between surface area of the woodlice and its desiccation resistance (Dias et al. 2013) therefore, desiccation resistance will be lower for juveniles. However, we can at least use it as relative measure to compare drought resistance between populations.

Data analysis

All data were analysed using the statistical software of R (R Core Team 2016). The variation in regional species richness (γ-diversity) was quantified with species accumulation curves for woodlice and millipedes separately and for all regions separately. We used the *specaccum*-function from the *vegan*-package (Oksanen et al. 2015), with sites sampled in a random order for a total of 100 permutations. The activity densities of the two sampling periods were summed up to get one value per sample unit for all analysis, we calculated Shannon-diversity of woodlice and millipedes at the same level. We used a multilevel analysis of variance (Gelman and Hill 2007; Qian and Shen 2007) to give us insight into the relative importance of the different explanatory variables in explaining the variation in woodlouse and millipede activity-density and Shannon-diversity. Explanatory variables included region, landscape use intensity, window, fragment, continuity, size and location (within-fragment level i.e. edge vs. core). We also tested the interaction between landscape window and fragment size, fragment continuity or location within the forest to see if their effects depended on the characteristics of the sampled landscape window. The partitioning of the total variation in activity-density and Shannon-diversity into the above-mentioned components was done with the following multilevel model:

$$y_i = \beta^0 + \beta^{\mathrm{region}}_{j(i)} + \beta^{\mathrm{window}}_{k(i)} + \beta^{\mathrm{fragment}}_{l(i)} + \beta^{\mathrm{LUI}}_{m(i)} + \beta^{\mathrm{loc}}_{n(i)} + \beta^{window \times loc}_{k(i),n(i)} + \beta^{\mathrm{size}}_{k(i)}.size_i + \beta^{\mathrm{cont}}_{k(i)}.cont_i + \varepsilon_i$$

where y_i is the predicted activity-density or Shannon-diversity of woodlice or millipedes on sample unit i, β^0 is a grand mean of y, $\beta^{\mathrm{region}}_{j(i)}$ is an effect of region ($j = 1, \ldots, 7$), $\beta^{\mathrm{window}}_{k(i)}$ is an effect of landscape window ($k = 1, \ldots, 14$), $\beta^{\mathrm{fragment}}_{l(i)}$ is an effect of forest fragment ($l = 1, \ldots, 224$), $\beta^{\mathrm{LUI}}_{m(i)}$ is an effect of landscape use intensity ($m = 1$[lower intensity] or 2[higher intensity]), $\beta^{\mathrm{loc}}_{n(i)}$ is an effect of location in the forest ($n = 1$[edge] or 2[centre]), $\beta^{\mathrm{window} \times \mathrm{loc}}_{k(i),n(i)}$ is an effect of the interaction between landscape window and location in the forest, $\beta^{\mathrm{size}}_{k(i)}.size_i$ is the effect when we allow the slope of size to differ between landscape windows, $\beta^{\mathrm{cont}}_{k(i)}.cont_i$ is the effect when we allow the slope of continuity to differ between landscape windows. Residual error was modelled from a normal distribution ($\varepsilon_i \sim N(0, \sigma^2)$) and β's were modelled from separate non-zero normal distributions (e.g., $\beta_{j(i)}^{\text{region}} \sim N(0, \sigma_{\text{region}}^2)$, with σ_{region}^2 the between-region "biogeographic" variance). Variance components were calculated as finite-population standard deviations of the effects β (e.g., s_{region}), with 95% and 68% credibility intervals (Gelman and Hill 2007). Posterior distributions were derived from 5,000 Markov chain Monte Carlo (MCMC) sampling iterations. The model was implemented with the probabilistic programming language *Stan* (Carpenter et al. 2015), called from the *RStan* package. The importance of the explanatory variables was visualized using a graphical ANOVA table (Gelman and Hill 2007).

