Voor Kas en Thor,
zodat ze weten dat hun papa toch al iéts kan…

Supervisors: Prof. Dr. Ir. Kris Verheyen
Ghent University, Department of Environment, Forest & Nature Lab
Prof. Dr. Dries Bonte
Ghent University, Department of Biology, Terrestrial Ecology Unit
Prof. Dr. Martin Hermy
KU Leuven, Department of Earth and Environmental Sciences, Division of Forest, Nature and Landscape
Dean: Prof. Dr. Ir. Marc Van Meirvenne
Rector: Prof. Dr. Ir. Rik Van de Walle

Pallieter De Smedt

Edge effects on the distribution of litter-dwelling arthropods in small forest fragments in agricultural landscapes

Thesis submitted in fulfillment of the requirements

For the degree of Doctor (PhD) in Applied Biological Sciences:

Forest and Nature management

Dutch translation of the title:
Bosrandeffecten op de verspreiding van strooiselbewonende arthropoden in kleine bosfragmenten in Europese landbouwlandschappen

Illustration on the cover:

Front: *Armadillidium pulchellum* (Gert Arijs)

Back: Agricultural landscape of Brakel, Belgium (Edwin Brosens)

Design: Kaat Van Ongeval

Citation:
De Smedt P (2018) Edge effects on the distribution of litter-dwelling arthropods in small forest fragments in agricultural landscapes. PhD-thesis, Ghent University, Ghent, Belgium

ISBN 9789463571111

DANKWOORD

29 mei 2018, het ligt er! Zes jaar van mijn leven aan dit boekje gewerkt en ik ben er heel trots op. Trotser ben ik op het feit dat dit tot stand is gekomen dankzij samenwerking met een heleboel fantastische mensen. Ik ging een kort dankwoord schrijven...

Kris, Ik had me geen betere promotor kunnen bedenken. Bedankt voor alle vrijheid en vertrouwen die ik kreeg van jou om mijn eigen onderzoek op mijn manier uit te bouwen. Daarnaast wil ik je ook bedanken voor de flexibele houding ten opzichte van mijn persoonlijke leven. Twee kindjes en een verbouwing op één doctoraat was heftig, maar mede dankzij jouw begrip heb ik dit tot een goed einde kunnen brengen. **Martin** en **Dries:** ook jullie wil ik enorm bedanken voor de fijne samenwerking en het vertrouwen. De combinatie van jullie drie als promotoren, en jullie persoonlijke begeleiding heeft ervoor gezorgd dat ik steeds weer nieuwe energie had om verder te werken.
Ik wil ook de leden van de doctoraatscommissie enorm bedanken om die taak ter harte te nemen en zich door mijn 250 pagina's te worstelen. Er zijn weinig mensen die al zoveel pagina's over pissebedden gelezen hebben. Bedankt **Pascal Boeckx**, **Patrick De Clercq**, **Frederik Hendrickx**, **Dirk Maes** en **Steven Sleutel**.

I would like to thank the whole **smallFOREST-consortium** for the opportunity to collect data from several regions in Europe in close collaboration. Special thanks to **Jörg**, **Sara** and **Sabine** for the beautiful field trip. **Emilie**, thanks for the fruitful collaboration on data management.

Het **FWO** (Fonds Wetenschappelijk Onderzoek) wil ik bijzonder bedanken voor de beurs die ik kreeg om dit onderzoek uit te voeren.

Ik had het geluk om mijn doctoraat op een prachtige werkplek met **fantastische collega's** uit te voeren. **An**, jij zorgde ervoor dat ik me meteen thuis voelde en nog steeds kan ik voor raad en daad bij jou terecht. **Lander**, van een vlotte samenwerking gesproken! Bedankt voor alle hulp en goede werksfeer in Lier alsook de goede niet-werksfeer op de trein en de fiets, vechtend tegen de polar vortex. **Pieter**, via jou kreeg ik mijn eerste vacature binnen. Fantastisch dat dit het resultaat mag zijn. We moeten alvast eens samenzitten om mottenproject 2.0 uit te werken. **Margot**, een rots in de branding. Bedankt voor alle naleeshulp en de goede raad, altijd perfect wanneer ik het nodig had. **Safaa**, thanks for the efficient contribution to the data-analysis of the soil fauna experiment. **Karen**, bedankt om mij te introduceren tot de wondere wereld van de bosranden. **Luc en Kris**, zelden zo'n duo tegengekomen dat steeds paraat staat. Mannen om op te bouwen! Bedankt voor alle hulp. Verder heb ik met veel collega's heel fijn mogen samenwerken en mooie momenten beleeft. Bedankt allemaal!

Matty, bedankt voor de mooie samenwerking en de fijne excursies. Hopelijk kunnen we deze samenwerking nog een tijdje verderzetten.

Johan, ik kwam steeds met veel plezier naar jou toe om nieuwe stalen te brengen of data op te halen, die we dan uitgebreid konden bespreken. Jouw enthousiasme voor taxonomie werkt aanstekelijk en jouw onmeetbare spinnenkennis heeft me weten boeien vanaf de eerste keer dat we samen op pad gingen in het Kollintenbos, toen ik 11 was. Zonder mensen als jij kunnen grote projecten het wel helemaal vergeten om op een correcte manier aan biodiversiteitonderzoek te doen. Ik heb veel respect voor jouw kennis en manier van werken. Hopelijk kunnen we in de toekomst nog veel samenwerken. Ik noteer alvast april 2036 voor de start van het derde spinnenonderzoek op het Bos van Aa.

Ik heb het plezier gehad om zes fantastische, gemotiveerde masterstudenten te mogen begeleiden. **Willem**, **Rieneke**, **Tom**, **Sam**, **Rani** en **Warre** bedankt voor de fijne tijden in het veld en het lab en de grote hulp bij het determineren en de dataverwerking. Willem, bijzonder bedankt voor de vlotte detritivore samenwerking. Je kan nog steeds de nieuwe Kime worden of dé Proesmans van de beerdiertjes. Sam, jou moet ik eigenlijk niet als thesisstudent bedanken, we hebben veel meer samen gedaan dan dat. Het is fantastisch om mijn passie voor kleine beestjes te kunnen delen met één van mijn beste vrienden.

Jonah, data van tienduizenden pissebedden die moesten ingevoerd worden in datafiles: zonder jou had ik daar nog lange dagen op moeten zwoegen. **Bart,** merci voor de hulp met de lay-out van dit boekje.

Mama en **papa**, bedankt om mij de liefde voor de natuur mee te geven. Die leeft voort in mij, en daarmee in dit boekje. Bedankt voor de vrijheid die ik van jullie kreeg om mijn eigen weg in te slaan, en jullie oeverloze vertrouwen in mij.
Mijn broers en zussen, mijn schoonouders, vrienden, bedankt voor de steun op verschillende vlakken de afgelopen jaren.

Maarten en **Naomi**, bedankt dat ik steeds bij jullie terecht kon om mijn hart te luchten over weer een nieuwe rejection of eindelijk een major revision. Op naar rustigere tijden om met de tractor te rijden, bomen te zagen, lekker te eten en te genieten op de (verbouwde) Leeuwerkhoeve.

Pepijn, **Gert**, **Stijn** en **Oliver**, hoe fantastisch dat ik vier andere nerds kon vinden om in de weekends pissebedden te gaan zoeken. “Spinicornis” kan dankzij jullie als één van de meest productieve natuurstudiewerkgroepen in België gerekend worden. Ik kijk al uit naar de projecten die we nog zullen realiseren en naar de vele excursie op de mooiste en lelijkste plekjes van ons land. Ook wij hebben een duidelijke afspraak om in de zomer van 2020 onze pissebeddenatlas voor te stellen op het 11de internationale pissebeddencongres in Tsjechië.

Wim, **Jens**, **Tom**, **Cappy** en **Geert**: Een geschenk uit de hemel dat jullie (dé desperate wannabe's) mijn dikste vrienden zijn. Ik wist altijd dat ik vol op jullie kon rekenen.

Kas en **Thor,** jullie hebben dit doctoraat tot een extra uitdaging gemaakt. Thor, merci om toch al een maand te hebben doorgeslapen op anderhalf jaar. Kas, bedankt om slechts 11 maanden van je eerste jaar dag en nacht te wenen… Het hadden er ook 12 kunnen zijn. Jullie kapoenenlach is wat mij de gelukkigste mens maakt op deze wereld. Ik kijk al uit naar nog meer kriebelbeestjesplezier samen.

Kaat, ik kan je voor je uiteenlopende bijdrage bedanken: de lay-out van dit boekje, het voorbereiden van de receptie, mijn kapsel op de grote dag… Maar het is vooral voor alles wat niet met dit doctoraat te maken heeft, waarvoor ik je wil bedanken. Dat we dit allemaal doorgeworsteld hebben is grotendeels aan jouw doorzettingsvermogen en vastberadenheid te danken. Ik bewonder je elke dag.

Pallieter

CONTENTS

SUMMARY

Humans strongly affect landscapes via land-use changes. Forests have been profoundly fragmented around the world due to land conversion for agriculture. Hence, many landscapes consist of small, isolated forest fragments embedded in an agricultural matrix, which puts severe pressure on the forests' biodiversity and the multiple ecosystem services they can provide. Within the European Union, no less than 40% of the forest habitat lies within 100 m of other land use types and can thus be regarded as forest edge. Small forest fragments suffer from strong edge effects because of their large edge-to-interior ratio. Forest edges differ from forest interiors in abiotic conditions. Forest edges are characterised by higher light levels, wind speeds, air and soil temperatures, lower air humidity and soil moisture and increased soil pH. Forest edges also receive higher nutrient inputs through higher litter fall quantity and quality, via spill-over from adjacent land-use types such as agricultural fields and through higher atmospheric deposition. These environmental differences between forest edge and interior impact the distribution of biota which is relatively well studied for plants, birds, or above-ground invertebrates, but have remained poorly explored for the soil fauna community.

Despite its extreme diversity, soil associated taxa are poorly studied. A good knowledge on taxonomy is essential to understand and study species-specific distribution patterns; therefore, we start with contributing taxonomical knowledge of woodlice (a dominant letter-dwelling arthropod taxa) in Belgium in **Chapter 2**. We compiled a new checklist and assessed the status of occurrence of all Belgian species, contributing to the current knowledge on a large share of the Western-European woodlice fauna. This was done based on a review of 142 papers on Belgian woodlice, re-identifying museum collections and performing extensive field surveys. We added nine species (25%) to the Belgian checklist and assessed for the first time the state of occurrence of all Belgian species.

Based on good taxonomical knowledge we studied species-specific distribution patterns of woodlice and millipedes along forest edge to interior gradients in six forest stands in Northern Belgium **(Chapter 3)**. Woodlice abundance strongly decreased from the forest edge towards the forest interior, while millipede abundance only decreased after a few meters inside the forest along the same gradient. The patterns strongly differed per species and could be linked to species' desiccation resistance as well as to some key environmental factors such as litter quality, leaf area index, pH and soil nutrients. Abundance along forest edge to interior gradients across all species were independent from forest stand or dominating tree species, while dominating tree species strongly influenced species composition.

We hypothesized that species-specific distribution along forest edge-to-interior gradients could be predicted based on species' desiccation resistance because of the strong differences in temperature and soil moisture content between forest edges and forest interiors. We tested this for woodlice distribution across 10 landscapes in Europe covering 160 forest patches **(Chapter 4)**. We saw that drought sensitive species reduce their activity-density in forest edges while drought resistant species flourish. Resulting in higher overall activity-density in forest edges.

To disentangle the importance of increased temperature and reduced moisture for macro-detritvore functi-

oning in the forest ecosystem we performed a full-factorial field experiment in a deciduous forest fragment in Northern Belgium **(Chapter 5)**. We installed microcosms with four detritivore treatments (woodlice, millipedes, both woodlice and millipedes and a control) under four environmental treatments being a reduced moisture treatment (using a rainout shelter above the microcosms), an increased temperature treatment (using open top chambers), a combination of both treatments and a control. We added low and high quality litter to test for litter breakdown by macro-detritivores under the different treatments. We found mainly moisture availability to be a limiting factor for litter breakdown of high quality litter, not for low quality litter. Macro-detritivore identity proved to be important for the breakdown of low quality litter, not for high quality litter. Relative consumption rates of macro-detritivores were not influenced by any environmental treatment but depended on macro-detritivore identity for low quality litter. Woodlice were more efficient for the breakdown of low quality litter compared to millipedes.

The next step was to identify drivers of macro-detritivore distribution across spatial scales. In 224 forest patches in 14 landscapes in Western Europe, we explored woodlice and millipede distribution at within-fragment level (forest edge vs forest interior), fragment level and landscape level **(Chapter 6)**. Distribution of woodlice and millipedes was mainly affected by differences between forest edges and interiors and the landscape disturbance intensity. Forest edges had higher activity-density of woodlice and millipedes. Forest fragments located in high disturbance landscapes (high land use intensity) had higher activity-density compared to forests located in lower disturbance landscapes. In high disturbance landscapes, macro-detritivores probably profit from higher atmospheric nitrogen input and spill over of fertilizers from adjacent fields in forest edges embedded in high disturbance landscapes.

We investigated forest edge-to-interior distribution patterns for multiple litter-dwelling arthropod taxa in 192 forest patches in 12 landscapes in Western Europe **(Chapter 7)**. Next to woodlice and millipedes, also spiders are more abundant in forest edges compared to forest interiors, while there was no difference for carabid beetles, harvestmen and centipedes. Older forests showed stronger edge effects when the distance between forest edge and interior increased, while the strength of the edge effect did not increase in recent forests. Species composition differed more with increasing distance between edge and interiors in older forests and southern forest edges while there was no effect in recent forests and northern forest edges. Edges bordering more structural continuous habitat (i.e. grasslands) showed stronger edge effects for carabid beetles and spiders compared to higher edge contrast (i.e. edges bordered by croplands).

In conclusion, edge effects strongly influence abundance and species composition of litter-dwelling arthropods in small forest fragments in Europe (1). Species-specific desiccation resistance, which we identified as a key response trait, can explain litter-dwelling arthropod distribution patterns (2). Forest edges filter species based on their response traits, resulting in a different community composition between forest edges and interiors with associated differences in species effect traits (e.g. feeding rate). This so-called response-and-effect-trait framework gives us a powerful tool to understand litter-dwelling arthropod distribution and predict the effects on ecosystem functioning (via effect traits) such as nutrient cycling, carbon sequestration etc.

SAMENVATTING

Mensen hebben een grote impact op landschappen in Europa via veranderingen in landgebruik. Bossen, bijvoorbeeld, zijn sterk gefragmenteerd door omzetting naar landbouwgrond. Dit resulteert in landbouwlandschappen met versnipperde kleine bosfragmenten, wat een grote druk zet op de biodiversiteit in deze bosfragmenten en de ecosysteemdiensten die ze vervullen. Binnen de Europese Unie ligt 40% van de bosoppervlakte binnen 100 m van land gebruikt voor andere doeleinden en kan dus beschouwd worden als bosrand. Kleine bosfragmenten zijn onderhevig aan sterke randeffecten doordat ze in verhouding meer bosrand hebben dan boskern. Het milieu van bosranden verschilt sterk van boskernen. Bosranden zijn gekenmerkt door meer licht, hogere windsnelheden, hogere lucht- en bodemtemperaturen en een hoger bodem-pH, maar ook door een lagere lucht- en bodemvochtigheid. Bosranden zijn nutriëntenrijker dankzij een hogere strooiselinput en hebben een betere strooiselkwaliteit. Ze zijn eveneens onderhevig aan hogere stikstofdepositie uit de lucht en via spillover van meststoffen uit de omliggende landbouwprecelen. Het contrasterende milieu tussen bosranden en kernen beïnvloedt de verspreidingspatronen van organismen. Deze verspreidingspatronen zijn redelijk goed bestudeerd voor planten, vogels en bovengrondse geleedpotigen, maar slecht onderzocht voor bodemfauna. Nochtans spelen die een belangrijke rol in het functioneren van bosecosystemen.

Desondanks de grote diversiteit aan bodemfauna, zijn de meeste groepen erg weinig onderzocht. Goede taxonomische kennis is essentieel om soort-specifieke verspreidingspatronen te bestuderen en te begrijpen. In **Hoofdstuk 2** starten we daarom met een bijdrage aan deze taxonomie voor pissebedden (een dominante strooiselbewonende groep) in België. De Belgische pissebeddenfauna dekt een groot deel van de soortenpool in West-Europa. We stellen een nieuwe checklist samen en beoordelen – voor het eerst – de status van alle Belgische pissebeddensoorten. Deze studie is gebaseerd op een review van 142 papers over Belgische pissebedden, controle van museumcollecties en uitgebreid veldonderzoek. We voegen negen soorten toe aan de Belgische checklist; dit is maar liefst 25% van de 36 Belgische soorten.

Goede taxonomische kennis stelt ons in staat soort-specifieke verspreidingspatronen van pissebedden en miljoenpoten (macro-detritivoren) te bestuderen. We doen dit langsheen bosrand-boskern gradiënten in zes bossen in het noorden van België (**Hoofdstuk 3**). Pissebeddenabundantie neemt sterk af van de bosrand naar de boskern, terwijl miljoenpotenabundantie pas afneemt na een paar meter van de bosrand. De verspreidingspatronen van macro-detritivoren in bosranden verschillen sterk per soort en kunnen zowel gelinkt worden aan soort-specifieke droogtetolerantie als aan karakteristieken van het milieu zoals strooiselkwaliteit, bladoppervlakte-index (LAI), bodem-pH en nutriëntenbeschikbaarheid. De abundantiepatronen bestaan onafhankelijk van het onderzochte bos en de dominante boomsoort. De dominante boomsoort heeft wel een sterke invloed op de soortensamenstelling van macro-detritivoren.

We testen de link tussen droogtetolerantie en de verspreiding van pissebedden in bosranden in 160 kleine bosfragmenten in 10 landschappen in West-Europa (**Hoofdstuk 4**). Droogtegevoelige soorten komen minder voor in bosranden en nemen in aantal en activiteit af richting de boskern, terwijl droogteresistente soorten net grote populaties opbouwen in bosranden. We verklaren het verspreidingspatroon van de soorten pissebedden op basis van één functionele eigenschap.

