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# Strength of forest edge effects on litter-dwelling macro-arthropods across Europe is influenced by forest age and edge properties

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## Abstract

**Aim:** Forests are highly fragmented across Western Europe, making forest edges important features in many agricultural landscapes. Forest edges are subject to strong abiotic gradients altering the forest environment and resulting in strong biotic gradients. This has the potential to change the forest's capacity to provide multiple ecosystem services such as nutrient cycling, carbon sequestration and natural pest control. Soil organisms play a key role in this perspective; however, these taxa are rarely considered in forest edge research.

**Location:** A latitudinal gradient of 2,000 km across Western Europe.

**Methods:** We sampled six dominant taxa of litter-dwelling macro-arthropods (carabid beetles, spiders, harvestmen, centipedes, millipedes and woodlice) in forest edges and interiors of 192 forest fragments in 12 agricultural landscapes. We related their abundance and community composition to distance from the edge and the interaction with forest age, edge orientation and edge contrast (contrast between land use types at either side of the edge).

**Results:** Three out of six macro-arthropod taxa have higher activity-density in forest edges compared to forest interiors. The abundance patterns along forest edge-to-interior gradients interacted with forest age. Forest age and edge orientation also influenced within-fragment compositional variation along the forest edge-to-interior gradient. Edge contrast influenced abundance gradients of generalist predators. In general, older forest fragments, south-oriented edges and edges along structurally more continuous land use (lower contrast between forest and adjacent land use) resulted in stronger edge-to-interior gradients while recent forests, north-oriented edges and sharp land use edges induced similarity between forest edge and interior along the forest edge-to-interior gradients in terms of species activity-density and composition.

**Main conclusions:** Edge effects on litter-dwelling macro-arthropods are anticipated to feedback on important ecosystem services such as nutrient cycling, carbon sequestration and natural pest control from small forest fragments.

KEYWORDS

agricultural landscapes, beta diversity, edge effects, forest fragmentation, natural pest control, nutrient cycling, soil fauna

## 1 | INTRODUCTION

Many landscapes around the world show increasing amounts of forest edges because of extensive forest fragmentation, due to land conversion for agriculture, infrastructure or residential areas (Ibisch et al., 2016; Wade, Riiters, Wickham, & Jones, 2003). In Western Europe, this fragmentation has led to scattered small forest fragments within an agricultural matrix (Decocq et al., 2016; Kolb & Diekmann, 2004) putting severe pressure on forests' biodiversity and the multiple ecosystem services it can provide (Haddad et al., 2015; Krauss et al., 2010). Altered ecological conditions due to an increased forest edge-to-interior ratio of small forest fragments are major drivers of negative effects of forest habitat fragmentation (Harrison & Bruna, 1999), in particular for forest interior specialist species (Pfeifer et al., 2017).

Forest edges have very different abiotic conditions compared to interiors for example, higher temperature, litter input… (Delgado, Arroyo, Arévalo, & Fernández-Palacios, 2007; Gehlhausen, Schwartz, & Ausperger, 2000; Matlack, 1993) generally favouring biotic activity (De Smedt et al., 2016; Remy, Wuyts, Verheyen, Gundersen, & Boeckx, 2018) and therefore we can expect strong changes in community compositions and ecosystem processes along forest edge-to-interior gradients (De Smedt, Baeten, Berg et al., 2018). Furthermore, forest edges are ecotones on the brink of forest and the adjacent land use where species from both habitats can co-occur (Boetzl, Schneider, & Krauss, 2016; Madeira et al., 2016). The strength (magnitude and depth) of the edge influence on species distribution patterns is highly context-dependent and can be related to forest and edge characteristics. Forest age (successional development) influences abiotic gradients, with a cooler microclimate in older forest, which results in a stronger distinction between forest edge and interior conditions and thus higher strength of edge influence (Matlack, 1993). This stronger distinction between forest edge and interior can result in higher differences in community composition between forest edge and interior in old compared to young forests (De la Peña et al., 2016). Similar patterns are detected for forest orientation. Microclimatic edge gradients are more extreme in south-oriented compared to north-oriented edges (Chen, Franklin, & Spies, 1995; Matlack, 1993). The shaded north-oriented edges more closely resemble forest interior resulting in a lower divergence in community composition between forest edge and interior. Next to forest age and edge orientation, edge contrast with the adjacent land use type is an important factor determining the strength of edge effects with high edge contrast if the land use types at either side of the edge are very different in structure, management intensity etc. It is generally assumed that "soft edges" (e.g., forest edges bordering other forest types or abandoned fields) manifest less strong edge effects compared to "hard edges" (e.g., forest edges bordering very intensive agricultural crop fields) (Peyras, Vespa Bellocq, & Zurita, 2013; Reino et al., 2009; Yekwayo, Pryke, Roets, & Samways, 2016).

More contrasting habitats have complementary species pools that can result in higher species richness in the edge ecotone. Therefore, community composition in small forest fragments can be driven by forest age, edge orientation and edge contrast but how the strength of edge effects change with distance from the forest edge has hardly been studied (Ries, Fletcher, Battin, & Sisk, 2004). Identifying the drivers of edge response strength is important for habitat conservation, because it can define the area of undisturbed interior forest habitat. Identifying unaffected interior habitat can provide more accurate predictions on population sizes, and consequently ecosystem functioning, compared to habitat area per se (Ewers & Didham, 2008).