Design variables explaining a large share of the variation in woodlouse and millipede total activity-density and diversity were further tested for their effects on the community structure (species' activity densities and composition). We performed a modelled-based analysis of the multivariate activity-density data, implemented in the *mvabund* package (Wang et al. 2016). We tested the effects of landscape use intensity, location within the forest and their interaction on the community structure. The approach allows making community-level inferences (based on species-level effects) about which factors are associated with the multivariate species activity-densities (Wang et al. 2016). The effects of the same predictors on the species composition (i.e., relative activity-densities within sampling units) were tested by adding a sampling unit effect to the same model (Warton et al. 2012). All regions were analysed separately because their species pool composition differed considerably. Activity-densities were modelled with a negative binomial error structure and the significance of the model terms was tested by comparing models with or without the explanatory variables (999 simulations), using analysis of variance (Wang et al. 2016).

We calculated the community weighted mean (CWM) *desiccation resistance* at sampling unit level using the *dbFD* function form the FD package (Laliberté et al. 2015). We used linear mixed effect models (*lme* function) from the lme4 package (Bates et al. 2016) to test the ln-transformed CWM desiccation resistance against landscape use intensity, location inside the forest and their interaction. We used forest ID nested in landscape window nested in region as random effects.

Results

Across the 224 forest fragments, 15001 millipedes (40 species) and 97026 woodlice (27 species) were sampled, respectively. A total of 28 millipede species and 19 woodlouse species were represented with more than ten individuals in the dataset. In terms of geographic distribution, only six millipede species and two woodlouse species were found across all seven regions, whereas 14 millipede species and 11 woodlouse species were represented in only one region (Online resource 1, appendix 4). Species accumulation curves were near saturation for most regions (except for woodlice in northern France), indicating that for both woodlice and millipedes the majority of the species in the regional forest species pool are included in the data set (Fig. 2). Woodlice regional species richness (γ-diversity) followed a latitudinal gradient (Fig. 2a) with the highest species richness in France, intermediate values for Belgium and Germany, and relatively low values for southern and central Sweden. This pattern was not observed for millipedes (Fig. 2b), which showed the highest species richness in the centre regions (Belgium and northern France) and lower species richness in the other regions.

Distribution patterns

Region, window and fragment explained about the same amount of variation compared with the unexplained residual variation for the activity-density, indicating that region, window and fragment characteristics (other than continuity and size) were important for both woodlouse and millipede total activity-density as well as for Shannon-diversity patterns (Fig. 3). Landscape use intensity and location were important design variables in explaining variation in the activity-density, with landscape use intensity explaining even more than the interregional variation and location explaining more than half of the interregional variation for woodlice (Fig. 3a). This means, for instance, that the variation in total activity-density between the higher- versus lower-intensity landscapes was more important than variation between the