Om het belang te ontrafelen van hogere temperaturen en een lager vochtgehalte in bosranden op het functioneren van macro-detritivoren, voerden we een full-factorial veldexperiment uit in een loofbos in het noorden van België (**Hoofdstuk 5**). We installeerden microkosmossen met vier macro-detritivore behandelingen (pissebedden, miljoenpoten, beide en een controle zonder fauna), onder vier omgevingsbehandelingen: lager vochtgehalte (hierbij werd regen opgevangen via dakjes boven de microkosmossen), verhoogde temperatuur (via open-top chambers), een combinatie van beide en een controle. We voegden strooisel van hoge en lage kwaliteit toe als voedsel voor de macro-detritivoren. Vochtbeschikbaarheid was de voornaamste limiterende factor voor de afbraak van hoogkwalitatief strooisel (niet voor laagkwalitatief strooisel). De soort macro-detritivoor was belangrijk voor de afbraak van laagkwalitatief strooisel (niet voor hoogkwalitatief strooisel). Pissebedden zijn efficiënter in het afbreken van laag kwalitatief strooisel in vergelijking tot miljoenpoten. De omgevingsbehandeling had hier geen invloed op.

Bij de volgende stap bestudeerden we factoren die de verspreiding van macro-detritivoren bepalen op verschillende ruimtelijke schalen. We onderzochten verschillen in de verspreiding van pissebedden en miljoenpoten binnen bosfragmenten (rand vs kern), tussen bosfragmenten en tussen landschappen. Dit onderzochten we voor 224 bosfragmenten in 14 landschappen in West-Europa (**Hoofdstuk 6**). De verspreiding van macro-detritivoren werd naast rand vs kern ook sterk bepaald op landschapsniveau, met meer pissebedden en miljoenpoten in bosfragmenten gesitueerd in intensief gebruikte landschappen. In deze intensief gebruikte landschappen kunnen macro-detritivoren waarschijnlijk profiteren van de hogere atmosferische stikstofdepositie en spillover van meststoffen uit naburige landbouwpercelen.

In het voorlaatste hoofdstuk bestuderen we verspreidingspatronen van zes groepen strooiselbewonende geleedpotigen in 192 bosfragmenten in 12 landschappen in West-Europa (**Hoofdstuk 7**). Naast pissebedden en miljoenpoten vertonen ook spinnen hogere abundantie in bosranden vs boskernen, terwijl abundantie van loopkevers, hooiwagens en duizendpoten niet verschilt tussen bosrand en kern. Oudere bossen veroorzaken sterkere randeffecten op abundantie en soortensamenstelling van strooiselbewonende geleedpotigen ten opzichte van jonge bossen. Zuidgerichte bosranden veroorzaken sterkere randeffecten enkel op de soortensamenstelling van strooiselbewonende geleedpotigen ten opzichte van noordgerichte bosranden. Bosranden grenzend aan grasland vertoonden sterke randeffecten op loopkevers en spinnen, bosranden grenzend aan akkers niet.

Tot slot: bosranden hebben een sterke invloed op strooiselbewonende geleedpotigen in kleine bosfragmenten in West-Europa (1). Droogtetolerantie is een belangrijke soortspecifieke reactie-eigenschap (response trait) die verspreidingspatronen van strooiselbewonende geleedpotigen kan verklaren (2). Bosranden selecteren soorten op basis van deze reactie-eigenschap wat resulteert in een verschillende soortengemeenschap in bosranden ten opzichte van boskernen. Deze verschillen in gemeenschapssamenstelling gaan gepaard met verschillende effect-eigenschappen (effect traits) (bijv. voedingssnelheid). Dit zogenaamde “response-effect-trait framework” kan ons helpen om de verspreiding van bodemfauna te begrijpen en de consequenties voor ecosysteemfuncties, zoals de nutriëntenkringloop en koolstofopslag te interpreteren.

Parikebos | Edwin Brosens

LIST OF ABBREVIATIONS

AD: Activity-density
BE: Belgium
CWM: Community weighted mean
ES: Estonia
FN: Northern France
FS: Southern France
GE: Eastern Germany
GW: Western Germany
LAI: Leaf Area Index
OTC: Open top chamber
RCR: Relative consumption rate
SC: Central Sweden
SS: Southern Sweden

Chemical compounds
Al: Aluminium
C: Carbon
Ca: Calcium
C/N-ratio: Ratio of Carbon divided by Nitrogen
Fe: Iron
N: Nitrogen
P: Phosphorous

Everbeekse bossen | Edwin Brosens

Chapter 1

INTRODUCTION

Forest fragmentation and edge effects

Forests worldwide have been heavily fragmented due to human-induced land-use change (Wade et al. 2003). The change of one land-use type (e.g. forest) into another (e.g. urban areas or agricultural fields) results in isolated forest fragments embedded in an anthropogenic matrix (Decocq et al. 2016) and is one of the major drivers of global biodiversity changes (Foley et al. 2005, Pereira et al. 2010). Europe experienced more human-induced forest fragmentation during the last centuries than other regions in the world (Wade et al. 2003). Yet, although forest cover is declining worldwide, a slow increase in forest cover is occurring in large parts of Europe, because of afforestation projects and the abandonment of low-productive agricultural fields (Hansen et al. 2013). Across Europe, forest fragments thus strongly differ in characteristics such as size and age (Valdés et al. 2015).

Due to the high degree of forest fragmentation in Europe, forest edges have become dominant features in European landscapes. In the European Union, 40% of the forest area lies within 100 m of a forest edge (Estreguil et al. 2013), compared to 20% worldwide (Haddad et al. 2015). Forest biodiversity strongly suffer from forest fragmentation (Pfeifer et al. 2017), which results in a decreasing potential to deliver ecosystem services for which biodiversity is of key importance (such as crop pollination and water purification, Haddad et al. 2015). This raises the question to what extent small forest fragments are capable to sustain biodiversity and fulfil multiple ecosystem services compared to large, continuous forest (Krauss et al. 2010).

Forest edges strongly differ from forest interiors in multiple ways (Murcia 1995, Ries et al. 2004). Along transects from forest edge to interior, we see strong gradients in a multitude of abiotic variables (see Table 1.1). These abiotic variables affect several ecological processes, which results in altered ecosystem services in the forest edge, e.g. for nutrient cycling and carbon sequestration (Remy et al. 2016, Reinmann & Hutyra 2017) or biomass production (Reinmann & Hutyra 2017). The strength of the abiotic gradients within forest edges is influenced by forest edge characteristics (such as forest edge orientation and forest age) and the surrounding land-use. The edge contrast is low when the land-use at either side of the edge is similar and high when the adjacent land-use types strongly differ (Ries et al. 2004). Forest edges bordered by more intensively cultivated arable land can be subject to higher inputs of pesticides or fertilizers compared to more extensive land-use types such as grasslands (Didham et al. 2015).

The abiotic gradients from forest edge to forest interior are primary drivers of biotic gradients in forest edges. Gradients in plant species abundance and composition are studied best: the environmental conditions in forest edges result in increased plant biomass, higher species richness but different community composition compared to forest interiors (Honnay et al. 2002, Harper et al. 2005, Chabrerie et al. 2013, Normann et al. 2016). In response to the increased biomass and species richness of primary producers, higher trophic levels can also increase their biomass and abundance, as has been observed for many aboveground arthropods (Jokimäki et al. 1998). A large part of the plant biomass is not consumed as living tissue and enters the detrital food web (cf. Moe et al. 2005) as forest litter. In this detrital food web, soil organisms play a crucial role; they are the actual decomposers and facilitate nutrient mineralisation (David 2014). Insight in the detrital food web is crucial to understand nutrient cycling in forest edges (Osler & Sommerkorn 2007). Besides, soil organisms influence a multitude of other ecosystem services (Table 1.2). Yet, the difference in abundance and community composition of different chains of the detrital food web from forest edge to forest interior is still a black box.

Table 1.1. *Important abiotic variables in forest edges and the gradient from edge to interior.* ↘ *indicates decreasing levels of the abiotic variable from edge to interior,* ↗ *indicates increasing levels of the abiotic variable from edge to interior.*

Abiotic variable	Gradient	References
Light availability	↘	Honnay et al. 2002, Delgado et al. 2007
Wind speed	↘	Wuyts et al. 2008
Air and soil temperature	↘	Honnay et al. 2002, Heithecker & Halpern 2007, Delgado et al. 2007
Humidity and soil moisture	↗	Chen et al. 1995, Gehlhausen et al. 2000
pH	↘	Honnay et al. 2002, Wuyts et al. 2013
Atmospheric deposition	↘	Weathers et al. 2001, De Schrijver et al. 2007

The soil food web

Food webs visualise the complex relations of consumption and energy flow between communities of animals, plants and microbes. Soil food webs differ from aboveground food webs because the primary consumers are saprophytic organisms instead of herbivores. Soil food webs are commonly called detrital or brown food webs because the major input is detritus or dead organic material and not green leaves. The different components of the soil food web are known for their extremely high biodiversity - with millions of species and billions of individuals per square meter of soil surface - and significantly contributes to the world's biodiversity (Bardgett & van der Putten 2014).

Functions of the soil fauna

Soils are vital for a wide array of functions and associated ecosystem services in forests (see e.g. Lavelle et al. 2006, Jeffery et al. 2010, Wall et al. 2012). The delivery of these ecosystem services is directly or indirectly linked to functions performed by soil organisms. For instance, soil organisms can affect the growth and primary production of vascular plants, thus influencing the ecosystem service 'primary production'. This influence can be direct, through mycorrhiza networks (Mosse 1973) or herbivory on plant roots (Blossey & Hunt-Joshi 2003), or indirect, via the decomposition of soil organic matter, the first step in making nutrients again available to plants (Schue 2003, De Deyn et al. 2003). The most widely recognised function of soil organisms is their effect on the chemical and physical properties of the soil, which is key for supporting ecosystem services such as soil formation. Besides, soil organisms contribute to provisioning ecosystem services (e.g. water supply, wood production), regulating ecosystem services (e.g. water quality, erosion control, natural pest control) and cultural ecosystem services (e.g. flagship species for the soil ecosystem) (Haygarth & Ritz 2009, Table 1.2).

The soil community is frequently divided into groups according to their body size: micro- (less than 0.1 mm), meso- (0.1 - 2 mm) and macro-organisms (2 – 20 mm) (Jeffery et al. 2010, Wall et al. 2012). For the soil macro-fauna, over 50% of the estimated number of species across the world have been described; for the micro-organisms, only about 1% (Wall et al. 2012, Orgiazzi et al. 2016). This illustrates how limited our knowledge is about belowground organisms, despite the important ecosystem functions they provide. Although the macro-fauna are amongst the best-studied soil organisms, our knowledge on their ecology and distribution is still limited (David & Handa 2010, Carpenter et al. 2012). Macro-fauna belong to a wide array of taxonomic groups (Fig. 1.1), i.e. the four arthropod subphyla (Chelicerata, Crustacea, Myriapoda and Hexapoda) and some groups of lower animals such as slugs and snails (Mollusca) and earthworms (Annelida). They comprise multiple trophic levels: decomposers, herbivores, predators and so-called ecosystem engineers. Ecosystem engineers are organisms that alter the resource availability for other organisms directly or indirectly by changing the physical state of a system's (a)biotic conditions (Jones et al. 1994). Well-known examples in temperate biomes are earthworms and ants; they shape the physical state of the soil by burrowing and mixing. The macro-fauna often plays an important role as first initiators of soil processes and functions (cf. Table 1.2). Macro-detritivores, for example, reduce the size of dead organic matter on the forest floor (Anderson 1988, Grelle et al. 2000), thereby increasing the accessible surface area for further decomposition by micro-organisms.

Soil community simplification due to species loss impairs effective delivery of ecosystem services such as litter decomposition and nutrient cycling (Wagg et al. 2012). It remains unclear, however, whether taxonomic or functional diversity loss drives this process (Bardgett & van der Putten 2014). If functional diversity of the soil community is an important driver of belowground ecosystem functioning, we can expect that changes in community composition will drive the effective delivery of ecosystem services. When taxonomic diversity is the main driver, we can expect species loss to decrease the effective delivery of ecosystem services. If we aim to understand how soil organisms mediate ecosystem processes in fragmented forest and their edges in particular, a first step is to investigate their distribution patterns and community composition (Wall et al. 2012) along forest edge-to-interior gradients.

Figure 1.1. (next page) *Dominant macro-fauna taxa from temperate forests: (a) Spiders (*Diplostyla concolor *(Wider, 1834)), (b) Harvestmen (*Phalangium opilio *Linnaeus, 1758), (c) Millipedes (*Proteroiulus fuscus *(Stein, 1857)), (d) Centipedes (*Lithobius dentatus *C.L. Koch, 1844), (e) Carabid beetles (*Badister lacertosus *Sturm, 1815), (f) Ants (*Formica rufa *Linnaeus, 1761), (g) Woodlice (*Armadillidium pictum *Brandt, 1833), (h) Earthworms (*Lumbricus rubellus *Hoffmeister, 1843) and (i) Slugs (*Malacolimax tenellus *O.F. Muller, 1747). Pictures: Anne Krediet (a,b,c,d,e,g,I), Theodoor Heijerman (f), Gert Arijs (h).*

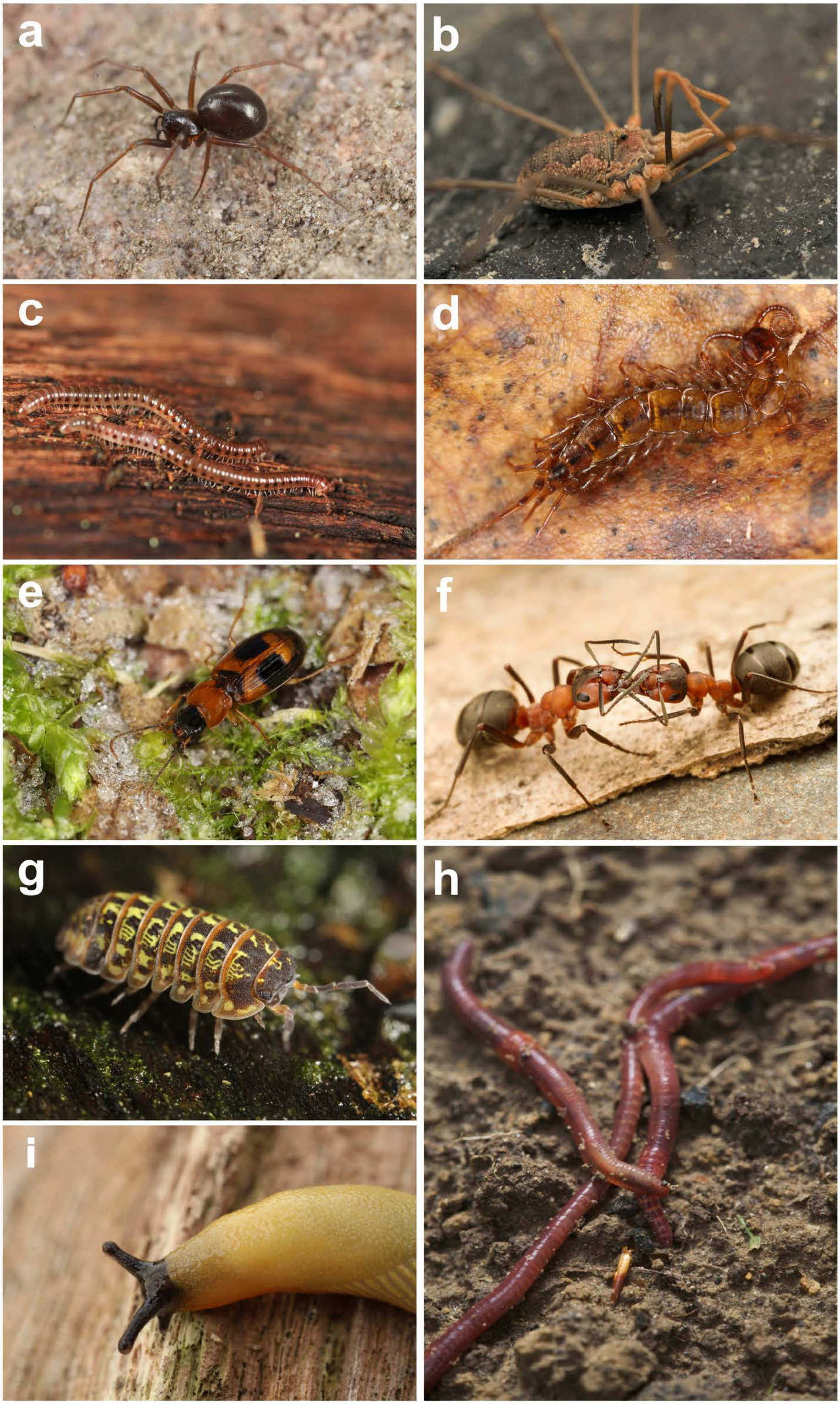

a
b
c
d
e
f
g
h
i

Table 1.2. *Ecosystem services and functions of macro-fauna, with indication of whether they are directly or indirectly responsible for the functioning (extracted from Haygarth & Ritz 2009 and Orgiazzi et al. 2016).*

	Ecosystem service	**Function**	**Direct/Indirect**
Supporting	Primary production	Interaction with vascular plants (e.g. root herbivory)	Direct
		Nutrient availability	Indirect
	Nutrient cycling	Organic matter decomposition and incorporation in the soil	Indirect
		Physical mixing of the soil	Direct
Provisioning	Water storage	Enhancing soil structure (porosity)	Indirect
	Biomaterials	Enhancing plant growth	Indirect
	Refuge	Enhancing soil structure (porosity)	Indirect
	Biodiversity	Gene reservoir	Direct
	Food for higher taxa	Bulk food source	Direct
Regulating	Water supply regulation	Soil structure (porosity)	Indirect
	Atmospheric gas regulation	Carbon dioxide regulation	Indirect
	Pest control	Preying on pest species	Indirect
	Erosion control	Enhancing soil structural stability	Direct
Cultural	Cognitive	Flagship species soil ecosystem	Direct
	Recreation Education Health and wellbeing	Via supporting, provisioning and regulating services	Indirect

Distribution of soil organisms

Global patterns of biodiversity have been suggested to be less clear for belowground biodiversity than for aboveground biodiversity (Wardle 2006, Bardgett & van der Putten 2014). Indeed, the distributional patterns of micro-organisms such as fungi and bacteria are influenced at extremely small scales, and many micro-organism species remain undescribed (Decaëns 2010). Macro-fauna, in contrast, show a biodiversity pattern consistent with many aboveground taxa (Gaston 2000). They seem to be most diverse in the tropics and show a decrease in species richness with increasing latitudes (Orgiazzi et al. 2016). In Europe, for instance, the number of macro-fauna species generally decreases from the Mediterranean towards northern latitudes (Decaëns 2010, Jeffery et al. 2010), probably driven by macro-climatic variables (Gaston 2000). Many macro-fauna are large litter-dwellers. They live in the litter layer instead of belowground, and therefore show comparable macro-ecological distribution patterns as aboveground taxa. At geographic scales smaller than a continent, the distributional patterns can strongly deviate from the macro-ecological pattern. At the landscape scale (distance measured in kilometres), the macro-fauna distribution depends on variation in soil type, land use type and topography. Rutgers et al. (2016) illustrated this for earthworm distribution in Europe. They showed that land use, which differed strongly between European countries, influenced earthworm abundance and species richness. Countries, such as Ireland, with a high cover of grasslands (most favourable earthworm habitat) had higher abundance and species richness of earthworms compared to countries with a higher proportion of forest and cropland compared to grasslands, such as France. At local scale (meters), distributional patterns are shaped by soil physical and chemical properties (such as soil water quality and nutrient availability), litter quality and micro-climatic variables (for different litter-dwelling fauna see e.g. Scheu & Poser 1996, David et al. 1999, Jabin et al. 2004, Dauber et al. 2005, Topp et al. 2006, Entling et al. 2007, Bardgett & van der Putten 2014, Wenk et al. 2016, Schelfhout et al. 2017).