Soil organisms and litter-dwelling fauna are key for ecosystem functioning and involved in multiple ecosystem services such as nutrient cycling, carbon sequestration and natural pest control (Costanza et al., 2017; de Vries et al., 2013; Jeffery et al., 2010). However, beside natural pest control agents (see e.g. Rand, Tylianakis, & Tscharntke, 2006; Tscharntke et al., 2012), the different components of the soil food web are rarely considered in forest edge research. Therefore, we studied the effect of edge characteristics (edge orientation and edge contrast) and the larger forest fragment context (fragment age and distance from the forest edge) on the abundance and community composition of different litter-dwelling macro-arthropods. We focussed on two dominant trophic levels of the soil fauna food web being predators, represented by most of the carabid beetles (Insecta, Coleoptera, Carabidae), spiders (Arachnida, Araneae), harvestmen (Arachnida, Opiliones) and centipedes (Chilopoda), and detritivores being millipedes (Diplopoda) and woodlice (Malacostraca, Isopoda).

Within forest fragments, we expect higher abundance of litter-dwelling macro-arthropods in forest edges compared to forest interiors (H1). We expect this contrast to become higher with increasing distance from the forest edge as well as increased dissimilarity in community composition between edge and interior (H2). Furthermore, we hypothesize that this distance effect is modulated by forest age and edge properties (edge orientation and edge contrast with the adjacent land use) (H3).

## 2 | METHODS

### 2.1 | Study area and selected forest fragments

The study was carried out in six regions across the temperate forest biome of Western Europe (Figure 1), along a latitudinal gradient spanning more than 2,000 km. In every region, we selected two 5 × 5 km landscape windows of different land use intensity (n = 12 landscape windows) (see Valdés et al., (2015) for more information about landscape characteristics and Supporting Information Appendix S1 for climate data from the regions). Within each landscape window, 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 determined the current size and historical forest continuity of all fragments using a digitized 1:25,000 map and a series of historical land use maps (from the 18th, 19th, 20th centuries), respectively, within a geographic information system environment (ArcGis® v.10.2, ESRI). Forest size ranged from 0.08 ha to 28.19 ha with a median of 1.31 ha. Forest temporal continuity (hereafter called forest age) ranged from 12 years to 269 years with a median of 51 years and was quantified by a weighted average of different stand ages (based on stand area, Valdes et al., 2015). We made two categories of forest age: older forests (at least 100 years forested; 31% of forests) and "recent" forests established on former agricultural land less than 100 years ago (69% of the forests). The forest fragments occurring in a given landscape window were evenly distributed among four categories based on forest age and area (this varied between regions): small-recent, small-older, large-recent and large-older. Four fragments per category and per landscape window were retained for field sampling: hence, 16 fragments per landscape window and 192 fragments across Western Europe were selected.

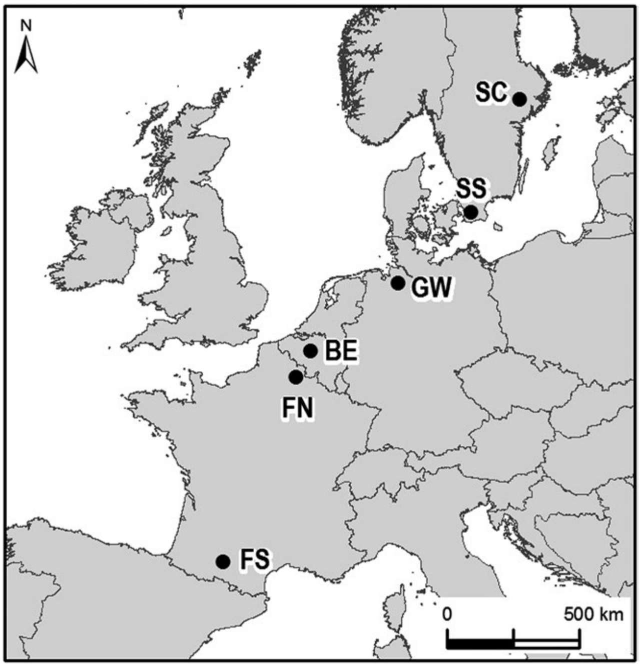

**FIGURE 1** Overview of the studied regions across Western Europe. FS: southern France; FN: northern France; BE: Belgium; GW: western Germany; SS: southern Sweden; SC: central Sweden

### 2.2 | Litter fauna sampling

Litter-dwelling arthropods were sampled using pitfall traps (Ø 10 cm, depth 11 cm) buried into the soil to blind-in with the litter environment. Litter properties are variable between regions and presented in the Supporting Information Appendix S2. Pitfall trap catches are a composite measure of activity and abundance of organisms (see e.g., Woodcock, 2004), so we will therefore use the term "activity-density" instead of abundance. The pitfall traps contained *ca.* 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 interior (centre) of each forest fragment as well as at the edge, that is, we have two sample points for each forest fragment for a total of 384 sample points. One sample point consisted of two sample units spaced five metres apart, resulting in four sample units per forest fragment (see De Smedt, Baeten, Proesmans et al. (2018) for more details on trap setup). We selected south-oriented or east-oriented edges (hereafter south-oriented edges, 75% of sample size), which are supposed to favour macro-arthropods because of the warmer microclimate (Chen et al., 1995). If this aspect was not suitable (e.g., edge bordered by a ditch, road or other physical barrier), we used west-oriented or north-oriented edges (hereafter north-oriented edge, 25% of sample size). Edge contrast depended on the land use intensity of the adjacent land and was classified in two categories: cropland (55% of the adjacent land use types) or grasslands (45%). Cropland can be seen as a more intensive form of agriculture with regular ploughing and a more intensive use of pesticides, hence a higher land use contrast at edge (hereafter edge contrast).