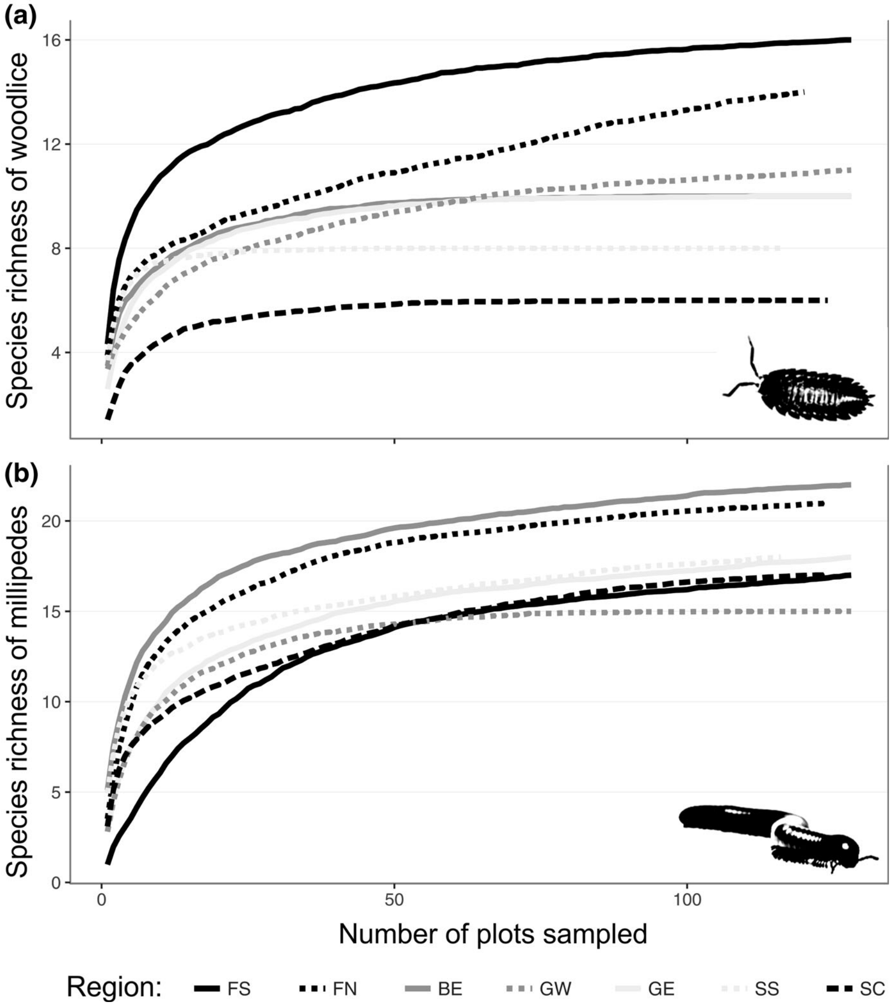
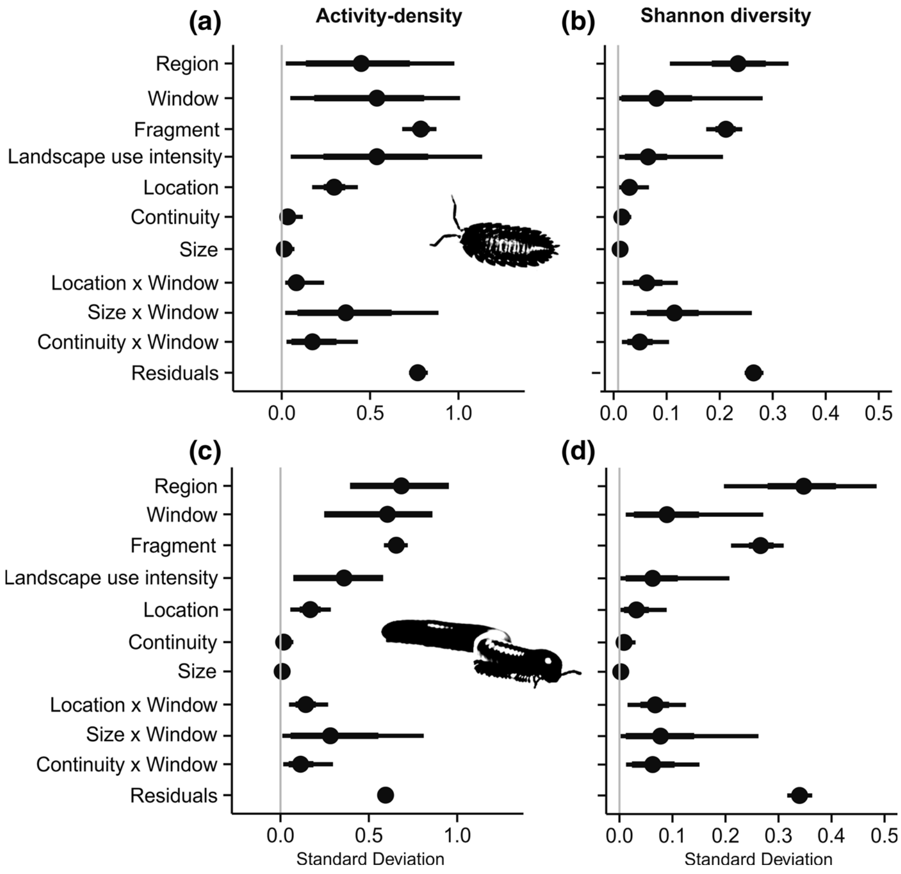