Litter-dwelling arthropods in forest edges

Knowledge on the distribution of litter-dwelling arthropods in forest edges is limited; most research has been about so-called natural pest control agents such as carabid beetles and spiders. The majority of invertebrates are not able to fulfil their life cycle on agricultural fields and need (semi-)permanent vegetation, such as forest edges, for reproduction. From the forest edge, they can recolonise agricultural fields to prey on pest species. Studies have pointed out weak positive, weak negative or neutral responses of species assemblages of natural pest control agents to forest edges (Rainio & Niemelä 2003, Pearce & Vernier 2006). However, most of these studies have been carried out on a limited geographic scale and at coarse spatial resolution (only sampling forest edge, forest interior and agricultural field), not covering the whole gradient in between. In addition, studies on litter-dwelling arthropods other than spiders and carabid beetles are scarce.

Compared to forest interiors, forest edges have environmental characteristics assumed to be favourable for macro-arthropod activity and life history. Forest edges have higher air and soil temperatures, preferred by macro-arthropods (Ziesche & Roth 2008, Gillingham et al. 2012) because it positively influences their activity and metabolic rate and results in a shorter reproduction time (Gillooly et al. 2001). The soil of forest edges has a higher pH, which is preferred by soil macro-arthropods since it correlates with the presence of crucial chemical elements in the soil such as Calcium, Aluminium, Iron and Phosphorous (Van Straalen & Verhoef 1997). Forest edges produce more litter (Wuyts et al. 2011), which provides both food and habitat for macro-arthropods (Koivula et al. 1999, David & Handa 2010), and the higher litter quality in forest edges (i.e. through a lower C/N-ratio; Wuyts et al. 2011) makes it a favoured food for detritivore macro-arthropods (Hassall et al. 2002, Gerlach et al. 2014). However, the lower air and soil humidity in forest edges can counteract advantages of the forest edge environment. Many litter-dwelling arthropods such as woodlice and centipedes strongly depend on soil moisture for their survival (see e.g. Warburg 1964, Hornung 2011). Therefore, gaining insight into the relative contribution of the different (a)biotic drivers to the forest edge environment is of key importance to understand litter-dwelling arthropod distribution along the forest edge-to-interior gradients.

A thorough understanding of the distribution of litter-dwelling arthropods in forest edges can help us recognise the ability of small forest fragments to deliver multiple ecosystem services and functions. For this purpose, a solid research platform is crucial. The smallFOREST-consortium (https://www.u-picardie.fr/smallforest/uk/) provides a platform that spans a large environmental gradient and provides detailed information at forest fragment level for a diverse array of small forest fragments across the temperate forest biome in Western Europe. The ecosystem services of small forest fragments are studied in agricultural areas in eight regions (Fig. 1.2), in more than 700 forest fragments along a 2,000 km geographic range from Southern France to central Sweden (Valdés et al. 2015). Forest fragments were selected based on the forest age and size and the intensity of the land use in the surrounding landscape in order to cover a wide variety of environmental contexts.

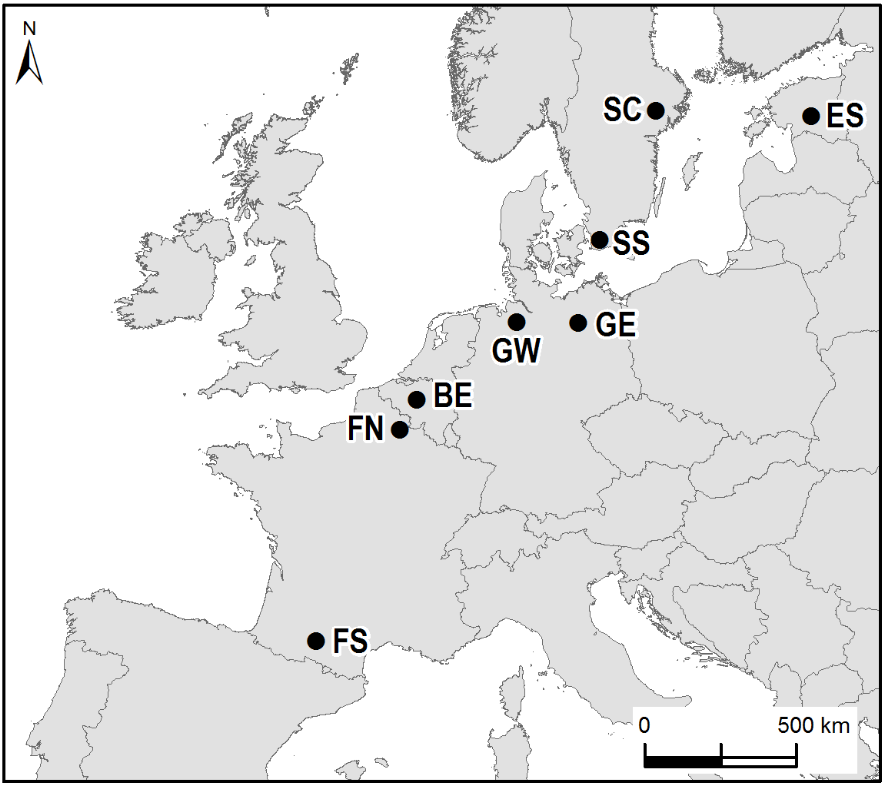


Figure 1.2. *Location of the eight study regions along a latitudinal gradient in Western Europe, covered by the smallFOREST-consortium (FS = Southern France; FN = Northern France; BE = Belgium; GW = Western Germany; GE = Eastern Germany; SS = Southern Sweden; SC = Central Sweden; ES = Estonia).*

Aims and research questions

The main aim of this thesis is to identify litter- dwelling arthropod distribution and its drivers in small forest fragments in Western Europe. To study species abundances and community composition, a thorough knowledge of taxonomy is key (Stribling et al. 2003). Many litter-dwelling arthropod groups have been poorly studied (see e.g. Carpenter et al. 2012), and for several taxa no recent or up-to-date checklists, atlases, catalogues, handbooks, identification keys are available. Identifying the species pool in Western Europe will contribute to the taxonomy of key litter-dwelling arthropods. With the right taxonomy and a correctly identified species pool at hand, we can then study species-specific distribution patterns and community composition from forest edge to forest interior and link the species distributions to the abiotic edge-to-interior gradients in the same forest fragments. To explain the response of particular species and the overall arthropod community to the specific environmental conditions in forest edges, we will look at functional species traits. The consequences of the key abiotic drivers and species traits for ecosystem functioning will be experimentally studied. Consistency of edge-to-interior responses of litter-dwelling arthropods will be tested at Western European scale and across different taxa. This results in five research questions (RQ) to be answered to accomplish the main aim:

RQ1: What is the species pool of key litter-dwelling arthropods in forest fragments across Western Europe?

RQ2: Do litter-dwelling arthropod species respond to abiotic forest edge-to-interior gradients in terms of species abundance and community composition?

RQ3: Can functional traits be used to predict species distributions along forest edge-to-interior gradients?

RQ4: What are the potential consequences of differences in species abundance and community composition of litter-dwelling arthropods for leaf litter decomposition?

RQ5: Are edge-to-interior responses of litter-dwelling arthropods consistent across multiple taxa and across Western Europe?

Thesis outline

The five research questions are tackled in six chapters that form the body of this thesis. Since soil arthropods are numerous and represented by a high number of species, it is hard to study all species. Therefore, we focussed on macro-detritivores (woodlice and millipedes) in five out of the six chapters (Fig. 1.3). We used woodlice and millipedes as model organisms for litter-dwelling arthropods, because of their dominance in temperate forests and their important functional role (David & Handa 2010).

Chapter 2 tackles the first research question. Belgium lies centrally in Western Europe, and has a rich geology despite its small size (Pirson et al. 2008). Many invertebrate taxa (such as butterflies, grasshoppers, dragonflies) have been well-studied in Belgium, but the different components of the soil community, woodlice for instance, have received only minor attention. Although the number of woodlouse species is low in Belgium, recordings have been limited (Wouters et al. 2000). Together with a newly established terrestrial isopod (woodlice) group, "Spinicornis" (www.spinicornis.be), extensive field surveys have been performed across Belgium in search for all Belgian woodlouse species. These surveys have been complemented with re-identification of museum collections and a review of all literature on Belgian woodlice. Hence, Chapter 2 gives a solid base of taxonomy and ecology of most woodlouse species occurring in forests in Western Europe (RQ1).

The extensive knowledge on species taxonomy and ecology gathered in Chapter 2 enabled us to perform the studies in the next two chapters. The differences in the ecology of woodlouse species (Chapter 2) and the strong environmental gradients observed in forest edges in previous PhDs (De Schrijver 2007, Wuyts 2009) lead to Chapter 3, in which we studied species-specific distribution patterns of macro-detritivores across the forest edges of six forest fragments in Northern Belgium, a region characterised by a highly fragmented forest cover. We linked macro-detritivore abundance to abiotic gradients along forest edge-to-interior gradients (RQ2)In Chapter 4, we then tried to explain the species-specific patterns of woodlice distribution based on a key functional trait, i.e. desiccation resistance, in small forest fragments in Western Europe (RQ3).

In Chapter 5, we performed a field experiment to disentangle the effects of abiotic drivers and the traits and abundance of macro-detritivores on leaf litter decomposition, an ecosystem function for which macro- detritivores are of key importance (RQ4). We established microcosms in a deciduous forest fragment in Northern Belgium and manipulated rainfall (as proxy for soil moisture), air and soil temperature, detritivore abundance and detritivore identity (a drought-resistant millipede vs a drought-sensitive woodlouse).

Finally, we tackled RQ5 in Chapter 6 and Chapter 7, where we looked for generalities across different spatial scales and for multiple taxonomic groups. In Chapter 6, we studied macro-detritivore distribution patterns and compositional differences at different spatial scales: within a forest fragment, at forest fragment level and at landscape level. The desiccation resistance of the macro-detritivore community was also tested at within-fragment and landscape scale. In Chapter 7, we investigated the abundance and community composition of six taxa of litter-dwelling macro-arthropods: macro-detritivores and invertebrate macro-predators (carabid beetles, spiders, centipedes and harvestmen). To combine all investigated groups into one chapter, we investigated edge-to-interior gradients at taxa level.

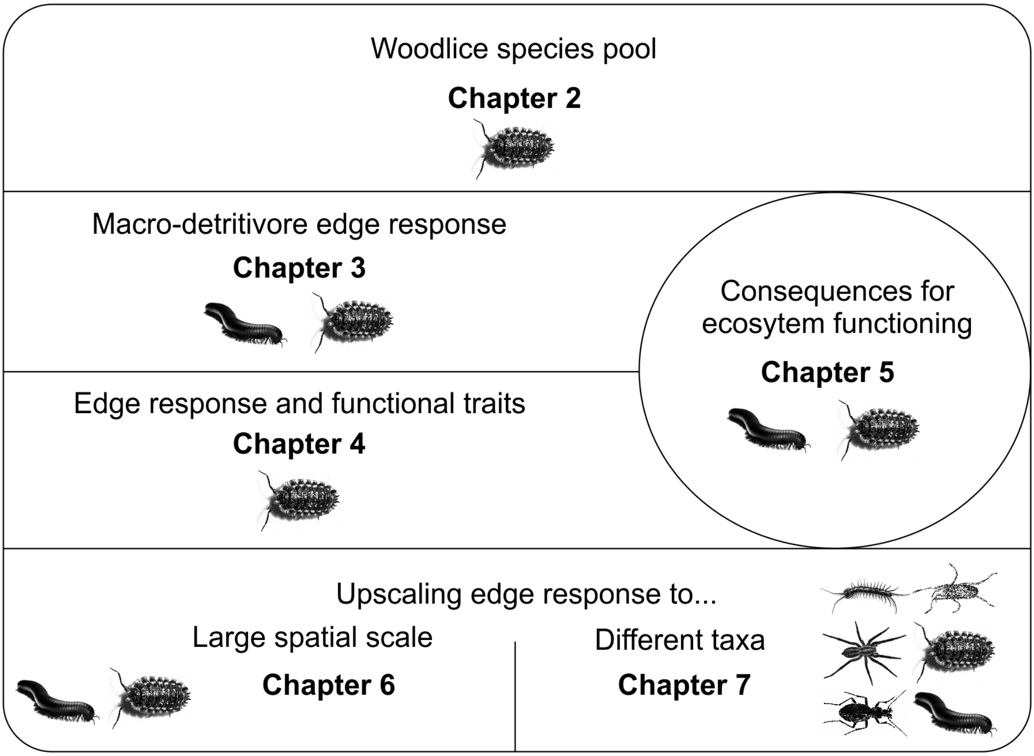


Figure 1.3. *Thesis outline. Chapter 2 starts with an overview of all Belgian woodlice literature and records in a checklist and bibliography of the country. Chapter 3 explores macro-detritivore abundance and community composition responses to forest edges and links this to environmental gradients along the same forest edges. Chapter 4 predicts woodlice distribution patterns along forest edge-to-interior gradients based on a species response trait. Chapter 5 experimentally tests the effect of environmental conditions and macro-detritivore abundance on ecosystem functioning. We looked for generalities of the observed patterns at European level (Chapter 6) and for multiple litter-dwelling arthropods (Chapter 7). Chapters 2 and 4 deal with woodlice (Malacostraca, Isopoda), Chapter 3, 5 and 6 with woodlice and millipedes (Diplopoda) and Chapter 7 with carabid beetles (Insecta, Coleoptera, Carabidae), spiders (Arachnida, Araneae), harvestmen (Arachnida, Opiliones), centipedes (Chilopoda), millipedes and woodlice.*

Philoscia affinis | Gert Arijs

Chapter 2

WOODLICE OF BELGIUM

AN ANNOTATED CHECKLIST AND BIBLIOGRAPHY

(ISOPODA: ONISCIDAE)

Adapted from: De Smedt P., Boerave P, Arijs G, Segers S. Woodlice of Belgium: An annotated checklist and bibliography (Isipoda: Oniscidae). Accepted to Zookeys.

Abstract

Woodlice are key organisms for nutrient cycling in many terrestrial ecosystems, however knowledge on this invertebrate group is limited as for other soil fauna taxa. Here, we present an annotated checklist of the woodlice of Belgium, a small but densely populated country in Western Europe. We reviewed all 142 publications on Belgian woodlice, the oldest dating back to 1831 and re-identified all doubtful specimens from the Royal Belgian Institute of Natural Sciences (RBINS) collection. These data is complemented with observations from extensive field surveys dating from March 2014 until December 2017. We report 36 species of terrestrial woodlice with free-living populations for Belgium. Nine species can be added compared to the latest checklist published in 2000 being *Hyloniscus riparius* (C. Koch, 1838), *Miktoniscus patiencei* Vandel, 1946, *Trichoniscoides sarsi* Patience, 1908, *Haplophthalmus montivagus* Verhoeff, 1941, *Porcellio monticola* Lereboullet, 1853, *Metatrichoniscoides leydigii* (Weber, 1880), *Trichoniscus alemannicus* Verhoeff, 1917, *Eluma caelata* (Miers, 1877) and *Philoscia affinis* Verhoeff, 1908. Two species are deleted from the checklist (*Ligidium germanicum* Verhoeff, 1901 and *Armadillidium depressum* Brandt, 1833) because records are doubtful and no material has been preserved. Additionally the data of the field surveys is used to determine a species status of occurrence in Belgium. For each species, we provide a short overview of their first records is provided and their confirmation as part of the Belgian fauna, their current status as well as a complete bibliography of the species in Belgium.

Introduction

Woodlice (Isopoda: Oniscidea) are amongst the largest representatives of the soil invertebrate community in European terrestrial ecosystems (Jeffery et al. 2010). They fragment dead organic material on the forest floor (Anderson 1988, Grelle et al. 2000) and their activity significantly contributes to nutrient cycling in many terrestrial ecosystems (see e.g. David 2014). However, despite their functional importance, they are still poorly studied (David & Handa 2010). In Belgium, distribution data on many species are very scarce (Wouters et al. 2000) in contrast to extensive work in neighbouring countries like the Netherlands (Berg et al. 2008), Great Britain (Gregory 2009), Germany (Gruner 1965) and France (Vandel 1960, 1962, Sechet & Noël 2015). The latest Belgian checklist only reported 27 species with confirmed free-living populations (Wouters et al. 2000) and by comparing this with neighbouring countries it can be assumed that many species could be added to this list (see. e.g. Lock & Durwael 2000, De Smedt et al. 2015, Boeraeve et al. 2017).