Macro-arthropods were sampled twice between April and August 2013 during fourteen consecutive days, in each forest fragment. To make data 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. All individual carabid beetles, spiders, harvestmen, centipedes, millipedes and woodlice were identified to species level. Harvestmen and Centipedes were not taken into account in samples from Southern France, because of sample storage problems. Since carabids represent a beetle family with both predators, herbivores and omnivores we extracted feeding guild data from carabids.org (Homburg, Homburg, Schäfer, Schuldt, & Assmann, 2013). We found this data for 91.3% of the species covering 99.8% of the individuals. Of these individuals, the vast majority (91.8%) were predators. We will therefore discuss this taxonomic group together with the other predatory taxa.

## 2.3 | Data analysis

### 2.3.1 | Activity-density

Sampling periods and sample units (replicates) were pooled at sample point level, resulting in one activity-density value for the forest edge and one for the forest interior per forest fragment and per taxon. These two values were used to calculate an effect size expressing the strength of the edge effect, as the change in activity-density (AD) from interior to edge. Here, we used the natural logarithm of the response ratio ADs (Hedges, Gurevitch, & Curtis, 1999): $\ln(AD_{edge}/AD_{interior})$. This response ratio will be referred to as edge effect on activity-density throughout the manuscript. This edge effect on activity-density was only calculated for a taxon if at least one individual was sampled in the forest edge and one in the forest interior. This resulted in 182 forests retained for carabid beetles (95%), 183 for spiders (95%), 144 for harvestmen (90%), 72 for centipedes (45%), 168 for millipedes (88%) and 183 for woodlice (95%). First, we tested whether the edge effect on activity-density deviated from zero and differed between taxa, using a linear multilevel model (*lmer*-function of the *lme4*-package; Bates et al., 2016). An edge effect on activity-density above zero indicates higher activity-density in forest edges compared to interiors, while an edge effect on activity-density below zero indicates the opposite. We used landscape window nested in region as a random effect to account for variability between landscapes. We used the *summary*-function (*t*-test) of our model to test whether the taxa specific edge effect differed from zero. Second, we tested whether the strength of the edge effect on activity-density (i.e., the effect size) depended on the distance between forest edge and interior, the forest age (older vs. recent), edge orientation (south-oriented vs. north-oriented) and edge contrast (crop vs. grassland). We also included the interaction between distance and forest age, distance and edge orientation, and distance and edge contrast, in order to test whether the effect of forest and edge characteristics on AD and community composition depended on distance between forest edge and interior. Distance was log-transformed and centred to average to zero across all regions. We used again a linear multilevel model (*lmer*-function) with landscape window within region as random effect and allowed the distance effects to vary between taxa by including an interaction effect. Individual taxa were tested according to the same procedure (see Supporting Information Appendix S3).

### 2.3.2 | Community composition

To quantify the within-forest fragment compositional variation between forest edge and interior, we calculated the Sørensen dissimilarity index between the two sampling points within each fragment and the two additive components of this dissimilarity (Baselga, 2010): the true turnover component (spatial replacement of species; Simpson index) and a nestedness component resulting from richness differences (*betapart*-package; Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2017). We only included taxon data from forests where at least 10 individuals of that particular taxon were sampled (e.g., 10 spiders, 10 centipedes etc.) to avoid many "0" and "1" values for the dissimilarity index. This resulted in 179 forests retained for carabid beetles (93%), 183 for spiders (95%), 127 for harvestmen (79%), 25 for centipedes (16%), 152 for millipedes (79%) and 181 for woodlice (94%). First, for the three components of community composition, that is, Sørensen dissimilarity index (referred to as compositional variation), species turnover and nestedness, we used a linear multilevel model (*lmer*-function) to test for differences between taxa. We used landscape window nested in region as a random effect to account for differences between landscapes. To get pairwise comparisons between taxa, we performed a Tukey post hoc comparison with the *glht*-function from the *multcomp*-package (Hothorn et al., 2016) (see Supporting Information Appendix S4). Second, we tested whether compositional variation depended on distance between forest edge and interior, forest age, edge orientation and edge contrast according to the same procedure as used for the activity-density model.

We tested individual taxa for compositional variation according to the same procedure as the activity-density model (see Supporting Information Appendix S5). All analyses were performed within the statistical software of R (R Core Team, 2017).

## 3 | RESULTS

Across all six taxa, we identified 182,118 individuals covering 598 species of which are 29,100 carabid beetles (150 species), 29,632 spiders (331 species), 23,378 harvestmen (25 species), 13,327 millipedes (39 species), 909 centipedes (26 species) and 85,769 woodlice (27 species) (see Supporting Information Appendix S6 for complete species lists).

### 3.1 | Edge effect on activity-density

The edge effect on activity-density differed significantly between taxa ($F_{(6,141)} = 15.12$, $p < 0.001$) (Figure 2). Spiders ($t_{182} = 6.27$, $p < 0.001$), millipedes ($t_{201} = 3.51$, $p < 0.001$) and woodlice ($t_{182} = 6.22$, $p < 0.001$) had higher activity-density in forest edges compared to interiors. Harvestmen activity-density tended to be higher in forest interiors compared to forest edges (but note that $t_{211} = -1.81$, $p = 0.07$). Activity-density of carabid beetles ($t_{184} = 1.19$, $p = 0.24$), and centipedes ($t_{412} = -0.02$, $p = 0.98$) did not differ between forest edges and interiors.