Fig. 2 Regional species accumulation curves for woodlice (**a**) and millipedes (**b**) for the different regions; FS: southern France, FN: northern France, BE: Belgium, GW: western Germany, GE: eastern Germany, SS: southern Sweden and SC: central Sweden. Curves are based on random sampling of the different sampling units (100 permutations)

regions along this > 2000 km latitudinal gradient. Landscape use intensity and location explained less variation in the millipede activity-density data, respectively 50 and 25% of the interregional variation. Landscape use intensity and location explained less of the variation for woodlouse and millipede Shannon-diversity (Fig. 3b, d). The location effect seemed to be consistent over the different windows for woodlouse activity-density (low interaction effect), but depended on window for millipede activity-density. Forest continuity and size explained a low amount of the variation in woodlouse and millipede total activity-density and Shannon-diversity data. However, the interaction with window was more important, indicating that the effects of fragment continuity and size are probably context dependent. Since landscape use intensity and location showed the strongest correlation with activity-density (and to a lesser extent Shannon-diversity) of woodlice and millipedes, we focused on these two variables for further analysis. Focusing on the direction of the effects, woodlouse activity-density was found to be higher in forest edges and in higher land use intensity landscapes (Fig. 4). The effects are by far the most extreme in northern France (Online resource 1, appendix 5). Comparable patterns were found for millipede activity-density, although the differences were the most pronounced in central Sweden. The effects of location and landscape use intensity on Shannon-diversity were highly variable and depend strongly on the sampling region (Online resource 1, appendix 6).

Fig. 3 Variance components based on a multilevel analysis of variance presented as a graphical ANOVA. **a** Woodlouse activity-density, **b** woodlouse Shannon-diversity, **c** millipede activity-density and **d** millipede Shannon-diversity. Point estimates show posterior means, wide lines are the 68% posterior credible intervals and thin lines are the 95% posterior credible intervals