A complete overview of the history of woodlice research in Belgium is provided, by checking all existing literature on Belgian woodlice and re-identifying all doubtful or difficult to recognise species present in the collections from the Royal Belgian Institute of Natural Sciences (RBINS). These data are complemented with extensive field surveys carried out from March 2014 until December 2017 in order to produce a new checklist of Belgian woodlice. Additionally the data of the field surveys is used to determine a status of occurrence in Belgium for all species.

History of woodlouse records in Belgium

The oldest record of woodlice species in Belgium dates back to 1831 (Carlier 1831) (Fig. 2.1) and was published in a geographical monograph including all animal species from the province of Liège. This book mentions six species of which one was a synonym of *Armadillidium vulgare*, which was also mentioned in the list. Carlier (1831) mentions besides the latter species also the three common species being *Oniscus asellus, Philoscia muscorum* and *Porcellio scaber*. The fifth species is *Porcellio laevis*, which is surprising since the species is extremely rare nowadays in Belgium as in the UK (Harding 2016). Apparently, this species was much more common in previous centuries (see Harding 2016).

During the second half of the 19th century, there was a slow increase in the number of publications and recorded species with nine species in 1870 and the first checklist for Belgium (Plateau 1870) (Fig. 2.1). From the mid 1880's until 1910 there was a first peak in woodlouse interest and publications, mostly because of work published by A. Preudhomme de Borre (1886b) and R.S. Bagnall (1907). Preudhomme de Borre (1886b) published a second checklist with 15 species (Fig. 2.1). In 1910, 21 species were recorded (Fig. 2.1).

From the 1910's to the 1970's, most woodlouse research in Belgium focused on caves (see e.g. all publications by Leruth in the 1930's and Kersmaekers in the 1970's). Capart (1942) produced a third checklist but excluded *Ligia oceanica*, since this species was seen as a marine species by some authors (see e.g. the comments by Pelseneer in 1886). At the time of Capart (1942), 24 species were recorded from Belgium (Fig. 2.1). In the mid 1950's and 1960's, Ph. Polk (see e.g. Polk & Van Oye (1956)) undertook extensive field surveys and identifications and published the first distribution maps for eleven native species (Polk 1957). Despite the new observations, the maps were far from complete and only for a limited number of species. He published a fourth checklist (Polk 1959b) in 1959 but did not really add confirmed species to the list since he claimed *Haplophthalmus danicus* and *Metatrichoniscoides leydigii* as new species. Capart (1942) did not mention the first, as he did not cite the publication by Bagnall (1907) when the species was recorded for the first time in Belgium. *M. leydigii* could only be confirmed in 2015 (De Smedt et al. 2016a). Nevertheless, Ph. Polk made an important contribution to the knowledge of Belgian woodlice and compiled the first more extensive bibliography with 33 papers (Polk 1959b). Towards the end of the 20th century a lot of work was summarised under impulse of J.M. Tavernier and K. Wouters who published a fifth checklist, together with a bibliography (Tavernier & Wouters 1989), reporting 27 species that could be validated (Fig. 2.1). They produced a sixth (Tavernier & Wouters 1991) and seventh (Wouters et al. 2000) checklist but they did not add confirmed species. Wouters et al. (2000) produced an extensive bibliography of 81 papers. After Polk (1957), they were also the second authors to publish distribution maps and this for the 27 native species. However, the distribution data were mostly collected from literature, especially from the extensive but geographically limited field survey by Boon et al. (1993), and from the RBINS collection. Therefore, only few new observations were added, resulting in insufficient data to assess the status of occurrence of all woodlice species in Belgium.

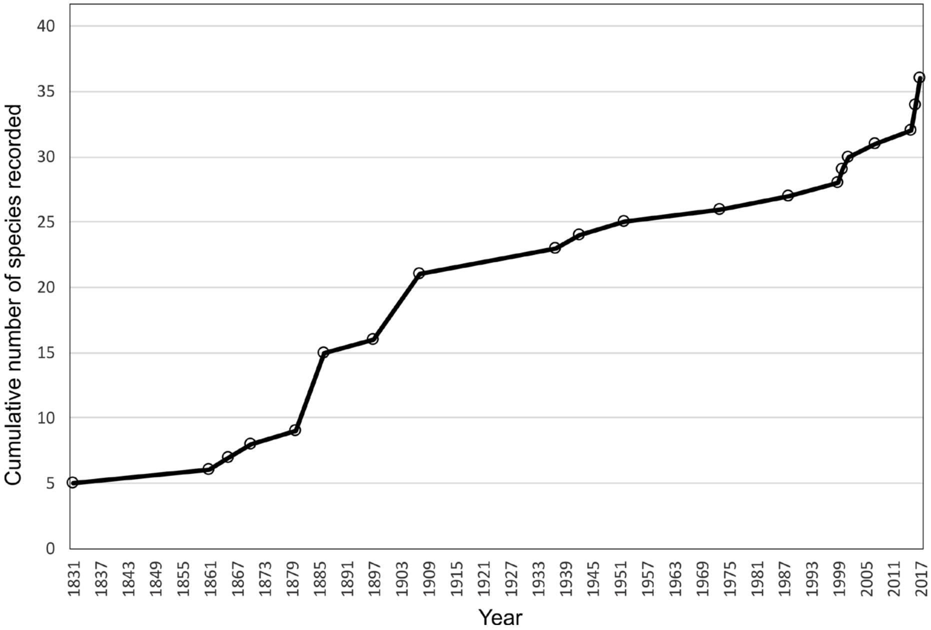


Figure 2.1. *Cumulative number of species published as part of the native fauna of Belgium between 1831 (five species) and 2017 (36 species). Exotic species exclusively living in greenhouses were omitted.*

At the start of the 21st century, there was a renewed interest in woodlouse research with the discovery of four new species for Belgium by K. Lock (Fig. 2.1). In 2014, a national terrestrial isopod group "Spinicornis" was founded by the authors of this paper. They aimed to survey the entire territory of Belgium at 10x10 km square resolution by 2020. This led to the discovery of four new species for the fauna of Belgium and finally the confirmation of *M. leydigii* (De Smedt et al. 2016a). This brings the current number of woodlouse species for Belgium at 36 (Fig. 2.1). Additionally the field surveys undertaken by Spinicornis since 2014 resulted in many new records for almost all Belgian woodlice species. This enables to assess the status and countrywide distribution of all Belgian species for the first time.

Methods

Study area

Belgium is a rather small country (ca. 30,500 km^2) in Western Europe, but despite its small size, the country shows a rich geology (Pirson et al. 2008). There is a small shoreline (approx. 65 km) and its territory penetrates up to 290 km inland. Along this gradient, the country evolves from a largely flat Atlantic region in the north with Holocene and Pleistocene deposits, towards a more continental hilly landscape (up to 694 m elevation) in the east and south with much older (Mesozoic and Palaeozoic) deposits. This varied gradient across such a small country gives the opportunity for many species to establish. This is also the case for woodlice, finding coastal species (Kersmaekers 1988, Lock & Durwael 2000) up to alpine ones (De Smedt et al. 2016b) within this small country.

Checklist

Literature

All existing literature published or accepted about Belgian woodlice was reviewed if containing distribution data, descriptions and ecology up to the end of 2017. Our search was based on old bibliographies from Belgium (Polk 1959b, Wouters et al. 2000), all volumes from journals produced by the Royal Belgian Entomological Society (SRBE/KBVE) and through Web of Science and Google Scholar using the keywords ["Belgium" AND "Woodlice"/"Isopod(a)"]. The same searches were carried out for Dutch and French translations respectively ["België" AND "Pissebed(den)"/"Isopod(a)"] and ["Belgique" AND "Cloporte(s)"/"Isopod(a)"]. Subsequently, all articles were scanned on the citing of Belgian woodlice species. Relevant MSc-theses were also included. The retrieved papers are the base for the checklist used to confirm species records by checking original descriptions. All used manuscripts are listed in the bibliography at the end of this paper. Our search resulted in 142 publications (Appendix 2.1) of any scientific significance published on Belgian woodlice from 1831 until 2017 (Fig. 2.2). There has been a steady increase in number of publications since 1830, with only a small dip around World War I. While the first literature records of Belgian woodlice were done in 1831, it increased to 14 publications by the beginning of the 20th century and to 101 at the beginning of the 21st century. Currently, there are 142 publications dealing with Belgian woodlice (Fig. 2.2).

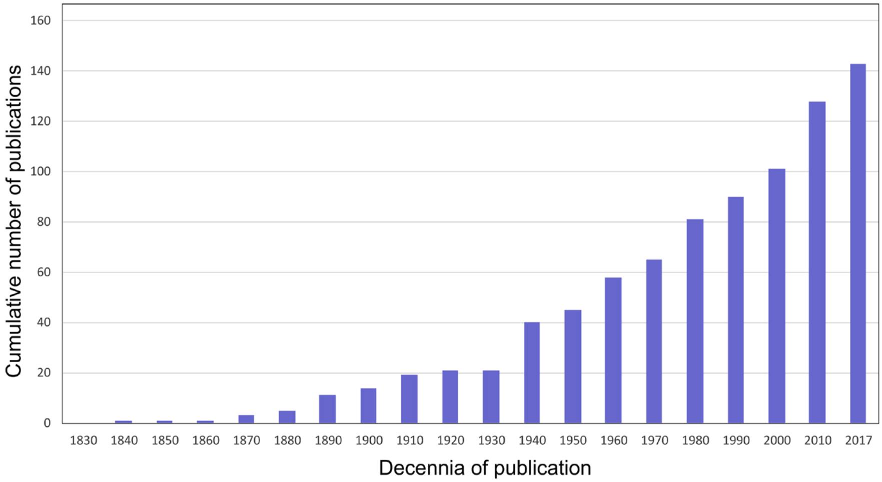


Figure 2.2. *Cumulative number of publications on Belgian woodlice from 1831 until 2017.*

Museum collections

All individuals of 18 species present in the collections of the RBINS were re-identified. *Armadillidium nasatum, A. opacum, A. pictum, A. pulchellum, Cylisticus convexus, Haplophthalmus danicus, H. mengii, Philoscia muscorum, Porcellium conspersum, Trachelipus rathkii, Trichoniscus pusillus, T. pygmaeus and Trichoniscoides helveticus* were checked because these species can easily be misidentified or because closely resembling species were only discovered many years later. *Androniscus dentiger, Porcellio dilatatus, P. laevis, Porcellionides pruinosus and Trichoniscoides albidus* were checked because only very limited knowledge is available for these species on both the historical and current distribution and ecology. Records labelled with *Armadillidium album* and *Trichoniscus provisorius* were not present in the collections. Records of *Ligia oceanica, Ligidium hypnorum, Oniscus asellus, Plathyarthrus hoffmannseggii, Armadillidium vulgare, Porcellio scaber,* and *P. spinicornis* are widespread and easy to recognise therefore they are expected to be correct. This re-identification enabled us to check the presence of all species and to verify literature references.

Field survey and status

Field surveys were carried out over a four-year period from March 2014 until December 2017 by the authors together with other volunteers from "Spinicornis". During these surveys, firstly searches for all known Belgian species on locations of old records and for species that could be expected to ccur in Belgium based on their preferred habitat in neighbouring countries.

Secondly, systematic searches of squares of the UTM 10x10 km grid were carried out in order to map species distribution patterns across Belgium. Main woodlice biotopes were visited in every square. The biotopes visited were (1) an (ancient) forest, (2) a wetland/rivers edge or swamp forest and (3) synantropic habitat (e.g. public park, garden, graveyard…) if present in the 10 km square. These three biotopes cover the habitat niches of most woodlouse species. Additionally, 10 km squares containing a shoreline were surveyed for coastal habitats (e.g. dunes) as well. In some regions, old farms or old quarries have also been visited when present. Woodlice were hand collected by turning stones/dead wood and by sieving the litter layer.

By the end of 2017, the field survey campaign has not been completed but enough data has already been collected to assess the current status of occurrence for all species. In order to give a first indication of the distribution pattern this status is not only determined for the complete territory but also for three different topographical regions. The three regions are roughly based on the Belgian topography with lowlands in the north, hilly landscape in the center and uplands (up to 694m) in the south (Fig. 2.3, next page).

Data of the field surveys were used to assess the status of all species but only observations made in sufficiently surveyed squares were withhold. The criterion for a square to be sufficiently surveyed was at least five species recorded in the square. In some parts of Belgium this is about the maximum number of species that can be found so a higher lower-limit would exclude well searched squares in those parts of Belgium. Records from heated greenhouses and of specimens only identified to genus-level were removed from the dataset. The resulting dataset contains 5110 records from March 2014 until December 2017.
For every region, at least 59.6% of the squares have been sufficiently surveyed, with a total of 254 visited

squares out of 381 (66.7%) (Table 2.1, below). The field surveys took place across the seasons in every region (Table 2.2, next page).

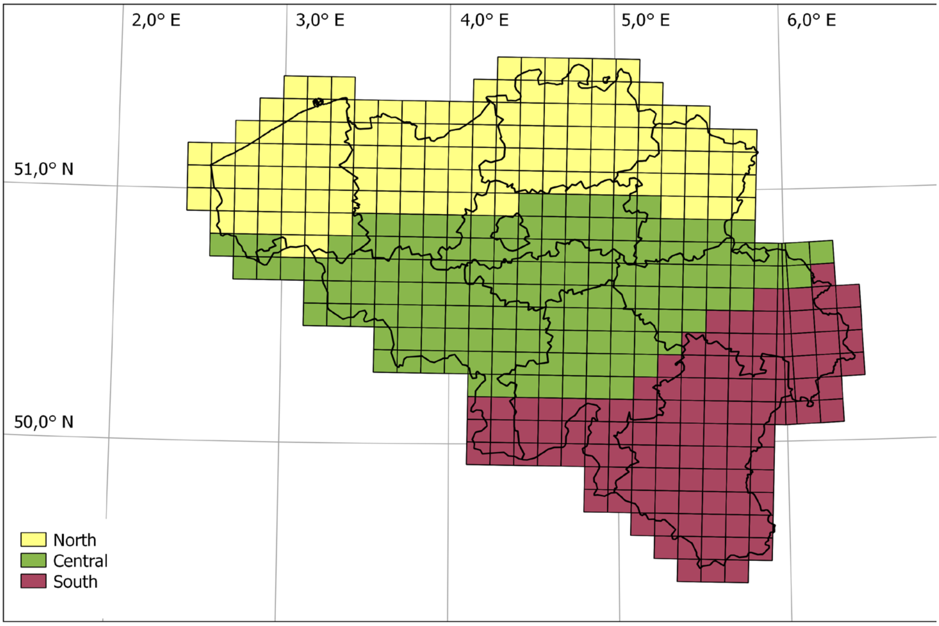


Figure 2.3. *Map of Belgium with the UTM 10x10 km grid. The different colours indicate the different topographical regions used to determine the species status.*

Table 2.1. *Number of squares of the UTM 10x10 km grid per region and number and percentage of squares surveyed between March 2014 and December 2017.*

Region	***squares in region***	***squares surveyed***	
		#	%
North	127	89	70.1
Centre	140	97	69.3
South	114	68	59.6
Total	381	254	66.7

Table 2.2. *Number of records per region and per three-month period, corresponding with the seasons of the year.*

	North	*Centre*	*South*	*Total*
December – February (Winter)	525	617	174	1316
March – May (Spring)	472	395	164	1031
June – August (Summer)	237	469	428	1034
September – November (Autumn)	727	624	378	1729
Total	**1961**	**2005**	**1144**	**5110**

The status was assessed based on the number of squares of the UTM 10x10 km grid in which the species was recorded compared to the number of squares that have been surveyed. Six different categories are distinguished from "not present" (0% of the squares) to "very common" (more than 31.5% of the squares) (Table 2.3).

Table 2.3. *Status categories for the Belgian woodlice, together with the lower and upper limits for the percentage of squares where a species was recorded between March 2014 and December 2017 in a certain region.*

Status	*No. of squares*	*Rel. no. of squares*
Not present (NP)	0	0%
Very rare (VR)	1 - 5	< 1.3%
Rare (R)	6 – 15	1.3% - 3.9%
Rather common (RC)	16 - 40	3.9% - 10.5%
Common (C)	41 – 120	10.5% - 31.5%
Very common (VC)	> 120	> 31.5%

Results

Checklist

Since 1831, seven checklists have been published about Belgian woodlice (Plateau 1870, Preudhomme de Borre 1886b, Capart 1942, Polk 1959b, Tavernier & Wouters 1989, 1991, Wouters et al. 2000). The last checklist includes 27 confirmed native species. Here we add nine species to this new checklist being *Hyloniscus riparius* (C. Koch, 1838), *Miktoniscus patiencei* Vandel, 1946, *Trichoniscoides sarsi* Patience, 1908, *Haplophthalmus montivagus* Verhoeff, 1941, *Porcellio monticola* Lereboullet, 1853, *Metatrichoniscoides leydigii* (Weber, 1880*), Trichoniscus alemannicus* Verhoeff, 1917, *Eluma caelata* (Miers, 1877) and *Philoscia affinis* Verhoeff,

1908. The new checklist below reports 36 species from 19 genera and nine families. Exotic species that were exclusively found in greenhouses are mentioned with an asterisk (*) but are not counted as Belgian species. New species are underlined.