Across all taxa, the edge effect on activity-density was influenced by the distance between forest edge and interior (Table 1) but only in older forest, not in recent forest (Figure 3). In older forest, larger distances between forest edges and interiors led to stronger increases in activity-density from interior to edge (more positive log-ratio). Fragments bordered by grasslands showed edge effects for carabid beetles and spiders (Supporting Information Table S3.1). However, both taxa show an opposite pattern. For carabid beetles, larger distances between forest edges and interiors led to more neutral responses (response of 0) in activity-density from interior to edge when edges were bordered by grasslands. At large distances from the forest edge, interior communities have even higher activity-density compared to edge communities (Supporting Information Figure S3.1). The edge effect on activity-density for spiders increased when distances between forest edges and interiors became larger (Supporting Information Figure S3.2). For carabid beetles and spiders, there was no response for edges bordered by cropland. The edge effect on activity-density depended on edge orientation for spiders, with larger distances between forest edges and interiors leading to stronger decreases in activity-density from interior to edge for north-oriented edges while opposite for south-oriented edges (Supporting Information Figure S3.3). Edge effect on millipede activity-density increased with increasing distance from the forest edge (Supporting Information Figure S3.4). Edge effects on woodlice activity-density showed a similar pattern as the overall trend (Supporting Information Figure S3.5). No significant trends were observed for harvestmen and centipedes (Supporting Information Table S3.1).

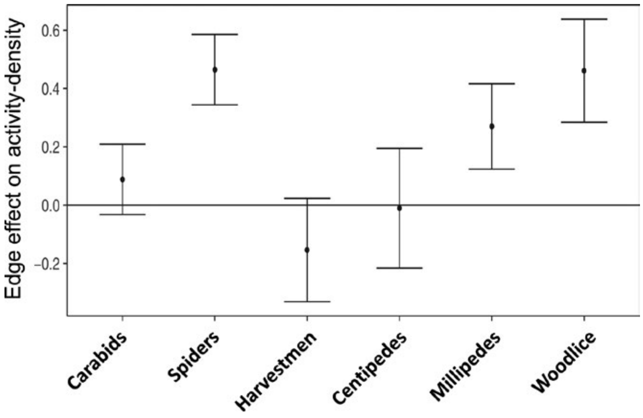

**FIGURE 2** Edge effect on activity-density, calculated as a log response ratio effect size, on six taxa of litter-dwelling macro-arthropods across Western Europe. A response ratio of zero indicates equal activity-density in forest edges and forest interiors and positive (negative) values higher (lower) activity-density at the forest edge. Points and error bars represent mean effects ±1 *SE*

### 3.2 | Edge effect on community composition

Edge effects on community composition (compositional variation) within forest fragments differed between taxa ($F_{(5,822)} = 108.84$, $p < 0.001$), with spiders showing the highest overall compositional variation, followed by carabid beetles (Figure 4a). Centipedes and millipedes had a lower overall compositional variation, but higher compared to harvestmen and woodlice (Figure 4a) (see Supporting Information Appendix S4). For carabid beetles and spiders, the compositional variation between forest interior and edge was mostly derived from turnover (70% and 83%, respectively). For the other taxa, compositional variation was derived from both turnover and nestedness (Figure 4). Species turnover patterns were similar compared with overall compositional variation (Figure 4b). Nestedness was lower for spiders compared to all other taxa, except woodlice (Figure 4c) and lower for woodlice compared to millipedes (Figure 4c) (see Supporting Information Appendix S4).

**TABLE 1** Results of the multilevel model testing the effect of distance (log-transformed), forest age, edge contrast and edge orientation on log-ratio activity-density of forest edge versus forest interior from six taxa and across Western Europe. Results (*F*-values and degrees of freedom) of linear multilevel models

| Explanatory variable | *F*-value | |
|---|---|---|
| Distance (Dist) | $F_{(1,644)}$ | 4.27* |
| Forest age (Age) | $F_{(1,381)}$ | 0.04 |
| Edge contrast (Cont) | $F_{(1,100)}$ | 0.21 |
| Orientation (Or) | $F_{(1,656)}$ | 1.16 |
| Dist × Age | $F_{(1,861)}$ | 11.40*** |
| Dist × Cont | $F_{(1,754)}$ | 0.03 |
| Dist × Or | $F_{(1,719)}$ | 0.75 |

$^{*}p < 0.05$, $^{***}p < 0.001$.