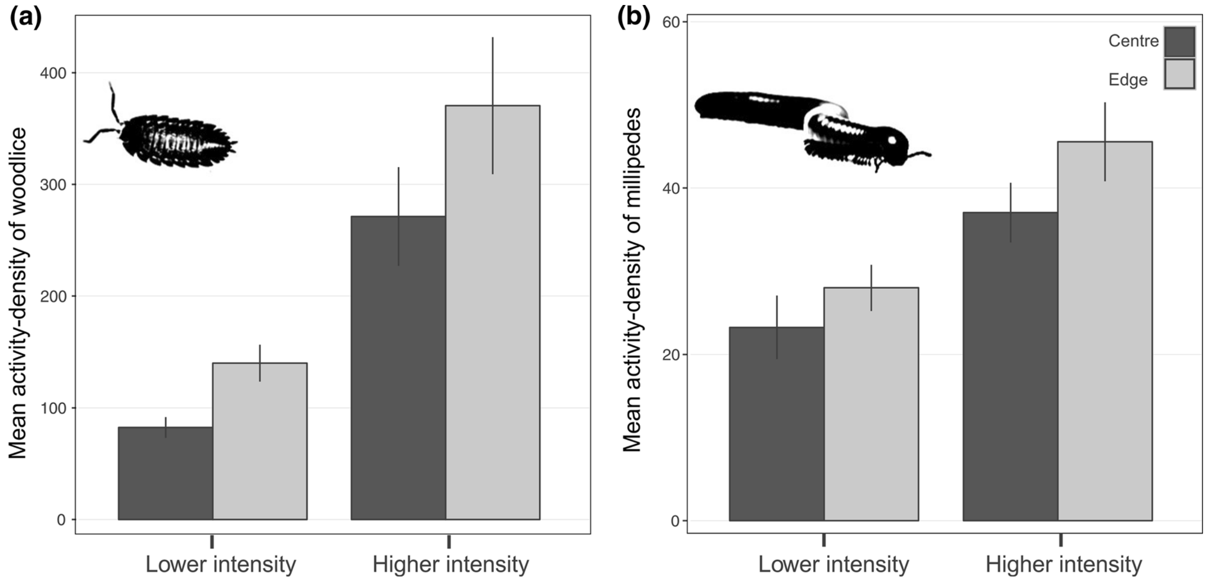


Fig. 4 Mean activity-density of **a** woodlice and **b** millipedes in forest edges and forest centres at the sample unit level in lower land use intensity (LUI) landscapes and higher land use intensity (LUI) landscapes. Error bars represent ± 1 standard error

Community variation

The multivariate species activity-densities differed significantly between landscapes with different landscape use intensity in all regions for woodlice and in six out of seven regions for millipedes (Fig. 5). In three out of seven regions, we found woodlouse species activity-densities to differ between forest edges and interiors, while none of the regions showed any difference for millipedes. However, focusing on the community composition effects (i.e. relative activity-densities), the importance of landscape use intensity diminished and was only significant for two regions for woodlice and in two regions for millipedes (Fig. 5). The sampling location in the forest had no effect on community compositional patterns for woodlice in any region but it had for millipedes in all regions. The interaction effect of landscape use intensity x location on community composition was only significant in few occasions for both woodlice (eastern Germany) and millipedes (Belgium).

Desiccation resistance

The CWM desiccation resistance differed significantly between forest edge and forest interior (lme, df = 187, F = 65.55, P < 0.001). Forest edges were characterised by communities with a higher average desiccation resistance (Fig. 6). No significant differences in desiccation resistance (lme, df = 5, F = 1.88, P > 0.05) was found between landscapes differing in landscape use intensity. The interaction