Family Ligiidae

1. *Ligia oceanica* (Linnaeus, 1767)
2. *Ligidium hypnorum* (Cuvier, 1792)

Family Trichoniscidae

3. *Androniscus dentiger* Verhoeff, 1908
4. *Haplophthalmus danicus* Budde-Lund, 1880
5. *Haplophthalmus mengii* (Zaddach, 1844)
6. *Haplophthalmus montivagus* Verhoeff, 1941
7. *Hyloniscus riparius* (C. Koch, 1838)
8. *Metatrichoniscoides leydigii* (Weber, 1880)
9. *Miktoniscus patiencei* Vandel, 1946
10. *Trichoniscoides albidus* (Budde-Lund, 1880)
11. *Trichoniscoides helveticus* (Carl, 1908)
12. *Trichoniscoides sarsi* Patience, 1908
13. *Trichoniscus alemannicus* Verhoeff, 1917
14. *Trichoniscus provisorius* Racovitza, 1908
15. *Trichoniscus pusillus* Brandt, 1833
16. *Trichoniscus pygmaeus* Sars, 1898

Family Styloniscidae

**Cordioniscus stebbingi* (Patience, 1907)

Family Oniscidae

17. *Oniscus asellus* Linnaeus, 1758

Family Philosciidae

18. *Philoscia affinis* Verhoeff, 1908
19. *Philoscia muscorum* (Scopoli, 1763)

Family Platyarthridae

20. *Platyarthrus hoffmannseggii* Brandt, 1833

**Trichorhina tomentosa* (Budde-Lund, 1893)

Family Armadillidiidae

21. *Armadillidium album* Dollfus, 1877
22. *Armadillidium nasatum* Budde-Lund, 1885
23. *Armadillidium opacum* (C. Koch, 1841)

24. *Armadillidium pictum* Brandt, 1833
25. *Armadillidium pulchellum* (Zencker, 1798)
26. *Armadillidium vulgare* (Latreille, 1804)
27. *Eluma caelata* (Miers, 1877)

Family Armadillidae

**Reductoniscus costulatus* Kesselyák, 1930

Family Cylisticidae

28. *Cylisticus convexus* (De Geer, 1778)

Family Porcellionidae

29. *Porcellio dilatatus* Brandt, 1833
30. *Porcellio laevis* Latreille, 1804
31. *Porcellio monticola* Lereboullet, 1853
32. *Porcellio scaber* Latreille, 1804
33. *Porcellio spinicornis* Say, 1818
34. *Porcellionides pruinosus* (Brandt, 1833)

Family Trachelipodidae

**Nagurus cristatus* (Dollfus, 1889)

35. *Porcellium conspersum* (C. Koch, 1841)
36. *Trachelipus rathkii* (Brandt, 1833)

Field survey and status

During the field surveys, 5110 records of woodlice in Belgium are collected between March 2014 and December 2017. For 35 of the 36 Belgian species there is at least one record in the database (Table 2.4). Only the species *Miktoniscus patiencei* was not found during the field surveys. The number of species per square of the UTM 10x10 km grid ranged between five and 19 (Fig. 2.4). At national level, one species was not recorded, six species are very rare, two are rare, three are rather common, fourteen are common and nine are very common (Table 2.4). Based on percentage occurrence in the number of visited UTM-squares (Table 2.3) the status of each species per region is given in the discussion.

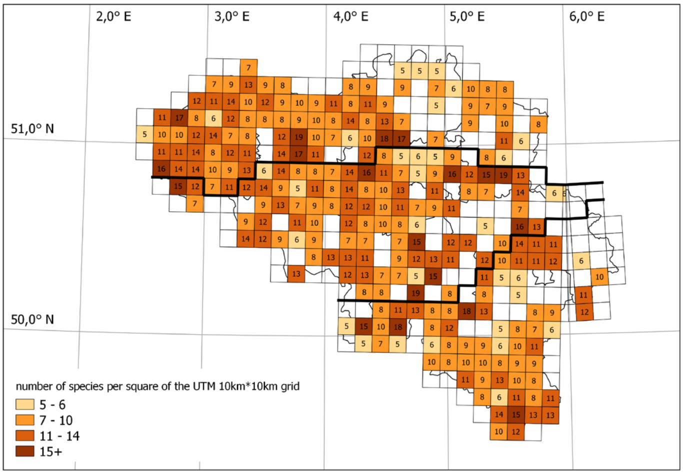


Figure 2.4. *Map of Belgium with the number of species per square of the UTM 10x10 km grid.*

Table 2.4. *Number of visited squares where a certain species is recorded and their relative occurrence per region and countrywide. Their countrywide status is given between brackets: NP = Not present, VR = Very rare, R = Rare, RC = Rather common, C = Common, VC = Very Common.*

	North		Centre		South		Belgium	
Species	#	%	#	%	#	%	#	%
Androniscus dentiger (C)	9	10.1	44	45.4	18	26.5	71	28.0
Armadillidium album (VR)	1	1.1	0	0.0	0	0.0	1	0.4
Armadillidium nasatum (VC)	27	30.3	46	47.4	31	45.6	104	40.9
Armadillidium opacum (C)	0	0.0	7	7.2	22	32.4	29	11.4
Armadillidium pictum (C)	0	0.0	11	11.3	20	29.4	31	12.2
Armadillidium pulchellum (C)	2	2.2	13	13.4	12	17.6	27	10.6
Armadillidium vulgare (VC)	62	69.7	53	54.6	16	23.5	131	51.6
Cylisticus convexus (R)	2	2.2	0	0.0	4	5.9	6	2.4
Eluma caelata (VR)	3	3.4	0	0.0	0	0.0	3	1.2
Haplophthalmus danicus (VC)	44	49.4	29	29.9	7	10.3	80	31.5
Haplophthalmus mengii (C)	30	33.7	15	15.5	4	5.9	49	19.3
Haplophthalmus montivagus (C)	1	1.1	34	35.1	37	54.4	72	28.3
Hyloniscus riparius (C)	11	12.4	26	26.8	10	14.7	47	18.5

Ligia oceanica (VR)	2	2.2	0	0.0	0	0.0	2	0.8
Ligidium hypnorum (VC)	37	41.6	63	64.9	63	92.6	163	64.2
Metatrichoniscoides leydigii (RC)	9	10.1	2	2.1	0	0.0	11	4.3
Miktoniscus patiencei (NP)	0	0.0	0	0.0	0	0.0	0	0.0
Oniscus asellus (VC)	89	100.0	92	94.8	68	100.0	249	98.0
Philoscia affinis (C)	3	3.4	34	35.1	10	14.7	47	18.5
Philoscia muscorum (VC)	87	97.8	90	92.8	62	91.2	239	94.1
Platyarthrus hoffmannseggii (VC)	38	42.7	26	26.8	18	26.5	82	32.3
Porcelio dilatatus (R)	2	2.2	4	4.1	0	0.0	6	2.4
Porcelio laevis (VR)	0	0.0	1	1.0	0	0.0	1	0.4
Porcelio monticola (VR)	0	0.0	0	0.0	3	4.4	3	1.2
Porcelio spinicornis (VC)	88	98.9	93	95.9	65	95.6	246	96.9
Porcellio scaber (VC)	65	73.0	77	79.4	62	91.2	204	80.3
Porcellionides pruinosus (RC)	13	14.6	7	7.2	2	2.9	22	8.7
Porcellium conspersum (C)	0	0.0	4	4.1	29	42.6	33	13.0
Trachelipus rathkii (C)	37	41.6	29	29.9	8	11.8	74	29.1
Trichoniscoides albidus (C)	40	44.9	20	20.6	0	0.0	60	23.6
Trichoniscoides helveticus (RC)	0	0.0	10	10.3	7	10.3	17	6.7
Trichoniscoides sarsi (C)	32	36.0	15	15.5	0	0.0	47	18.5
Trichoniscus alemannicus (VR)	0	0.0	1	1.0	2	2.9	3	1.2
Trichoniscus provisorius (VC)	55	61.8	36	37.1	7	10.3	98	38.6
Trichoniscus pusillus (VC)	69	77.5	64	66.0	55	80.9	188	74.0
Trichoniscus pygmaeus (C)	23	25.8	39	40.2	14	20.6	76	29.9

Discussion

Although many papers have been published on woodlice, many records remained doubtful and the reference collection at the RBINS contained a considerable number of identification errors. Additionally, the number of species recorded in Belgium was relatively low compared to neighbouring countries. This new checklist adds nine species to the last checklist published only 17 years ago (Wouters et al 2000). In this section, the first record of all species with free-living populations in Belgium are discussed, their current status and a complete bibliography per species. The bibliography reports all papers mentioning the particular species. Papers in bold represent the first confirmed Belgian records. Underlined papers include information about the species ecology or distribution.

Certain exotic species are in Belgium only recorded from greenhouses and do not have free-living populations. These species are discussed in a recent paper dedicated to greenhouse species in Belgium (De Smedt et al. 2017a) and only briefly in a separate section of this discussion as they are not considered as part of the Belgian fauna.

Order Isopoda

Suborder Oniscidea

Section Diplocheta

Family Ligiidae

Genus LIGIA Fabricius, 1798

1. *Ligia oceanica* (Linnaeus, 1767)

Van Beneden (1861) first mentioned this species in 1861 as being abundant between stones were they reach the seawater. Since this is a strictly littoral species, certain authors (e.g. Plateau (1870) and Capart (1942) did not consider it as part of the terrestrial isopod fauna (see e.g. Pelseneer (1886) for a discussion about this). Nevertheless, it is nowadays fully considered as a terrestrial isopod because it can inhabit higher littoral zones and within this genus, there are a few species that are not bound to coastal conditions (Schmalfuss 2003).

Status: Coastal species, rare in the north of the country.

Bibliography: **Van Beneden (1861)**, Bellynck (1865), Pelseneer (1886), Preudhomme de Borre (1886b), Lameere (1895), Maitland (1897), Gilson (1900), Bagnall (1907), Lameere (1909, 1913, 1931, 1938), Leloup & Miller (1940), Gils (1947), Holthuis (1950), Kesteloot (1956), Lefevere et al. (1956), Leloup & Konietzko (1956), Polk & Van Oye (1956), Leloup (1957), Polk (1959a,b), Leloup et al. (1963), Polk (1963), Lefevere (1965), Polk (1965), Leloup & Polk (1967), Daro (1969), Jocqué & Van Damme (1971), Polk (1976), Van Gompel & Rabaut (1976), Rappé (1977), Eneman (1984), Tavernier & Wouters (1986), Rappé (1989a,b), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Mares (1994), Lock & Durwael (2000), Wouters et al. (2000), Engledow et al. (2001), Jonckheere & Van Rillaer (2001), Huwae & Rappé (2003), Maelfait et al. (2004), Vandepitte et al. (2010), Segers (2015), De Smedt et al. (2017b)

Genus LIGIDIUM Brandt, 1833

2. *Ligidium hypnorum* (Cuvier, 1792)

Plateau (1870, 1873) was the first to mention the species from Belgium in the 1870's as *Ligidium persoonii* (Brandt) (Plateau 1870) and *Ligidium agile* (Plateau 1873). Since this publication, the species has been mentioned in many papers.

Status: Very common across the country.

Bibliography: **Plateau (1870**, 1873), Pelseneer (1886), Preudhomme de Borre (1886b), Lameere (1895), Maitland (1897), Bagnall (1907), Leruth (1937f), Lameere (1938), Leruth (1939), Capart (1942), Polk & Van Oye (1956), Polk (1957), Leloup & Van Meel (1958), Polk (1959a,b), Delhez & Kersmaekers (1973), Kersmaekers & Deroeck (1973), Kersmaekers (1973d), Gysels et al. (1976), Tavernier (1981), Tavernier & Kerwyn (1982), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Branquart et al. (1995), Delhez et al. (1999), Devaere (1999), De Bakker et al. (2000), Schollen (2000), Wouters et al. (2000), Baeté et al. (2003a), Vandekerckhove et al. (2003), Baeté et al. (2004), Dekoninck et al. (2005), Baeté et al. (2006a,b), Van De Vyver (2009), Dethier & Hubart (2010), Segers (2015), De Smedt et al. (2016b,c), Nijs et al. (2016), Boeraeve et al. (2017), De Smedt et al. 2018a,b)

Section Synocheta

Superfamily Trichoniscoidea

Family Trichoniscidae

Genus ANDRONISCUS Verhoeff, 1908

3. *Androniscus dentiger* Verhoeff, 1908

Expected to occur in Belgium by Preudhomme de Borre (1886b), but mentioned as *Trichoniscus roseus*. First recorded by Lameere (1897) near Thon-Samson (Namur). Vandel (1933) is the first author to mention the name *A. dentiger*. In the following years, both names are used by different authors. Capart (1942) is the first one to mention both species on het checklist, but indicates that the record of *Trichoniscus roseus* by Lameere (1897) is doubtful and could be *A. dentiger.* Finally, Polk (1957) indicates that the species identified as *T. roseus* is probably *A. dentiger*, and removes *T. roseus* from his checklist. *A. dentiger* specimens from the RBINS were re-identified and all specimens belonged to *A. dentiger* of which the oldest ones dated back to 1916 from Jemelle (Namur) and Schaerbeek (Brussels).

Status: Very common in the centre of the country, common in the south and rather common in the north.

Bibliography: Moniez (1886), Preudhomme de Borre (1886b), **Lameere (1897)**, Maitland (1897), Bagnall (1907, 1908), Vandel (1933), Leruth (1936a,b,c,d,e, 1937b,d,f), Lameere (1938), Leruth (1939), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Delhez & Houssa (1969), Delhez et al. (1973), Delhez & Kersmaekers (1973), Gilson & Hubart (1973), Kersmaekers & Deroeck (1973), Holthuis (1983), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Delhez et al. (1999), Wouters et al. (2000), Dethier & Hubart (2010), Segers (2015), De Smedt et al. (2017a)

Genus HAPLOPHTHALMUS Schöbl, 1860

4. *Haplophthalmus danicus* Budde-Lund, 1880

First mentioned from greenhouses by Bagnall (1907, 1908), but the species is not incorporated in the checklists from Lameere (1938) and Capart (1942). In 1956, Polk & Van Oye (1956) discovers the species in Ghent and claims the first record, despite citing Bagnall (1907, 1908). The species was discovered in a medieval basement in Brussels (Kersmaekers 1974), but it took until the 21st century for the first confirmed records from wild populations. *H. mengii* samples from the collections of RBINS were re-identified and the oldest samples of *H. danicus* dated back from 2002 (Ramioul, Liège) and 2004 (Cheratte, Liège). However, numerous observations after 2010 proved that the species is much more common than previously thought.

Status: Very common in het north and common to rather common in the rest of the country.

Bibliography: **Bagnall (1907,** 1908), Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers (1974), Tavernier & Wouters (1989,1991), Boon et al. (1993), Wouters et al. (2000), Lock (2007), Segers (2015), De Smedt et al. (2016c, 2017a)

5. *Haplophthalmus mengii* (Zaddach, 1844)

First mentioned by Maitland (1897) but unclear if the species was already recorded from Belgium or only from the Netherlands, therefore, the species is mentioned as new for the Belgian fauna by Bagnall (1907). He collected one specimen in a greenhouse in Antwerp. After investigating all museum specimens of *H. mengii*, a specimen collected in 1899 in Han-sur-Lesse (Namur) was discovered. The record consists of one male and one female specimen and is the first record of the species in Belgium. Specimens belonging to *Haplopthalmus mengii/montivagus* were also present in the collections from 1897 and 1898 but it was impossible to identify the species.

Status: Very common in het north and common to rather common in the rest of the country.

Bibliography: Maitland (1897), **Bagnall (1907),** Leruth (1937a,b,c,e,f, 1939), Capart (1942), Leleup (1948), Polk & Van Oye (1956), Leclercq (1957), Polk (1957, 1959a,b), Delhez et al. (1973), Delhez & Kersmaekers (1973), Kersmaekers & Deroeck (1973), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Branquart et al. (1995), Delhez et al. (1999), Wouters et al. (2000), Lock (2007), Dethier & Hubart (2010), Segers (2015), Nijs et al. (2016), De Smedt et al. 2017a

6. *Haplophthalmus montivagus* Verhoeff, 1941

First reported record of the species was done by Lock (2007) in 2006. This species closely resembles *H. mengii* and has probably been overlooked for a long time. After checking specimens of *H. mengii* from the collection of the RBINS, *H. montivagus* appeared to be collected in 1998 (Comblain-au-Pont, Liège) and 2002 (Stoumont, Liège).

Status: Very common in the centre and south of the country, very rare in the north.

Bibliography: **Lock (2007)**, Segers (2015), De Smedt et al. (2016b)

Genus HYLONISCUS Verhoeff, 1908

7. *Hyloniscus riparius* (C. Koch, 1838)

Discovered in Belgium through pitfall trap research in 1998 (Lock & Vanacker 1999). Recent observations indicated that the species is not rare in the country (Fig. 2.5c). All specimens of *Trichoniscus pusillus* s.l. from the RBINS were re-identified, because *H. riparius* could be easily confused with this species. However, no historical records from *H. riparius* could be discovered.

Status: Common across the country.

Bibliography: **Lock & Vanacker (1999)**, Lock & Durwael (2000), Lock (2001), Huwae & Rappé (2003), Lock (2007), Segers (2015)

Genus METATRICHONISCOIDES Vandel, 1942

8. *Metatrichoniscoides leydigii* (Weber, 1880)

Reported by Maitland (1897), but probably this is based on a record from the Netherlands. Polk & Van Oye (1956) found the first individuals of this genus, but the individuals were all females. Identification is only possible by checking male pleopods. Nevertheless, the species was mentioned on all subsequent checklists. A second observation was done in 2009, but it took until 2015 before the first males were observed and the species could be confirmed for the Belgian fauna (De Smedt et al. 2016a) (Fig. 2.5f).

Status: Rather common in the north of the country, very rare in the centre and absent from the south.

Bibliography: Maitland (1897), Polk & Van Oye (1956), Polk (1957, 1959a,b), Tavernier & Wouters (1989,1991), Boon et al. (1993), Wouters et al. (2000), Segers (2015), **De Smedt et al. (2016a)**

Genus MIKTONISCUS Kesselyák, 1930

9. *Miktoniscus patiencei* Vandel, 1946

Only two sightings of this species are known in Belgium. After its discovery in 1999 (Lock & Durwael 2000) a second record was done by Lock (2001). In 2015-2016 searches at the same locations where the first two sightings were done but could not rediscover the species. The area where the species was found strongly changed through restoration works. It is unclear if the species could be found on other locations in Belgium since the lack of suitable habitat (for details on habitat see Lock & Durwael 2000, Berg et al. 2008).