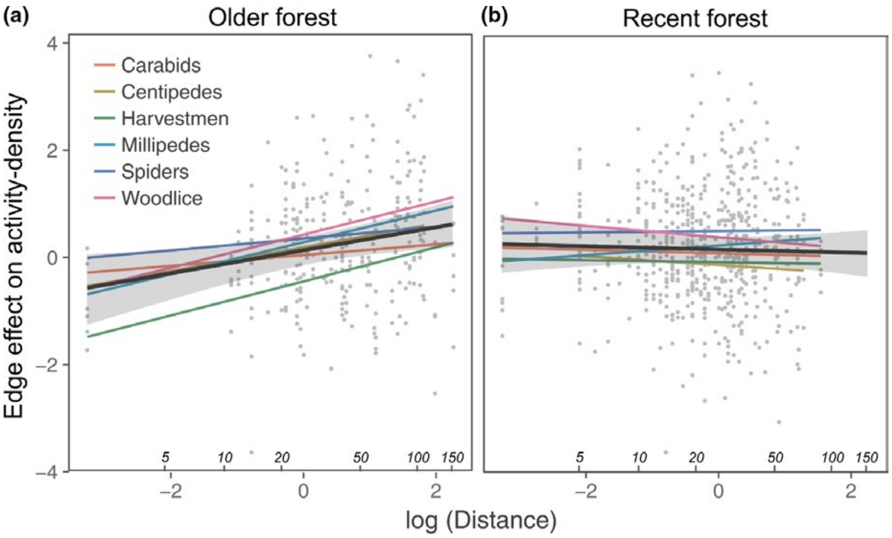

**FIGURE 3** Edge effect on activity-density, calculated as a log response ratio effect size, according to distance of the forest interior from the forest edge for (a) older forest fragments and (b) recent forest fragments across Western Europe. Different colours represent the six taxa of litter-dwelling macro-arthropods. Data based on 192 forest fragments in 12 landscapes across Western Europe. Black line represents mean ±1 *SE* (shaded area). Italic numbers represent non-transformed distances from the forest edge

Across all taxa, compositional variation and turnover were influenced by the actual distance between forest edge and interior (Table 2) in older forest (Figure 5a) and south-oriented forest edges (Figure 5d), not in recent forest (Figure 5b) or in north-oriented forest edges (Figure 5c). In older forest and south-oriented forest edges, larger distances between forest edge and interior led to stronger compositional variation between the forest edge and interior. Splitting-up the analysis for separate taxa revealed a significant increase of compositional variation for spiders with increasing distance from forest edge and interior, at least in south-oriented edges but not in north-oriented edges (Supporting Information Figure S5.1). Millipede compositional variation increased with increasing distance between forest edge and interior in older forest but not in recent forest (consistent with the overall pattern) (Supporting Information Figure S5.2).

## 4 | DISCUSSION

For three out of six litter-dwelling macro-arthropod taxa (i.e., spiders, millipedes and woodlice), activity-density was higher in forest edges compared to forest interiors. Carabid beetles, harvestmen and centipedes did not show a significant response. The contrast in activity-density between forest edges and interiors depended strongly on distance between forest edge and interior, which was also the case for compositional variation. The effect interacted for multiple groups with forest (edge) characteristics: responses were stronger in older forest, south-oriented edges and lower contrast edges that is, with grassland on the outside.

### 4.1 | Activity-density in forest edges versus interiors

The higher activity-density of different litter-dwelling taxa suggests that the habitat conditions in forest edges are more favourable for arthropods compared to forest interiors. Forest edges have higher temperatures (Delgado et al., 2007; Heithecker & Halpern, 2007), which increases arthropod activity, metabolic rate and results in a shorter reproduction time (Gillooly, Brown, West, Savage, & Charnov, 2001). Additionally, edge leaf litter has a lower C/N-ratio (De Smedt et al., 2016) resulting in better food quality for detritivore taxa, such as woodlice and millipedes (David & Handa, 2010). However, an important determinant of soil arthropod distribution and survival is humidity, which is lower at forest edges compared to interiors (Chen et al., 1995; Gehlhausen et al., 2000). Different studies have pointed out humidity as a key factor shaping soil arthropod distribution (Bogyó, Magura, Nagy, & Tóthmérész, 2015; David & Handa, 2010; Hornung, 2011; Pearce & Venier, 2006), and how well species can cope with low moisture levels is highly species-specific (Dias et al., 2013). This can help us to understand the distribution of harvestmen along forest edge-to-interior gradients. Harvestmen can be divided in two groups being true soil dwellers and vegetation dwellers. Pitfall traps, in particular sample soil dwellers (De Smedt & Van de Poel, 2017), which are more drought sensitive compared to the thermophilic shrub dwellers (Curtis & Machado, 2007). The used sampling technique, biased to soil dwellers, might therefore explain the observed tendency of harvestmen to be more common in forest interiors compared to forest edges. The observed distribution patterns are probably a net effect of species that have the ability to withstand dry conditions and built-up large populations in forest edges compared to drought-sensitive species that retreat to forest interiors. De Smedt, Baeten, Berg et al. (2018) investigated species-specific distribution patterns of woodlice along forest edge-to-interior gradients and discovered that the patterns could be explained based on species desiccation resistance. The most drought-sensitive species showed a negative activity-density response towards forest edges. This is also the species, which have the lowest number of eggs in their brood pouch and can be considered as woodlice K-strategists (Warburg, Linsenmair, & Bercovitz, 1984). The drought-resistant species from the forest edge on the contrary have higher number of eggs (r-strategists) enabling them to build up large populations in a short time-period (Warburg et al., 1984). The r/K strategy theory