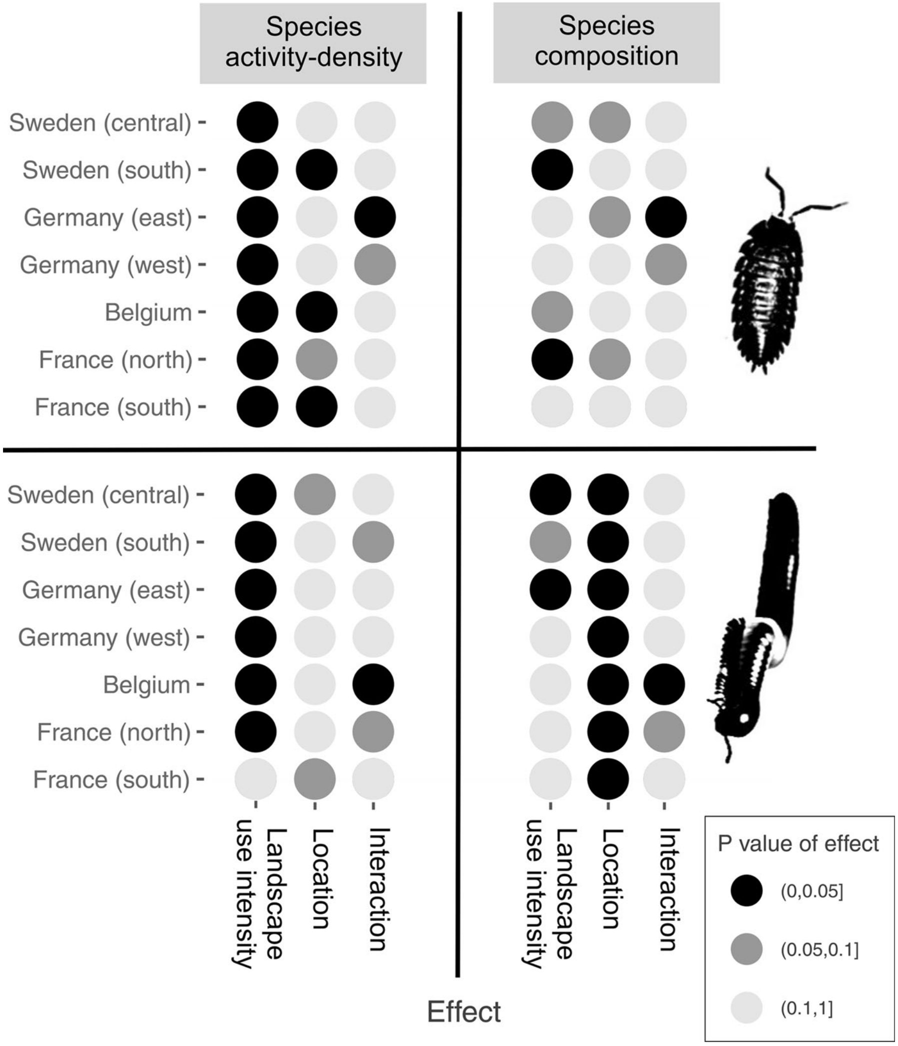


Fig. 5 Effects on landscape use intensity (lower vs. higher land use intensity landscapes), location (edge vs. centre) and their interaction on the community structure of woodlice and millipedes in fragmented forests. We tested which factors are associated with variation in the multivariate species activity-densities of the communities (left part) or the species composition of the communities (relative species activity-densities; right part)

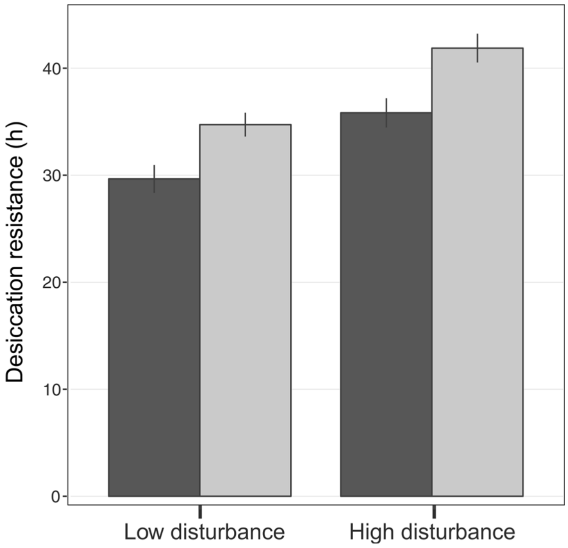


Fig. 6 Average community weighted mean desiccation resistance in survival time (in hours) under constant relative humidity of 85%. Error bars represent ± 1 standard error

between landscape use intensity and location was not significant for desiccation resistance (lme, df = 187, F = 0.87, P > 0.05).

Discussion

Macrodetritivore distribution

We performed a large scale study on the distribution patterns of macrodetritivores in forest fragments embedded in agricultural landscapes across Europe. We found higher activity-density of woodlice and millipedes in forest edges compared with forest centres and in landscapes with higher land use intensity, meaning that a large part of the variation in activity-density could be explained at the within-forest fragment scale and at the landscape scale. The within-forest fragment scale was also an important predictor for millipede species composition. Herewith, we add to the valuable knowledge of edge-effect theory, which is a prominent concept in landscape ecology theory since many decades (see Forman and Godron 1981; Harris 1988) and recognizing that forest edges strongly influence biodiversity and ecosystem service provisioning worldwide (Haddad et al. 2015; Pfeifer et al. 2017)".