Status: Coastal species, not recorded during the recent field surveys.

Bibliography: **Lock & Durwael (2000)**, Lock (2001, 2007), Huwae & Rappé (2003), Segers (2015), De Smedt et al. (2017b)

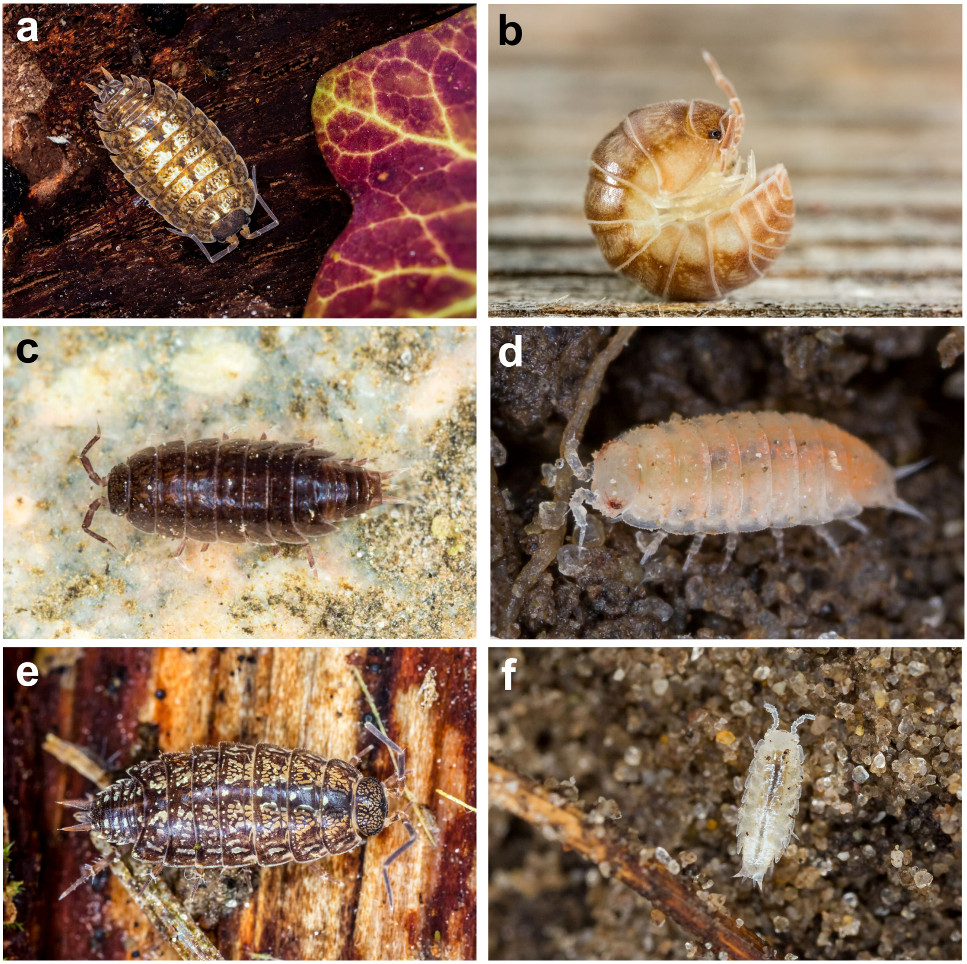


Figure 2.5. *Six of the nine species added to this new checklist, **a) Porcellio monticola**, **b) Eluma caelata**, c) **Hyloniscus riparius**, **d) Trichoniscoides sarsi**, **e) Philoscia affinis** and **f) Metatrichoniscoides leydigii**. Photos: Gert Arijs.*

Genus TRICHONISCOIDES Sars, 1898

10. *Trichoniscoides albidus* (Budde-Lund, 1880)

Expected to occur in Belgium by Preudhomme de Borre (1886b) and first recorded from Durbuy (Luxembourg) in 1933 by Leruth (1937f). In the collection of the RBINS a male from Rochefort (Namur) in 1929 was discovered, this is probably the first collected individual of this species in Belgium. Records of this species remained extremely scarce until the 21st century.

Status: Very common in the north of the country, common in the centre but absent from the south.

Bibliography: Preudhomme de Borre (1886b), **Leruth (1937f**, 1939), Capart (1942), Vandel (1952), Polk & Van Oye (1956), Leclercq (1957), Polk (1957, 1959a,b), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Delhez et al. (1999), Wouters et al. (2000), Segers (2015), De Smedt et al. (2017b, 2018a,b)

11. Trichoniscoides helveticus (Carl, 1908)

First individuals identified by Vandel (1933) from Jemelle (Namur), but the exact date is unknown. Records of this species before 2010 are very scarce.

Status: Absent in the north, rather common in the rest of the country.

Bibliography: **Vandel (1933**, 1952), Polk & Van Oye (1956), Polk (1957, 1959a,b), Delhez & Kersmaekers (1973), Kersmaekers (1973a), Kersmaekers & Deroeck (1973), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Delhez et al. (1999), Wouters et al. (2000), Lock (2001), Segers (2015)

12. Trichoniscoides sarsi (Patience, 1908)

First recorded by Lock (2001) (Fig. 2.5d). Probably, this species had been overlooked for a long time because of its close resemblance to *T. helveticus*.

Status: Very common in the north of the country, common in the centre but absent from the south.

Bibliography: Lock & Durwael (2000), **Lock (2001**, 2007), Huwae & Rappé (2003), Segers (2015), De Smedt et al. (2017b)

Genus TRICHONISCUS Brandt, 1833

13. Trichoniscus alemannicus Verhoeff, 1917

Discovered in 2015 (De Smedt et al. 2016b), but probably overlooked for a long time because of its close resemblance to *T. pusillus* and *T. provisorius*.

Status: Rare in the south of the country, very rare in the centre and absent from the north.

Bibliography: **De Smedt et al. (2016b)**

14. Trichoniscus provisorius Racovitza, 1908

First recorded by Kersmaekers (1973c) as a subspecies of *T. pusillus*. Nowadays, not longer considered as a subspecies (Schmalfuss 2003) and can be distinguished from *T. pusillus* by the different shape of the male first pleopod (see e.g. Vandel 1960, De Smedt et al. 2016b). It was not mentioned on the checklists of Tavernier & Wouters (1989, 1991) and only as a subspecies by Wouters et al. (2000). Recordings of this species are extremely scarce in Belgium, since the species was considered a subspecies for a long time. Therefore, all specimens (945 individuals) of *Trichoniscus pusillus* s.l. present at the RBINS were re-identified of which 15 males and 930 females. All males belonged to *T. provisorius*. Interestingly, all male specimens were recorded after 1980. Vandel (1960) reports the species as being expansive and comparing the historical data with the recent surveys it can be assumed that the species is nowadays much more widespread. Historical data from the RBINS collections until 1970 recorded 0% of males across the country while this is 0.04% between 1970 and 2000 and about 1% after 2010.

Status: Very common in the north and centre of the country, common in the south.

Bibliography: **Kersmaekers (1973c)**, Wouters et al. (2000), De Smedt et al. (2015), Segers (2015), De Smedt et al. (2016b, 2018a,b)

15. *Trichoniscus pusillus* Brandt, 1833

First mentioned by Preudhomme de Borre (1886b), but later on the species appeared to be two species *T. pusillus* and *T. provisorius*. Except for Kersmaekers (1973c), no author distinguished between the two species. For a sure identification, the first male pleopod needs to be examined, but males are extremely rare (about 1.6%) of the population in *T. pusillus* (Vandel 1960). Therefore, identification of this species is often done based on the sex ratio of a large sample of the population (see Fussey 1984, De Smedt et al. 2016b). All *T. pusillus* s.l. present in the RBINS collections were re-identified (see *T. provisorius*). No males of *T. pusillus* were detected, but from three localities populations with more than 30 female individuals were recorded and no males were present. These are from Brussels in 1941 (166 ind.), Wanze (Liège) in 1979 (70 individuals) and from Ethe (Luxembourg) in 1981 (109 ind.).

The bibliography presented below should be considered as a bibliography for the species complex *T. alemannicus/pusillus/provisorius*, except for references from 2015 onwards.

Status: Very common across the country.

Bibliography: Pelseneer (1886), **Preudhomme de Borre (1886b)**, Lameere (1895, 1897), Maitland (1897), Bagnall (1907), Leruth (1937a,b,d,e,f, 1939), Capart (1942), Leleup (1948), Leloup et al. (1954), Polk & Van Oye (1956), Polk (1957), Leloup & Van Meel (1958), Polk (1959a,b), Delhez & Kersmaekers (1973), Kersmaekers & Deroeck (1973), Kersmaekers (1973c), Tavernier (1981), Tavernier & Kerwyn (1982), Holthuis (1983), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Branquart et al. (1995), Delhez et al. (1999), Devaere (1999), Lock & Vanacker (1999), Lock & Durwael (2000), Schollen (2000), Wouters et al. (2000), Lock (2001), Baeté et al. (2002, 2003a,b, 2004), Dekoninck et al. (2005), Baeté et al. (2006a), Loones et al. (2008), Dethier & Hubart (2010), De Smedt et al. (2015), Segers (2015), De Smedt et al. (2016b,c, 2017a,b, 2018a,b)

16. *Trichoniscus pygmaeus* Sars, 1898

Bagnall (1907) recorded the first specimens in greenhouses of the Botanical Gardens in Antwerp (Antwerp) and Brussels. A year later, the same author reported free-living populations in Brussels (Bagnall, 1908).

Status: Very common in the centre of the country, common in the north and the south.

Bibliography: **Bagnall (1907**, 1908), Vandel (1933), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers (1973c), Kersmaekers & Deroeck (1973), Tavernier & Wouters (1989,1991), Boon et al. (1993), Delhez et al. (1999), Wouters et al. (2000), Segers (2015), De Smedt et al. (2016b, 2017a,b)

Section Crinocheta

Superfamily Oniscoidea

Family Oniscidae

Genus ONISCUS Linnaeus, 1758

17. Oniscus asellus Linnaeus, 1758

One of the first five species mentioned for the fauna of Belgium by Carlier (1831). From Bellynck (1865) until Preudhomme de Borre (1886b) referred to as *Oniscus murarius* (Cuvier). No less than 61 publications deal with this species, making it the third most cited species in Belgian literature references.

Status: Very common across the country.

Bibliography: **Carlier (1831)**, Bellynck (1865), Plateau (1870), Pelseneer (1886), Plateau (1886), Preudhomme de Borre (1886b), Lameere (1895, 1897), Maitland (1897), Schouteden (1901), Bagnall (1907), Leruth (1937f), Lameere (1938), Leruth (1939), Capart (1942), Leleup (1948), Leloup et al. (1954), Polk & Van Oye (1956), Leclercq (1957), Polk (1957, 1959a,b), Kersmaekers & Deroeck (1973), Kersmaekers (1973c), Gysels et al. (1976), Tavernier (1981), Tavernier & Kerwyn (1982), Holthuis (1983), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Branquart et al. (1995), Lambrechts (1997), Delhez et al. (1999), Devaere (1999), Boon & Wijns (2000), De Bakker et al. (2000), Schollen (2000), Wouters et al. (2000), Baeté et al. (2002, 2003a,b), Huwae & Rappé (2003), Hendrickx et al. (2003), Vandekerckhove et al. (2003), Baeté et al. (2004), Dekoninck et al. (2005), Baeté et al. (2006a,b), Loones et al. (2008), Van De Vyver (2009), Dethier & Hubart (2010), Segers (2015), De Smedt et al. (2016b,c), Nijs et al. (2016), Boeraeve et al. (2017), De Smedt et al. (2017a,b, 2018a,b)

Family Philosciidae

Genus PHILOSCIA Latreille, 1804

18. Philoscia affinis Verhoeff, 1908

Expected to occur in Belgium by De Smedt et al. (2015) and shortly afterwards discovered in 2014 (Boeraeve et al., 2017) (Fig. 2.5e). Boeraeve et al. (2017) checked all individuals present in the collection of the RBINS and discovered that the species was already collected in Belgium in 1938 but mis-identified as *P. muscorum*. In total, they discovered eight historic records. The species proved to be widespread in Belgium and was recorded in eight out of ten provinces after 2014.

Status: Very common in the centre of the country, common in the south and rare in the north.

Bibliography: De Smedt et al. (2015), Segers (2015), **Boeraeve et al. (2017)**

19. Philoscia muscorum (Scopoli, 1763)

One of the five first species mentioned for the fauna of Belgium by Carlier (1831) as *Philoscia sylvestris* (Latr.). This is the second most cited species in Belgian woodlouse literature with 63 publications mentioning the species.

Status: Very common across the country.

Bibliography: **Carlier (1831)**, Bellynck (1865), Plateau (1870, 1873), Pelseneer (1886), Plateau (1886), Preudhomme de Borre (1886b), Lameere (1895, 1897), Maitland (1897), Schouteden (1901), Bagnall (1907), Leruth (1937f), Lameere (1938), Leruth (1939), Capart (1942), Leleup (1948), Leloup et al. (1954), Leloup & Konietzko (1956), Polk & Van Oye (1956), Polk (1957, 1959a,b), Dumont & Gysels (1971), Kersmaekers & Deroeck (1973), Kersmaekers (1973c), Gysels et al. (1976), Tavernier (1981), Tavernier & Kerwyn (1982), Holthuis (1983), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Branquart et al. (1995), Lambrechts (1997), Devaere (1999), De Bakker et al. (2000), Lock & Durwael (2000), Schollen (2000), Wouters et al. (2000), Lock (2001), Baeté et al. (2002, 2003a,b), Huwae & Rappé (2003), Hendrickx et al. (2003), Vandekerckhove et al. (2003), Baeté et al. (2004), Maelfait et al. (2004), Dekoninck et al. (2005), Baeté et al. (2006a), Loones et al. (2008), Van De Vyver (2009), Dethier & Hubart (2010), Segers (2015), De Smedt et al. (2016b,c), Nijs et al. (2016), Boeraeve et al. (2017), De Smedt et al. (2017a,b, 2018a,b)

Family Platyarthridae

Genus PLATYARTHRUS Brandt, 1833

20. Platyarthrus hoffmannseggi Brandt, 1833

First recorded by Mac Leod (1880), and appeared to be common but undersampled (Lameere 1897, Adam & Leloup 1940) because the unusual habitat (ant nests) for a woodlouse. This is the only myrmecophilous woodlouse species in Belgium.

Status: Very common in the north of the country, common in the centre and south.

Bibliography: **Mac Leod (1880)**, Moniez (1886), Pelseneer (1886), Preudhomme de Borre (1886b), Lameere (1895, 1897), Maitland (1897), Schouteden (1901), Bagnall (1907), Massart (1912), Collart (1936), Lameere (1938), Adam & Leloup (1940), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers & Deroeck (1973), Tavernier (1981), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Wouters et al.

(2000), Deconinck et al. (2007), Segers (2015), De Smedt et al. (2017a), Parmentier et al. (2017)

Superfamily Armadilloidea

Family Armadillidiidae

Genus ARMADILLIDIUM brandt, 1833

21. Armadillidium album Dollfus, 1877

Discovered by Kersmaekers (1988), which is the only published faunistical record so far, but it was also recorded during our field surveys. The species is both mentioned on the marine and brackish water isopod checklist (Rappé 1989a) as on terrestrial isopod checklists (Tavernier & Wouters 1989, 1991, Wouters et al. 2000), because its restriction to coastal habitat.

Status: Coastal species, very rare in the north of the country.

Bibliography: **Kersmaekers (1988)**, Rappé (1989a), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Lock & Durwael (2000), Wouters et al. (2000), Huwaé & Rappé (2003), Maelfait et al. (2004), Hoffmann (2006), Segers (2015), De Smedt et al. (2017b)

22. Armadillidium nasatum Budde-Lund, 1885

Expected to occur in Belgium by Preudhomme de Borre (1886b) and first discovered by Bagnall (1907) in greenhouses in Brussels and Antwerp. In the collections of the RBINS records from 1941 and 1943 from the museum gardens and on a roadside verge are present, both anthropogenic environments. It took until 1972 before the first non-anthropogenic populations were discovered in the southern part of the country (Kersmaekers 1972).

Status: Very common in the centre and the south of the country, common in the north.

Bibliography: Preudhomme de Borre (1886b), Maitland (1897), **Bagnall (**1907, 1908), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers (1972), Kersmaekers & Deroeck (1973), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Wouters et al. (2000), Huwae & Rappé (2003), Segers (2015), De Smedt et al. (2017a)

23. Armadillidium opacum (C. Koch, 1841)

First mentioned by Preudhomme de Borre (1886b) as *A. sulcatum*, but he corrected the identification later on to *A. opacum* (Preudhomme de Borre 1886a, Capart 1942). Nevertheless, *A. sulcatum* instead of *A. opacum* was reported on the checklist of Maitland (1897) and by Bagnall (1907). The oldest individuals that could be re-identified from the RBINS collections were collected by A. Capart in the 1940's.

Status: Very common in the south of the country, rather common in the centre and absent in the north.

Bibliography: Pelseneer (1886), **Preudhomme de Borre (1886**a,b), Maitland (1897), Bagnall (1907), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Gysels et al. (1976), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Devaere (1999), Wouters et al. (2000), Vandekerckhove et al. (2003), Dekoninck et al. (2005), Segers (2015), Nijs et al. (2016), De Smedt et al. (2018a,b)

24. *Armadillidium pictum* Brandt, 1833

Mentioned for the first time for Belgium by Plateau (1870) but the species was re-identified by Preudhomme de Borre (1886) as being *A. pulchellum*. Also, Bagnall (1907) mentioned the species as occurring in Belgium but without any reference. Leruth (1937f) could therefore be the first one to record the species from Belgium. Belgian specimens from the RBINS were re-identified, which mostly originated from the surveys done by Capart (1942), and found both *A. pictum* and *A. pulchellum* in the samples. Both species are easily confused and historical records without preserved animals should be treated with caution.

Status: Common in the centre and south of the country, absent from the north.