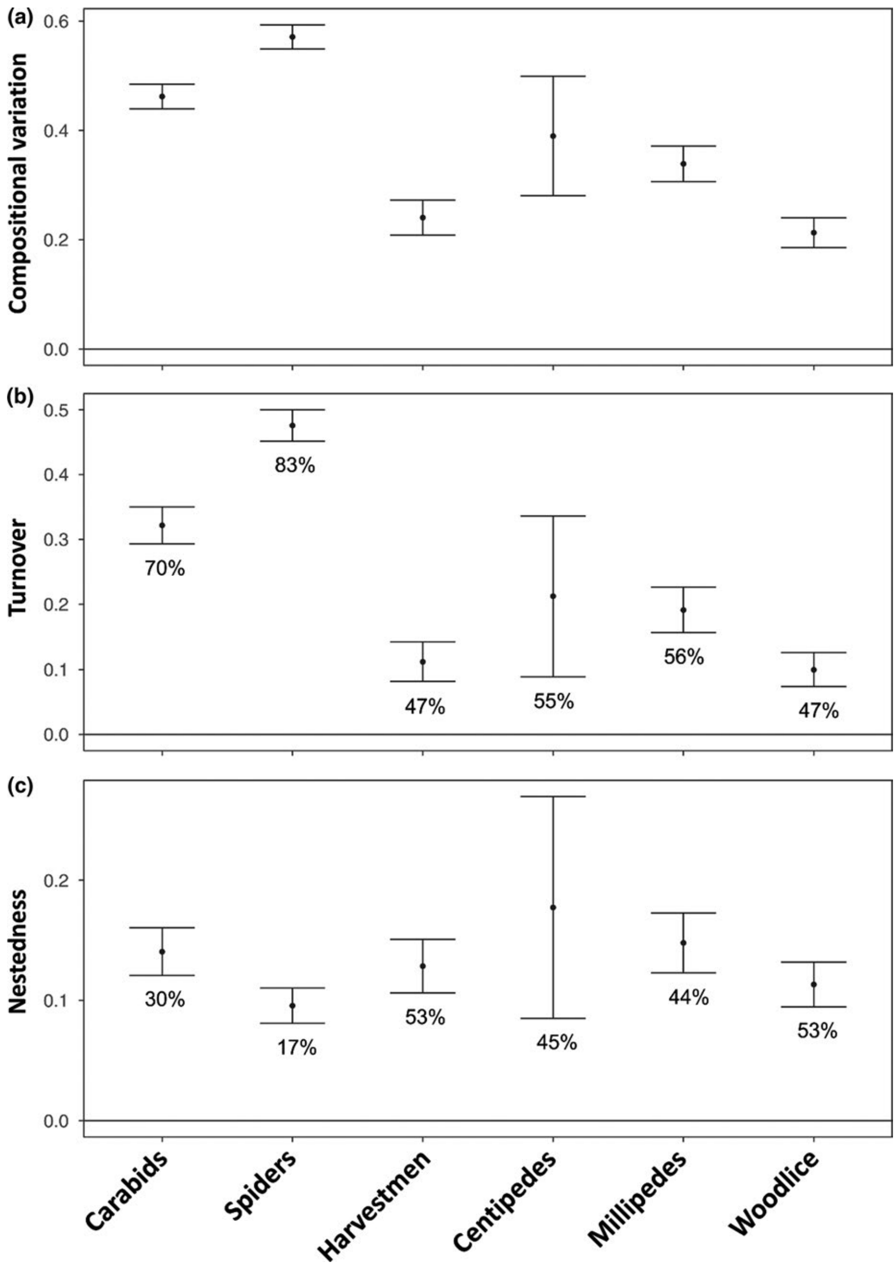

**FIGURE 4** Mean compositional variation (±1 *SE*) between the interior and edge community within forest fragments for six taxa of litter-dwelling macro-arthropods across Western Europe for (a) compositional variation (Sørensen dissimilarity index) and its two additive components: (b) turnover (Simpson Index) and (c) nestedness. Percentages report the proportion of community variation that is attributed to turnover or nestedness. Significance values between taxa can be found in Supporting Information Appendix S4

has also been established for plants in forest edges (Chabrerie, Jamoneau, Gallet-Moron, & Decocq, 2013). Next to, environmental conditions favouring fast population growth, the increased use of pesticides close to forest edges might also select for r-strategists (Chabrerie et al., 2013). Nevertheless, the net overall distribution pattern of the different taxa is a balance between the positive effects of suitable environmental and food conditions in forest edges and the negative response to decreased moisture availability.

### 4.2 | Activity-density contrast and community composition along edge-to-interior gradients

The edge response on activity-density depended on the distance between forest edge and interior across all taxa, in interaction with forest age (see below). This was also the case for compositional variation where distance between forest edge and interior always interacted with forest (edge) characteristics, proving the strong context-dependency of forest edge-to-interior gradients. Compositional variation between forest edge and interior was highest for species-rich taxa (spiders and carabid beetles) and lowest for species-poor taxa (woodlice and harvestmen). Local communities of species-rich taxa may be assembled from a larger species pool and show higher local site-to-site variation (Baselga, 2010). Species-poor taxa had low relative turnover rates, this could be explained by (a) interior communities being largely a subset of edge communities or (b) edge communities becoming more species rich because of spillover from adjacent agricultural land. De Smedt, Baeten, Berg et al. (2018) have supported the first for woodlice, where most species (despite some exceptions) decrease in activity-density from the forest edge to the interior with few typical forest interior species. However, typical interior communities have