Our result are in support by earlier research from Riutta et al. (2012) and De Smedt et al. (2016) showing that forest edges have a higher abundance of macrodetritivores. They also found species diversity to be higher in forest edges (especially for woodlice), but diversity was less affected by forest edge compared to forest centre than abundance. This could indicate that most woodlouse species show a consistent positive response in terms of abundance (Riutta et al. 2012; De Smedt et al. 2016) as well as activity-density (this study) towards forest edges, in contrast to millipedes, which show considerable interspecific variation in their edge response (De Smedt et al. 2016). This could also explain the strong difference between forest edges and forest interiors for millipede community structure.

The higher activity-density of detritivores in forest edges could be due to higher temperatures in forest edges (Delgado et al. 2007; Heithecker and Halpern 2007), which could counterbalance the negative effect of reduced soil moisture conditions in forest edges (Chen et al. 1995; Gehlhausen et al. 2000), both very important factors in macrodetritivore distribution and functioning (David and Handa 2010). However, an altered soil biogeochemistry due to regional intensive farming in forest edges could also contribute in explaining the observed patterns. Forest edges have on average higher N-concentrations (Didham et al. 2015) and lower C/N ratios of litter and mineral topsoil layers (Wuyts et al. 2011), offering a more optimal food source for detritivores (David and Handa 2010; Hornung 2011; Gerlach et al. 2014). The altered microclimate at forest edges also causes a more abundant and species rich herb layer richness (Normann et al. 2016), providing N-rich litter and more optimal nutritional conditions for macro-invertebrates (Zimmer 2002).

Higher N-concentrations could also be an explanation for the activity-densitiy observations at a landscape scale in our study. The inputs of nitrogen into small forest fragments is mediated by fertilization of the surrounding agricultural landscapes, with increasing soil nitrogen when fields are intensively used (Didham et al. 2015). Diekötter et al. (2010) indicate the importance of the surrounding landscape on woodlouse and millipede abundances, by showing that agricultural fields have higher activity densities if local and regional managements show a larger contrast (i.e., organic fields surrounded by conventional farming or vice versa).

Beside a spill-over of nutrients, there could also be a spill-over of organisms from one system to the other (Tscharntke et al. 2012; Boetzl et al. 2016; Madeira et al. 2016). This spill-over can be strongly dependent on the neighbouring landscape (Madeira et al. 2016). Few data are available for macrodetritivores, but low abundances of woodlice in intensively cultivated agricultural fields (Paoletti and Hassall 1999) makes it unlikely that a spill-over causes the differences in abundance of woodlice in small forest fragments. This could be different for millipedes, where some species of open habitats have been reported to be pest species in agricultural crops like *Blaniulus guttulatus*, *Cylindroiulus caeruleocinctus* and *Brachydesmus superus* (Brunke et al. 2012). These species are more abundant in forest patches embedded in higher land use intensity landscapes compared to lower intensity landscapes (See Appendix 4, Table A4.2). We can therefore assume a spill-over of these millipede species from agricultural fields to forest patches, locally increasing species richness.

Unlike the activity-density patterns, the effect of landscape use intensity on species diversity differed strongly between regions and landscape windows. In general, an increase in land use intensity decreases species richness of multiple taxa (Hendrickx et al. 2007; Van Calster et al. 2008; Allan et al. 2013; Haddad et al. 2015; Newbold et al. 2015), but this was not consistent for woodlice and millipedes in our study. Also Diekötter et al. (2005) could not find an effect of the surrounding land use on macrodetritivore species richness, while an effect was discovered by Dauber et al. (2005). Therefore, patterns remain unclear and more research is needed to assess the importance of the surrounding landscape on macrodetritivore species richness and diversity.