Bibliography: Plateau (1870), Preudhomme de Borre (1886b), Bagnall (1907), **Leruth (1937f**, 1939), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers & Deroeck (1973), Gysels et al. (1976), Holthuis (1983), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Wouters et al. (2000), Dekoninck et al. (2005), Dethier & Willems (2005), Segers (2015), De Smedt et al. (2016b)

25. *Armadillidium pulchellum* (Zencker, 1798)

Preudhomme de Borre (1886b) re-identified the specimens collected by Plateau (1870) and concluded that the species under consideration was *A. pulchellum* and not *A. pictum*. This is the first record of the species for Belgium. However, the species is easily confused with *A. pictum* (see section on A. pictum for additional information).

Status: Common in the centre and south of the country, and rare in the north.

Bibliography: **Preudhomme de Borre (1886**a,**b)**, Pelseneer (1886), Lameere (1895, 1897), Maitland (1897), Bagnall (1907), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Gysels et al. (1976), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Devaere (1999), De Bakker et al. (2000), Wouters et al. (2000), Vandekerckhove et al. (2003), Dekoninck et al. (2005), Segers (2015)

26. *Armadillidium vulgare* (Latreille, 1804)

One of the five first species on the Belgian list (Carlier 1831). Carlier (1831) mentions two species (*Armadillo vulgaris* Latr. and *Armadillo variegatus* Latr.) that eventually proved to be the same species (Schmalfuss 2003). Bellynck (1865) mentions *Armadillo triviale*, which also proves to be a synonym of *A. vulgare* (Schmalfuss 2003). Plateau (1870) reports both *Armadillidium vulgare* and *Armadillidium triviale*. Preudhomme de Borre (1886b) and Maitland (1897) mention *A. triviale* or *A. trivialis* as a subspecies of *A. vulgare*. This was also supported by Capart (1942). Afterwards, only *A. vulgare* has been mentioned in the Belgian literature. Interesting is the record by Troubleyn et al. (2009) from the remains of two woodlice, one unidentified woodlouse and the other one being *A. vulgare*, that were found in cesspits of on old prison at the main square of Malines dating back to the 14th century. This is the oldest record of a woodlouse in Belgium.

Status: Very common in the north and the centre of the country, common in the south.

Bibliography: **Carlier (1831)**, Bellynck (1865), Plateau (1870), Pelseneer (1886), Plateau (1886), Preudhomme de Borre (1886a,b), Lameere (1895, 1897), Maitland (1897), Schouteden (1901), Bagnall (1907), Senden (1936), Lameere (1938), Capart (1942), Leleup (1948), Leloup & Konietzko (1956), Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers & Deroeck (1973), Gysels et al. (1976), Tavernier (1981), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Branquart et al. (1995), Lambrechts (1997), Lock & Vanacker (1999), Lock & Durwael (2000), Schollen (2000), Wouters et al. (2000), Lock (2001), Baeté et al. (2003a), Huwae & Rappé (2003), Vandekerckhove et al. (2003), Maelfait et al. (2004), Troubleyn et al. (2009), Van De Vyver (2009), Dethier & Hubart (2010), Segers (2015), Nijs et al. (2016), De Smedt et al. (2017a,b, 2018a,b)

Genus ELUMA Budde-Lund, 1885

27. *Eluma caelata* (Miers, 1877)

Discovered for the first time in Belgium in 2016 (De Smedt et al. 2017b) (Fig. 2.5b). The species was expected to occur in Belgium since its discovery in the Netherlands close to the Belgian border (Lock & Durwael 2000), but it took more than 20 years since its first sighting in the Netherlands, to find the first Belgian specimens. It is still unclear if the species is truly native or naturalised in Belgium after colonisation from the Netherlands, where it could be accidentally introduced (De Smedt et al. 2017b). Berg et al. (2008) mentions the species from Belgium based on a reference of Lock in 2000, but this publication does not exist and can be classified as a typo.

Status: Rare in the north of the country, absent from the centre and the south.

Bibliography: Lock & Durwael (2000), Huwae & Rappé (2003), **De Smedt et al. (2017b)**, Boeraeve et al. (2017)

Family Cylisticidae

Genus CYLISTICUS Schnitzler, 1853

28. *Cylisticus convexus* (De Geer, 1778)

Expected to occur in Belgium by Preudhomme de Borre (1886b) and recorded for the first time in the same year by Moniez (1886). Records of this species have always been scarce with a peak during field research from Capart (1942); he collected specimens from at least six locations in the south of the country. Our recent observations indicate that the species is still scarce in the south of the country but was discovered as some isolated populations in the north as well.

Status: Rather common in the south of the country, rare in the north and absent from the centre.

Bibliography: Preudhomme de Borre (1886b), **Moniez (1886)**, Bagnall (1907), Leruth (1937f, 1939), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers & Deroeck (1973), Tavernier & Wouters (1989,1991), Boon et al. (1993), Wouters et al. (2000), Segers (2015), De Smedt et al. (2017a)

Family Porcellionidae

Genus PORCELLIO Latreille, 1804

29. *Porcellio dilatatus* Brandt, 1833

First mentioned by Plateau (1870), but according to Preudhomme de Borre (1886b), the identifications by Plateau (1870) were not correct and appeared to be *P. scaber* (see also Plateau 1886). Therefore, Preudhomme de Borre (1886) does the first record in 1886. Rre-identification of specimens from the RBINS dated back to 1898 from Charleroi (Hainaut). Sightings of the species are very rare and mostly associated to manmade structures like old horse and cow stables.

Status: Rather common in the centre of the country, rare in the north and absent from the south.

Bibliography: Plateau (1870), Pelseneer (1886), Plateau (1886), **Preudhomme de Borre (1886b)**, Lameere (1895), Maitland (1897), Bagnall (1907), Leruth (1937f, 1939), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers & Deroeck (1973), Holthuis (1983), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Delhez et al. (1999), Wouters et al. (2000), Segers (2015), De Smedt et al. (2017a)

30. *Porcellio laevis* Latreille, 1804

One of the first five species mentioned for the country by Carlier (1831). He mentions that the species could be found frequently under stones. Records from the 20th century are extremely rare and the only literature records are from Schouteden (1901), Polk & Van Oye (1956) and Boon et al. (1993). In the collection of the RBINS some individuals collected in Belgium in 1916 in Leuven (Flemish-Brabant) and the 1940's in the Museum Garden (a zoo at that time) (Brussels) were found. Since 2000, in the species has only been recorded from Wellen (Limburg) in 2015 in an old horse stable. However, despite an intensive search in 2017, after the buildings at the site were renovated, the species could not be rediscovered.

Status: Very rare in the centre, absent from the rest of the country.

Bibliography: **Carlier (1831)**, Plateau (1870), Pelseneer (1886), Preudhomme de Borre (1886a,b), Lameere (1895,1897), Maitland (1897), Schouteden (1901), Bagnall (1907), Capart (1942), Polk & Van Oye (1956), Polk (1957,1959a,b), Tavernier & Wouters (1989,1991), Boon et al. (1993), Wouters et al. (2000), Segers (2015)

31. *Porcellio monticola* Lereboullet, 1853

Expected to occur in Belgium by Preudhomme de Borre (1886b) (mentioned as *Porcellio lugubris*), but only recently discovered in Belgium in 2014 (De Smedt et al. 2015) (Fig. 2.5a).

Status: Rather common in the south, absent from the rest of the country.

Bibliography: Preudhomme de Borre (1886b), **De Smedt et al. 2015**, Segers (2015), Boeraeve et al. (2017)

32. Porcellio scaber Latreille, 1804

One of the first five species mentioned for the fauna of Belgium by Carlier (1831). This species is mentioned in 64 publications on Belgian woodlice, making it the most cited species.

Status: Very common across the country.

Bibliography: **Carlier (1831)**, Bellynck (1865), Plateau (1870), Pelseneer (1886), Plateau (1886), Preudhomme de Borre (1886b), Lameere (1895, 1897), Maitland (1897), Schouteden (1901), Bagnall (1907), Senden (1936), Leruth (1937f), Lameere (1938), Leruth (1939), Capart (1942), Leleup (1948), Leloup et al. (1954), Leloup & Konietzko (1956), Polk & Van Oye (1956), Polk (1957, 1959a,b), Delhez & Kersmaekers (1973), Kersmaekers & Deroeck (1973), Gysels et al. (1976), Tavernier (1981), Holthuis (1983), Tavernier & Wouters (1989, 1991), Donker & Bogert (1991), Donker (1992), Boon et al. (1993), Donker et al. (1993), Branquart et al. (1995), Lambrechts (1997), Delhez et al. (1999), Devaere (1999), Lock & Vanacker (1999), Lock & Durwael (2000), Schollen (2000), Wouters et al. (2000), Lock (2001), Baeté et al. (2003a), Huwae & Rappé (2003), Hendrickx et al. (2003), Vandekerckhove et al. (2003), Baeté et al. (2004), Maelfait et al. (2004), Dekoninck et al. (2005), Dethier & Willems (2005), Baeté et al. (2006a), Swiecicka & Mahillon (2006), Loones et al. (2008), Van De Vyver (2009), Dethier & Hubart (2010), De Smedt et al. (2015), Segers (2015), De Smedt et al. (2016b,c), Nijs et al. (2016), Boeraeve et al. (2017), De Smedt et al. (2017a,b, 2018a,b)

33. Porcellio spinicornis Say, 1818

First mentioned by Bellynck (1865) with the French name “Porcellion peint”. The first checklist by Plateau (1870) refers to the publication of Bellynck (1865) as the only observation up to that date. Afterwards, almost exclusively recorded from antropogenic habitats.

Status: Very common across the country.

Bibliography: **Bellynck (1865)**, Plateau (1870), Pelseneer (1886), Preudhomme de Borre (1886b), Lameere (1895), Maitland (1897), Bagnall (1907), Leruth (1937f, 1939), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers & Deroeck (1973), Gysels et al. (1976), Holthuis (1983), Tavernier & Wouters (1989, 1991), Tavernier & Wouters (1991), Boon et al. (1993), Wouters et al. (2000), Dethier & Willems (2005), Segers (2015), De Smedt et al. (2015, 2017a)

Genus PORCELLIONIDES Miers, 1877

34. Porcellionides pruinosus (Brandt, 1833)

First observations from the 1870's and first mentioned by Preudhomme de Borre (1886b). Observations are scattered and Boon et al. (1993) carried out the bulk of the observations during an intensive field survey. They found the species in most of the old stables and compost heaps they visited. The species is always associated with anthropogenic environments (compost heaps, graveyards, old stables…).

Status: Common in the north of the country, rather common in the centre and rare in the south.

Bibliography: **Preudhomme de Borre (1886b)**, Pelseneer (1886), Lameere (1895, 1897), Maitland (1897), Schouteden (1901), Bagnall (1907), Capart (1942), Polk & Van Oye (1956), Polk (1957, 1959a,b), Holthuis (1983), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Wouters et al. (2000), Segers (2015), De Smedt et al. (2017a)

Family Trachelipodidae

Genus PORCELLIUM Dahl, 1916

35. Porcellium conspersum (C. Koch, 1841)

First recorded by Capart (1942) in 1941, confirmed based on individuals stored in the RBINS collections. Records remain very scarce until 2014, but targeted research shows that the species is more common than observed from the few records.

Status: Very common in the south of the country, rather common in the centre and absent from the north.

Bibliography: **Capart (1942)**, Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers (1974), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Branquart et al. (1995), Wouters et al. (2000), Dekoninck et al. (2005), Segers (2015)

Genus TRACHELIPUS Budde-Lund, 1908

36. Trachelipus rathkii (Brandt, 1833)

First mentioned by Preudhomme de Borre (1886b) as being common in the country. Since the species can easily be confused with e.g. different *Porcellio* species, all material present at the RBINS collections was re-examined (286 individuals from 78 records). However, no mis-identifications could be detected. The oldest individuals were from Leuven (Flemish-Brabant) in 1916.

Status: Very common in the north of the country, common in the centre and in the south.

Bibliography: Pelseneer (1886), **Preudhomme de Borre (1886b)**, Lameere (1895), Maitland (1897), Bagnall (1907), Capart (1942), Leleup (1948), Polk & Van Oye (1956), Polk (1957, 1959a,b), Kersmaekers & Deroeck

(1973), Tavernier (1981), Tavernier & Kerwyn (1982), Tavernier & Wouters (1989, 1991), Boon et al. (1993), Devaere (1999), Lock & Vanacker (1999), Wouters et al. (2000), Huwae & Rappé (2003), Dekoninck et al. (2005), Van De Vyver (2009), De Smedt et al. (2015), Segers (2015), Nijs et al. (2016), De Smedt et al. (2017b, 2018a,b)

Deleted species

Six species were mentioned on at least one of the previous checklists, but are not present anymore on the current checklist. Most species appeared to be mis-identifications or could not be confirmed because material was not preserved and literature references are incomplete.

- *Androniscus roseus* (C. Koch, 1838) was first mentioned by Lameere (1897), but after a lot of confusion between this species and *Androniscus dentiger* by different authors mentioning one of the two species, it became clear that only *A. dentiger* was recorded from Belgium (Polk 1957) (see *Andronicus dentiger* above).
- *Armadillidium depressum* Brandt, 1833 was first mentioned by Tavernier & Wouters (1989). The species was apparently collected on a graveyard in the province of East-Flanders near Ninove. However, the species could not be verified and even if the identification is correct the species can be assumed as imported e.g. from Great Britain where the species is common in the south (Gregory 2009) and the species has no current free-living populations in Belgium. Extensive searches for woodlice on Belgian graveyards did not reveal the presence of the species. The species was included in the checklists from Tavernier & Wouters (Tavernier & Wouters 1989, 1991, Wouters et al. 2000) and Huwae & Rappé (2003) mentioned the species based on the same references. Baeté et al. (2003b) found the species in the nature reserve Walenbos (Flemish-Brabant), but later on, this appeared to be *A. opacum*. Finally, De Smedt et al. (2015) proposes to remove the species from the Belgian list.
- *Armadillidium sulcatum* Milne-Edwards, 1840 is a species from Northern Algeria (Schmalfuss 2003) and was mentioned by Preudhomme de Borre (1886b) as found in Belgium. However, after re-identification this specimen proved to be *A. opacum* (Preudhomme de Borre 1886a, Capart 1942).
- *Armadillidium triviale* Schöbl, 1861 mentioned by Bellynck (1865) and Plateau (1870) appeared to be *A. vulgare* (Preudhomme de Borre 1886b, Capart 1942). This species proved to be a synonym of *A. vulgare* (Schmalfuss 2003).
- *Ligidium germanicum* Verhoeff, 1901 was mentioned by Gysels et al. (1976), but was not mentioned on the checklists of Tavernier & Wouters (1989, 1991). However, the species appears on the checklist of Wouters et al. (2000) and is cited by Schmalfuss (2003). Wouters et al. (2000) already mentions the species as doubtful since no material has been preserved.*L. germanicum* was deleted from this new checklist because its presence could not be confirmed.
- *Eoniscus simplicissimus* Arcangeli was a specimen collected by Leruth (1937) and described as a new species to science in a new genus and family by Arcangeli (1935). Verhoeff (1937) re-examined the individual and concluded that it was a larvae of a species from the millipede genus *Polydesmus* (Polk & Van Oye 1956, Polk 1957).

Species from greenhouses

Literature on Belgian woodlice in greenhouses is very limited. Only five papers deal with inventories carried out in Belgian greenhouses and they are all from the northern part of the country. Up to date only four exotic species could be confirmed in Belgian greenhouses. Since they cannot be considered as part of the Belgian woodlice fauna, because of the lack of wild populations, and are not included in this checklist as Belgian species. However, they were included in previous checklists (see e.g. Capart 1942, Polk 1959a Wouters & Tavernier 1989, 1991, Wouters et al. 2000).

The first exotic species recorded from Belgian greenhouses is *Cordioniscus stebbingi* (Patience, 1907) by Bagnall in 1908 from a greenhouse in Brussels. Polk & Van Oye (1956) mention *Trichorhina tomentosa* (Budde-Lund, 1893) from Ghent. De Smedt et al. (2017a) mention *Nagurus cristatus* (Dollfus, 1889) and *Reductoniscus costulatus* Kesselyák, 1930 both from greenhouses in Ghent (East-Flanders) and the first species also from Meise (Flemish-Brabant). In addition, Polk & Van Oye (1956) mention an individual of the genus *Rhyscotus* Budde-Lund, 1885 and De Smedt et al. (2017a) mention an individual of the genus *Synarmadillo* Dollfus, 1892. However, both specimens were lost and could not be verified.

Greenhouse literature: Bagnall (1907,1908), Polk & Van Oye (1956), Kersmaekers (1973b), De Smedt et al. (2017a).

Species to be expected

Twenty-five percent of the Belgian woodlice species were added on this new checklist and all were discovered the last 20 years, therefore it is still possible that even more species can be discovered in Belgium. Below, some species recorded in neighbouring countries and relatively close to the Belgian border are listed:

- *Porcellio gallicus* Dollfus, 1904. This species is found to be abundant in small deciduous forest fragments in agricultural areas in the north of France (Landifay-et-Bertaignemont) only 45 km from the Belgian border (De Smedt et al. 2018b). Similar habitats are also present in the southern and central part of Belgium.
- *Porcellio montanus* Budde-Lund, 1885. Found in Germany (Wiesbaden) around 100 km from the Belgian border (edaphobase.org). Also reported from Grand Duchy of Luxembourg (Weber 2013) at only 18 km from the Belgian border. Hower, the latter record is not wel documented. According to Gruner (1965) the species occurs in forest edges, under bark of trees and stone heaps. The species could therefore be expect in the south of Belgium.
- *Androniscus roseus* (C. Koch, 1838). A species closely resembling *A. dentiger* and recorded about 160 km from the Belgian border in Frankfurt (Germany) (edaphobase.org). There the species is reported from riparian habitat and forest fringe communities. The species could be overlooked since its close resemblance to *A. dentiger* and can be expected in the eastern part of the country.
- *Trachelipus ratzeburgi* (Brandt, 1833). Another species that could be overlooked in Belgium be-

cause of its close resemblance to *T. rathkii*. The species occurs in all kinds of woodland and the closest records are from Herborn in Germany at 140 km from the Belgian border (edaphobase.org). Therefore, the species could be expected in the east of the country.