**TABLE 2** Results of the multilevel model testing the effect of distance (log-transformed), forest age, edge contrast and edge orientation on compositional variation (Sørensen dissimilarity index), turnover (Simpson index) and nestedness between forest edge and interior communities of litter-dwelling macro-arthropods from six taxa and across Western Europe. Results (*F*-values and degrees of freedom) of linear multilevel models

| Explanatory variable | *F*-value | |
|---|---|---|
| Compositional variation | | |
| Distance (Dist) | $F_{(1,816)}$ | 1.40 |
| Forest age (Age) | $F_{(1,563)}$ | 1.09 |
| Edge contrast (Cont) | $F_{(1,121)}$ | 1.94 |
| Orientation (Or) | $F_{(1,749)}$ | 2.00 |
| Dist × Age | $F_{(1,812)}$ | 11.55*** |
| Dist × Cont | $F_{(1,750)}$ | 1.73 |
| Dist × Or | $F_{(1,802)}$ | 5.40** |
| Turnover | | |
| Distance (Dist) | $F_{(1,809)}$ | 1.13 |
| Forest age (Age) | $F_{(1,552)}$ | 1.01 |
| Edge contrast (Cont) | $F_{(1,124)}$ | 0.50 |
| Orientation (Or) | $F_{(1,742)}$ | 0.00 |
| Dist × Age | $F_{(1,812)}$ | 13.49*** |
| Dist × Cont | $F_{(1,746)}$ | 1.29 |
| Dist × Or | $F_{(1,796)}$ | 3.19 |
| Nestedness | | |
| Distance (Dist) | $F_{(1,815)}$ | 0.02 |
| Forest age (Age) | $F_{(1,603)}$ | 0.02 |
| Edge contrast (Cont) | $F_{(1,150)}$ | 0.83 |
| Orientation (Or) | $F_{(1,764)}$ | 3.43 |
| Dist × Age | $F_{(1,815)}$ | 0.58 |
| Dist × Cont | $F_{(1,765)}$ | 0.04 |
| Dist × Or | $F_{(1,806)}$ | 0.33 |

$p < 0.1$,
**$p < 0.01$, ***$p < 0.001$.

been found for millipedes (De Smedt, Baeten, Proesmans et al., 2018) and centipedes (Lacasella et al., 2015). A species-rich taxon, like carabid beetles, showed a higher degree of typical interior species (Soga, Kanno, Yamaura, & Koike, 2013; Tóthmérész, Nagy, Mizser, Bogyó, & Magura, 2014), but this has hardly been found for the species-rich spiders (Kowal & Cartar, 2012; Lacasella et al., 2015). However, for these two groups spillover from adjacent fields to forest edges has been reported (Boetzl et al., 2016; Tscharntke et al., 2012), which can cause the higher compositional variation between forest edge and interiors for carabid beetles and spiders.

## 4.3 | Modulation of edge effects by forest (edge) characteristics

Distance between forest edge and interior influenced edge effects on activity-density in older forests. This can be associated to abiotic gradients in older forest being stronger, compared to recent forest fragments, with overall lower temperatures and higher humidity in older forest (longer successional development) compared to recent forest (Baker et al., 2014). Hence, abiotic gradients are less developed in recent fragments resulting in weaker gradients of arthropod abundance (Ng, Barton, Macfadyen, Lindenmayer, & Driscoll, 2018). Compositional variation showed an increase with distance from the forest edge in older fragments, but a neutral response in recent forest fragments. This indicates that larger distances between edge and interior communities lead to stronger compositional variation in older forest, but not in recent forest. In recent fragments, there is a degree of dissimilarity between edge and interior but this does not change when moving deeper into the forest fragment. This effect was found for both compositional variation and turnover, but not for nestedness. Therefore, turnover has a larger share in compositional variation at larger distance between edge and interior, indicative for increased species replacement in older forest. Interior communities are more stable compared to edge communities in older forest (Ewers & Didham, 2008), but this might not be the case for recent forest fragments, which can be more dynamic compared to older forest because of the ongoing forest succession. These recent forests lack, for example, characteristic older forest vegetation (Flinn & Vellend, 2005; Verheyen, Bossuyt, Honnay, & Hermy, 2003) and differ from older forest in microbial and micro-fauna community (de la Peña et al., 2016), providing different food and habitat properties for litter-dwelling macro-fauna.

Spiders are the only studied taxon in which the strength of activity-density response depended on edge orientation. As expected, the contrast between forest edges and interiors increases with distance in south-oriented forest edges, because of the more extreme abiotic gradients (Chen et al., 1995; Matlack, 1993). The reversed pattern in north-oriented forest edges is however difficult to explain, but could indicate that north-oriented forest edges have less favourable environmental conditions for spiders compared to forest interiors. Spider distribution is strongly related to vegetation structure because they need complexity for both hunting and web building (Hatley & Macmahon, 1980; Uetz, 1991) for example, in forest edges (Baldissera, Ganade, & Fontoura, 2004). Vegetation structure and plant community composition show a stronger gradient and larger penetration depth in south-oriented compared to north-oriented edges (Fraver, 1994; Honnay, Verheyen, & Hermy, 2002), which might explain the observed spider gradients. The same mechanisms are probably causing the observed compositional variation pattern for spiders, and all taxa combined. South-oriented edges provide therefore not only habitat for more individuals but also for different species compared to forest interiors.

All spiders and more than 90% of our carabid individuals are predators with great potential for natural pest control (Holland & Luff, 2000; Marc & Canard, 1997; Symondson, Sunderland, & Greenstone, 2002; Tscharntke et al., 2012). Carabid beetles and spiders showed a changing activity-density response along the forest edge-to-interior gradients at lower contrast edges (grasslands) but not on higher contrast edges (crop fields). Most of the studied