Although fragment identity was important, variation explained by fragment continuity and size on woodlouse and millipede activity-density and diversity was low. This in accordance with former research (David and Handa (2010) and references therein). The marginal effect of fragment size could be explained by the critical fragment size that can be very small for these soil dwelling arthropods (Tajovský et al. 2012) or alternatively that woodlice and millipedes are better dispersers than generally thought (David and Handa 2010). In our study the sampling effort was equal in small and large forest fragments in contrast to most studies on the effect of fragment size, when sampling intensity increases with increasing fragment size. This could mask the presence of a size effect. We quantified forest continuity as a weighted average of the different stand ages; and the week effect that we found could raises the question if we used a good measure to quantify forest continuity. Alternatively, Kolb and Diekman (2004) for example quantified forest continuity as the period when at least a part of the forest meets condition of temporal continuity and tested the effect on forest plant species. However, they found only a relatively weak effect on species composition of forest plants. Furthermore, it is not known which time in the past is important for community composition of different species groups and therefore the importance of forest continuity can easily be underestimated.

Desiccation resistance

We demonstrated, on a large geographic scale, that edge communities of detritivores are shifted towards dominance of more drought tolerant species. This pattern could be driven by the relative humidity and soil moisture being lower at the forest edge (Chen et al. 1995; Gehlhausen et al. 2000). Drought tolerant species can better withstand dry conditions and therefore benefit from higher temperatures in forest edges (Delgado et al. 2007; Heithecker and Halpern 2007) enhancing soil fauna activity (Zhang et al. 2008). These drought tolerant species are in general also bigger (Hadley 1994; Dias et al. 2013; Broly et al. 2014; Appendix S3). Larger species consume on average more compared with smaller woodlouse and millipede species (Reichle 1968). This could indicate that the carrying capacity for detritivores is higher in forest edges compared to forest centres, through higher input of organic matter [e.g., through increased Leaf Area Index (one-sided leaf area per unit of ground surface) (Beier and Gundersen 1989; Wuyts et al. 2008)] or increased herbaceous richness (N-rich litter) (Normann et al. 2016)). The net effect could result in altered nutrient cycling in forest edges resulting in e.g., higher N stocks (Didham et al. 2015; Remy et al. 2016). The question if the distribution patterns in our study are cause or consequence of altered biogeochemistry in small forest fragments in agricultural landscapes remains to be answered.

Conclusion

Summarising, we showed that macrodetritivore abundance and community composition is strongly altered by landscape use intensity and forest edges. Indicating the importance of both landscape context and within forest-patch gradients for macrodetritivore distribution. Although fragment characteristics are important for macrodetritivore distribution, this could not be explained by forest continuity or forest size. The observed patterns at multiple spatial scales could be linked to a key functional trait being desiccation resistance, a major driver in macrodetritivore distribution. Desiccation resistance is assumed to be an important filtering mechanism determining species occurrence. Altered environmental conditions in forest edges (temperature and humidity) influence community desiccation resistance at a local scale, while desiccation tolerant species (being larger) could benefit from higher nutrient input in higher land use intensity landscapes. Key functional traits can help us to predict changes in community structure in changing landscapes and the next challenge will be evaluating the impact of these community changes on ecosystem functioning.

Remy et al. (2017) have undertaken a first step in quantifying the effect of forest edge versus interior macro-detritivore communities for litter decomposition and nutrient cycling. They interchanged edge and interior litter, while mimicked abiotic edge conditions in forest centres to disentangle the effect of abiotic conditions and the detritivore community for leaf litter breakdown. Using this setup, they proved the importance of the specific detritivore edge community for accelerating leaf litter breakdown. A similar setup could be used to assess the effect of land use intensity on leaf litter breakdown by detritivores interchanging edge litter from higher and lower land use intensity landscapes. However, to understand the mechanisms behind these differences in leaf litter breakdown we propose a more controlled approach using field experiments with microcosms, manipulating macro-detritivore community composition and abundance in forest edges and interiors and across landscapes. In this way, we can link macro-detritivore community traits to litter decomposition in changing landscapes.

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