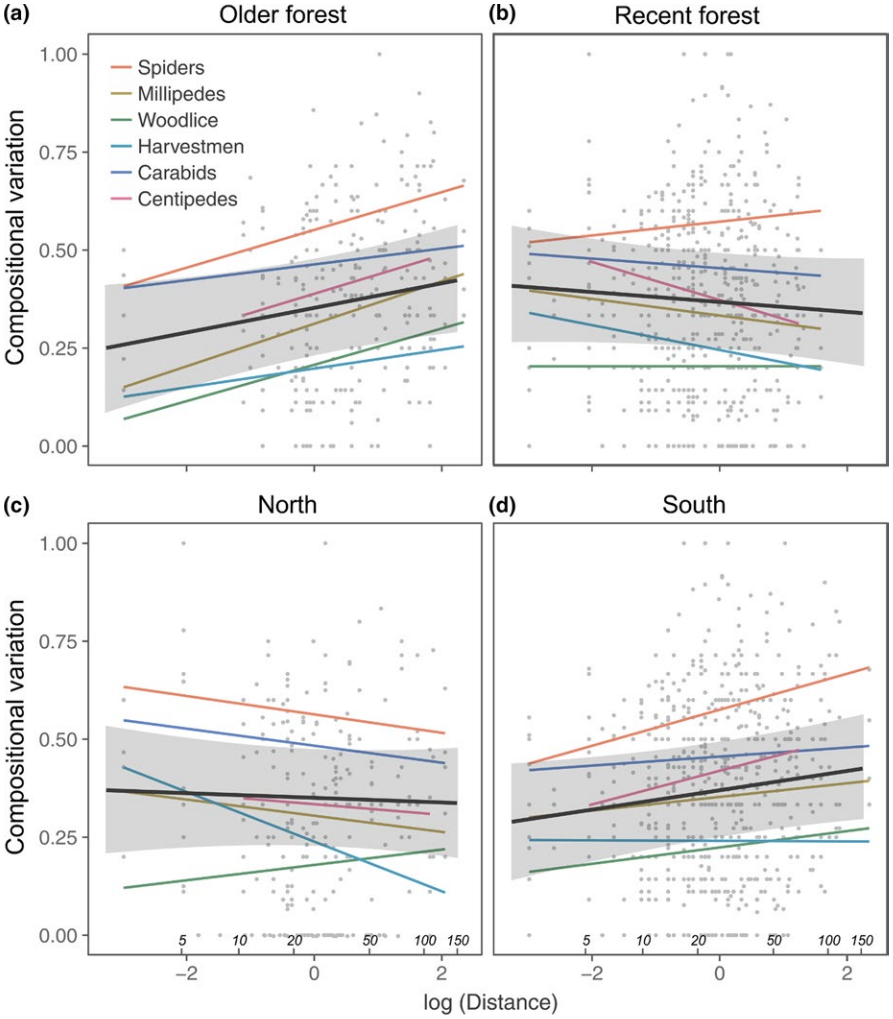

**FIGURE 5** Edge effect on the compositional variation between interior and edge communities of six taxa of litter-dwelling macro-arthropods according to distance between forest edge and interior for (a) older and (b) recent fragments according and (c) north- or (d) south-oriented edges across Western Europe. Different colours represent the six litter-dwelling macro-arthropods. Data based on 192 forest fragments in 12 landscapes across Western Europe. Black line represents mean ±1 *SE* (shaded area). Italic numbers represent non-transformed distances from the forest edge

arthropod predators cannot complete their life cycle on crop fields (Samu & Szinetár, 2002), while at least some species can on permanent grasslands. This could result in a more stable edge community, because of a more stable grassland community compared to crop fields at least for spiders (Birkhofer, Smith, Weisser, Wolters, & Gossner, 2015), resulting in a more constant spillover rate compared to crop fields. Croplands are dynamic because of annual soil management and more intensive use of pesticides and this could result in more temporal fluxes of predators. These findings support the potential of predatory taxa from the agricultural matrix to influence arthropod dynamics in semi-natural vegetation fragments through their edge (see e.g., Tscharntke, Rand, & Bianchi, 2005). However, the observed patterns might be explained by the fact that meadows and croplands have different arthropod communities (Jeanneret, Schüpbach, Pfiffner, & Walter, 2003; Samu & Szinetár, 2002), and species-specific responses might govern distributional patterns (Magura, 2002; Niemelä, Langor, & Spence, 1993).

### 4.4 | Conclusion

We showed strong edge responses of litter-dwelling arthropods with generally higher activity-density in forest edges. However, the strength of the edge effect depended on the actual distance between interior and edge and the interaction with forest age, edge orientation and edge contrast. Forest edge research has found strong abiotic gradients and there is increasing evidence that these gradients are translated into strong biotic gradients for an increasing number of taxa. This study shows this for dominant litter-dwelling macro-arthropods with consistent patterns in temperate forest fragments across Western Europe spanning a gradient of more than 2,000 km from Southern France up to central Sweden. In consequence, these strong gradients could have important consequences for ecosystem functioning. All studied taxa are important links in the detrital food web and therefore of key importance for nutrient cycling in forest habitats (Lavelle, 1997). Of the global net primary production, 80% enters the detrital food web. However this, food web receives far less attention compared to aboveground food webs (Moe et al., 2005). This fact stresses the need for detrital food web studies. Using a food web modelling approach, tracking nutrients and biomass across the detrital food web in forest edges and interiors, can give us important insights in how forest functioning is affected by forest edges. This can enable us to understand how forest edges affect the ecosystems ability to supply multiple ecosystem services (such as carbon sequestration, nutrient mineralization, water purification, natural pest control) in small forest fragments in agricultural landscapes.

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## DATA ACCESSIBILITY

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

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## BIOSKETCH

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Author contributions: All authors conceived the ideas and collected the data; P.D.S. and L.B. analysed the data; and P.D.S. led the writing.

## SUPPORTING INFORMATION

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

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