- *Chaetophiloscia cellaria* (Dollfus, 1884). This species has recently been discovered in Northern France at three localities of which two at 35 km from the Belgian border (Delasalle & Séchet 2014). The species was recorded in association with anthropogenic environments, like cemeteries. Therefore it is very likely that the species can also be found in similar habitat in Belgium.

Three of the last five new species on the Belgian list are large to medium-sized and therefore it is possible that also they are present and awaiting discovery.

Conclusion

With 36 species Belgium now has a comparable amount of species, relative to its size, to neighbouring countries like the Netherlands (33 species see Berg et al. (2008) and Berg & Krediet (2017)), Great Britain (41 species see Gregory (2009) and Segers et al. (2017)) and Germany (about 50 species see edaphobase.org). France (218 species including greenhouse species see Séchet & Noël (2015)) has far more species but this is due to the additional southern species and many endemics. Despite the large amount of published papers, Belgium lagged behind in number of species recorded, probably because of the lack of an interest group, as exists for Great Britain and the Netherlands. Belgium has caught up with its neighbouring countries, although there are still some species that may be present in Belgium. Future field surveys should fill the last "blank spots" in the distribution maps and will form the base of a first distribution atlas of woodlice in Belgium. This will be a valuable way forward to understand the ecology and habitat-preference of many Western European woodlouse species.

Acknowledgements

We are grateful to Yves Samyn and Wouter Dekoninck for giving us access to the collections of the RBINS. Oliver Mechthold is thanked for the help with fieldwork.

Appendix 2.1. Bibliography of Belgian woodlice

1. Adam W, Leloup E (1940) La distribution en Belgique de Leucochloridium paradoxum, Rhynchodemus terrestris, Arion intermedius, Platvarthrus hoffmannseggi et Atyaephyra desmaresti. Bulletin du Musée royal d'histoire naturelle de Belgique 16: 1-8.
2. Arcangeli A (1935) Eoniscus Simplicissimus, Un Pigmeo Degli Isopodi Terrestri, Appartenente a Nuova Specie, Nuovo Genere, Nuova Famiglia. Bolletino di zoologia 6: 203-212.
3. Baeté H, Christiaens B, De Keersmaeker L, Esprit M, Van de Kerckhove P, Vandekerkhove K, Walleyn R (2004) Monitoringprogramma Vlaamse bosreservaten - Bosreservaat Wijnendalebos - Basisrapport. IBW Bb 04.009. Instituut voor Bosbouw en Wildbeheer, Geraardsbergen, 125 pp.
4. Baeté H, Christiaens B, De Keersmaeker L, Esprit M, Van de Kerckhove P, Vandekerkhove K, Walleyn R (2006a) Bosreservaat Bos Ter Rijst (Heikruis) - Basisrapport. INBO.R.2006.15. Instituut voor Natuur- en Bosonderzoek, Brussel, 131 pp.
5. Baeté H, Christiaens B, De Keersmaeker L, Esprit M, Van de Kerckhove P, Vandekerkhove K, Walleyn R (2006b) Bosreservaat Jansheideberg (Hallerbos) - Basisrapport. INBO.R.2006.13. Instituut voor Natuur- en Bosonderzoek, Brussel, 131 pp.
6. Baeté H, De Keersmaeker L, Van de Kerckhove P, Christiaens B, Esprit M, Vandekerkhove K (2002) Monitoring-programma Vlaamse Bosreservaten–Bosreservaat Kersselaerspleyn (Zoniënwoud)–Monitoringrapport. Rapport IBW Bb 02.005. Instituut voor Bosbouw en Wildbeheer, Geraardsbergen, 172 pp.
7. Baeté H, De Keersmaeker L, Walleyn R, Van de Kerckhove P, Christiaens B, Esprit M, Vandekerkhove K (2003a) Monitoring-programma Vlaamse bosreservaten – Monitoring van een transect in het Vlaams natuurreservaat Hannecartbos – Basisrapport. IBW Bb 03.012. Instituut voor Bosbouw en Wildbeheer, Geraardsbergen, 81 pp.
8. Baeté H, De Keersmaeker L, Walleyn R, Van de Kerckhove P, Christiaens B, Esprit M, Vandekerkhove K (2003b) Monitoringprogramma Vlaamse bosreservaten – Monitoring van kernvlakte en transecten in het Vlaams Natuurreservaat Walenbos – Basisrapport. IBW Bb 03.014. Instituut voor Bosbouw en Wildbeheer, Geraardsbergen, 84 pp.
9. Bagnall RS (1907) On some terrestrial lsopod Crustacea new to the Fauna of Belgium. Annales de la Société royale zoologique et malacologique de Belgique 42: 263-266.
10. Bagnall RS (1908) On the occurrence in Belgium of a recently described terrestrial Isopod, Trichoniscus Stebbingi, Patience. Annales de la Société royale zoologique et malacologique de Belgique 43: 127-129.
11. Bellynck A (1865) Résumé du cours de zoologie professé au collège Notre Dame de la Paix à Namur. 1864-1865: 1-375.
12. Boeraeve P, De Smedt P, Arijs G, Segers S (2017) Philoscia affinis Verhoeff, 1908 new to Belgium (Isopoda: Philosciidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 153: 183-188.
13. Boon B, Wijns K (2000) ICP onderzoek op zware metalen in pissebedden van Vlaamse bossen. Eindwerk tot het behalen van de graad van gegradueerde in de Chemie, optie Milieuzorg. Erasmus Hogeschool Brussel.
14. Boon N, Lambrechts J, Stuckens J (1993) Landpissebedden. Verspreiding en Ecologisch Onderzoek. 22 UTM-hokken rond Tienen. Koninklijk Atheneum Tienen.
15. Branquart E, Kime RD, Dufrêne M, Tavernier J, Wauthy G (1995) Macroarthropod-habitat relationships in oak forests in South Belgium. 1. Environments and communities. Pedobiologia 39(3): 243-263.
16. Cappart A (1942) Note sur les isopodes terrestres de la faune Belge. I. Liste des espèces connues actuellement en Belgique. Bulletin du Musée royal d'histoire naturelle de Belgique 18: 1-5.
17. Carlier A (1831) Dictionnaire géographique de la province de Liége. Vander Maelen, Bruxelles, 365 pp.
18. Collart A (1936) Assemblée mensuelle du 6 juin 1936. Bulletin et Annales de la Société royale d'Entomologie de Belgique 76: 227-228.
19. Daro MH (1969) Etude écologique d'un brise-lames de la côte belge: 1. Description et zonation des organismes. Annales de la Société Royale Zoologique de Belgique 99: 111-152.

20. De Bakker D, Desender K, Grootaert P (2000) Determinatie en bioindicatie van bosgebonden ongewervelden. 1. Bioindicatie van standplaatsvariabelen. Onderzoeksopdracht B&G/29/98, AMINAL. Rapport ENT200001. KBIN, Brussel, 146 pp.
21. De Smedt P, Arijs G, Segers S, Boeraeve P (2017a) Woodlice of the green houses at Ghent Botanical Garden and Botanic Garden Meise with two new exotic species for Belgium (Isopoda: Oniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 153: 109-112.
22. De Smedt P, Baeten L, Berg MP, Gallet-Moron E, Brunet J, Cousins SAO, Decocq G, Diekmann M, Giffard B, De Frenne P, Hermy M, Bonte D, Verheyen K (2018a) Desiccation resistance determines distribution of woodlice along forest edge-to-interior gradients. European Journal of Soil Biology 85: 1-3.
23. De Smedt P, Baeten L, Proesmans W, Berg MP, Brunet J, Cousins SAO, Decocq G, Deconchat M, Diekmann M, Gallet-Moron E, Giffard B, Liira J, Martin L, Ooms A, Valdés A, Wulf M, Hermy M, Bonte D, Verheyen K (2018b) Linking macrodetritivore distribution to desiccation resistance in small forest fragments embedded in agricultural landscapes in Europe. Landscape Ecology 33: 407-421.
24. De Smedt P, Boeraeve P, Arijs G (2016a) Confirmation of Metatrichoniscoides leydigii (Weber, 1880) in Belgium, 60 years after discovery (Isopoda: Trichoniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 152: 18-21.
25. De Smedt P, Boeraeve P, Arijs G, Franken O, Mechtold O, Segers S, Berg MP (2017b) A long-expected finding: the first record of the isopod Eluma caelatum (Miers, 1877) from Belgium (Crustacea: Isopoda: Armadillidiidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 153: 89-93.
26. De Smedt P, Boeraeve P, Arijs G, Proesmans W (2016b) Trichoniscus alemannicus Verhoeff, 1917 a new species of woodlouse for Belgium (Isopoda: Trichoniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 152: 104-108.
27. De Smedt P, Boeraeve P, Arijs G, Segers S, Lock K (2015) Porcellio monticola Lereboullet, 1853 a new species for Belgium (Isopoda: Porcellionidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 151: 118-121.
28. De Smedt P, Wuyts K, Baeten L, De Schrijver A, Proesmans W, De Frenne P, Ampoorter E, Remy E, Gijbels M, Hermy M, Bonte D, Verheyen K (2016c) Complementary distribution patterns of arthropod detritivores (woodlice and millipedes) along forest edge-to-interior gradients. Insect Conservation and Diversity 9: 456-469.
29. Dekoninck W, Lock K, Janssens F (2007) Acceptance of two native myrmecophilous species, Platyarthrus hoffmannseggii (Isopoda: Oniscidea) and Cyphoderus albinus (Collembola: Cyphoderidae) by the introduced invasive garden ant Lasius neglectus (Hymenoptera: Formicidae) in Belgium. European Journal of Entomology 104(1): 159.
30. Dekoninck W, Maelfait J-P, Desender K, Grootaert P (2005) Comparative study of the Terrestrial Isopod Faunas of Ancient and Afferested Former Agricultural Fields. Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 75: 271-279.
31. Delhez F, Dethier M, Hubart J-M (1999) Contribution à la connaissance de la faune des grottes de Wallonie. Bulletin de la société royale belge d'études géologiques et archéologiques "Les chercheurs de la Wallonie" 39: 27-54.
32. Delhez F, Gilson R, Hubart JM (1973) Étude préliminaire de la faune de la grotte de Ramioul. Bulletin de la société royale belge d'études géologiques et archéologiques "Les chercheurs de la Wallonie" 22: 329-349.
33. Delhez F, Houssa M (1969) L'araine de Richeronfontaine à Liège. Etude écologique de la faune cavernicole d'un réseau souterrain artificiel. Les Naturalistes belges 50: 194-212.
34. Delhez F, Kersmaekers M (1973) Aspect Biologique de la Grotte de Pré-au-Tonneau à Rochefort. Speleologia Belgica 1: 3-9.
35. Dethier M, Hubart J-M (2010) Évolution de la fauna invertébrée des grottes de Ramioul (commune de Flémalle, province de Liège, Belgique). Bulletin des Chercheurs de la Wallonie hors-série 3: 15-44.
36. Dethier M, Willems L (2005) Les invertébrés des carrières souterraines de craie de la Montagne Saint-Pierre (Province de Liège, Belgique). Note préliminaire. Notes fauniques de Gembloux 57: 17-27.
37. Devaere N (1999) Het voorkomen en de ecologie van pissebedden (Oniscidea, Crustacea) in Vlaamse bossen. Universiteit Gent.
38. Donker MH (1992) Energy reserves and distribution of metals in populations of the isopod Porcellio scaber from metal-contaminated sites. Functional ecology 6(4): 445-454. doi:10.2307/2389282
39. Donker MH, Bogert CG (1991) Adaptation to cadmium in three populations of the isopod Porcellio scaber. Comparative Biochemistry and Physiology Part C: Comparative Pharmacology 100(1-2): 143-146.

40. Donker MH, Zonneveld C, Van Straalen NM (1993) Early reproduction and increased reproductive allocation in metal-adapted populations of the terrestrial isopod Porcellio scaber. Oecologia 96(3): 316-323.
41. Dumont H, Gijsels H (1971) Etude faunistique et écologique sur les criques de la Flandre orientale et le long de L'Escaut. Considérations sur leur chimisme, leur faune planktonique, entomologique et malacologique et discussion de leur état biologique actuel. Annales de la Société Royale Zoologique de Belgique 101: 157-182.
42. Eneman E (1984) Uit het Natuurhistorisch archief. De Strandvlo 4: 14.
43. Engledow H, Spanoghe G, Volckaert A, Coppejans E, Degraer S, Vincx M, Hoffmann M (2001) Onderzoek naar (1) de fysische karakterisatie en (2) de biodiversiteit van strandhoofden en andere harde constructies langs de Belgische kust: eindrapport van de onderhandse overeenkomst dd. 17.02.2000 i.o.v. de Afdeling Waterwegen Kust van het Ministerie van de Vlaamse Gemeenschap, Departement Leefmilieu en infrastructuur, Administratie Waterwegen en Zeewezen. Instituut voor Natuurbehoud, 110 + annexes pp.
44. Gils A (1947) Les Crustacés du Littoral belge. Les Naturalistes belges 7-8: 1-15.
45. Gilson G (1900) Exploration de la mer sur les côtes de la Belgique en 1899. Mémoires du Musée royal d'histoire naturelle de Belgique. Polleunis & Ceuterick, Bruxelles, 1-81.
46. Gilson R, Hubart JM (1973) Protection du biotope de la grotte Lyell. Bulletin de la société royale belge d'études géologiques et archéologiques "Les chercheurs de la Wallonie" 12: 367-681.
47. Gysels H, Vanfleteren J, Lippens P, Maertens D (1976) Tien jaar zoölogische stages in en om de Ardennen. Natuurwetenschappelijk tijdschrift 58: 3-68.
48. Hendrickx F, Maelfait JP, De Mayer A, Tack FM, Verloo MG (2003) Storage mediums affect metal concentration in woodlice (Isopoda). Environmental Pollution 121(1): 87-93. doi:10.1016/S0269-7491(02)00203-8
49. Hoffmann M (2006) Beheerplan VNR De Ijzermonding. 154 pp.
50. Holthuis LB (1950) Isopodes et Tanaidacés marins de la Belgique; remarques sur quelques espèces de la zone méridionale de la Mer du Nord. Bulletin de l'Institut royal des Sciences naturelles de Belgique 36: 1-19.
51. Holthuis LB (1983) De Pissebedden (Crustacea, lsopoda, Oniscidea) van de ondergrondse kalksteengroeven in Zuid-Limburg. Zoölogische bijdragen (Bijdragen tot de faunistiek van Nederland X) 29: 77-98.
52. Huwae P, Rappé G (2003) Waterpissebedden: een determineertabel voor de zoet-, brak- en zoutwaterpissebedden van Nederland en België. Wetenschappelijke Mededelingen van de Koninklijke Nederlandse Natuurhistorische Vereniging, 226. KNNV Uitgeverij, Utrecht, 55 pp.
53. Jocqué R, Van Damme D (1971) Inleidende oecologische studie van klei-en turfbanken in de getijdenzone te Raversijde (België). Biologisch Jaarboek Dodonaea 40: 157-190.
54. Jonckheere I, Van Rillaer L (2001) Strandexcursie op 12 maart 2001 in de Baai van Heist. De Strandvlo 21(2): 84-86.
55. Kersmaekers M (1972a) Note sur deux nouvelles stations pour la Belgique d'un Oniscoïde du genre Armadillidium, Armadillidium nasatum (Budde-Lund). Bulletin d'lnformation de l'Equipe Spéléologique de Bruxelles 51: 14-17.
56. Kersmaekers M (1972b) Un cas de tératologie chez un Oniscoïde (lsopode). Bulletin et Annales de la Société royale d'Entomologie de Belgique 109: 94-96.
57. Kersmaekers M (1973a) Communications a l'Assemblée mensuelle du 7 novembre 1973. Bulletin et Annales de la Société royale d'Entomologie de Belgique 109: 221-223.
58. Kersmaekers M (1973b) Note sur plusieurs captures d'un Oniscoïde du genre Trichorhina dans les serres du Jardin Botanique à Gand. Biologisch Jaarboek Dodonaea 41: 194-197.
59. Kersmaekers M (1973c) Nouvelle sous-espèce d'Oniscoïde pour la faune belge: Trichoniscus pusillus provisorius Racovitza, 1908. Bulletin et Annales de la Société royale d'Entomologie de Belgique 109: 305-307.
60. Kersmaekers M (1974) Communications a l' Assemblée mensuelle du 6 mars 1974. Bulletin et Annales de la Société royale d'Entomologie de Belgique 110: 34-35.
61. Kersmaekers M (1988) Communications a l'Assemblée mensuelle du 2 décembre 1987. Armadillidium (Duplocarinatum) album (Dollfus, 1889), nouvel Oniscoïde pour la faune belge (Crustacea, Isopoda). Bulletin et Annales de la Société royale d'Entomologie de Belgique 124: 67-69.

62. Kersmaekers M, Deroeck R (1973) Comparaison de la faune des Isopodes de deux massifs karstiques: Massif de Boine et Massif de Dieupart. Speleologia Belgica 2: 6-11.
63. Kesteloot E (1956) Zeebrugge: une curiosité biologique de notre littoral. Association Nationale des Professeurs de Biologie de Belgique 2: 9.
64. Lambrechts J (1997) Spinnen en pissebedden van autosnelwegbermen rond Gent en het voorkomen van zware metalen in deze organismen. Universiteit Gent.
65. Lameere A (1895) Manuel de la Faune de Belgique. H. Lamertin, Bruxelles, 639 pp. doi:10.5962/bhl.title.123557
66. Lameere A (1897) Documents pour la faune de Belgique. Annales de la Société Royale de Microscopie 22: 41-46.
67. Lameere A (1909) Assemblée mensuelle du 4 septembre 1909. Annales de la Société d'Entomologie de Belgique 53: 405-406.
68. Lameere A (1913) La faune du môle de Zeebrugge. Annales de la Société royale zoologique et malacologique de Belgique 44: 259-260.
69. Lameere A (1931) Excursion à Blankenberge. 25-26 mai 1931. Annales de la Société royale zoologique et malacologique de Belgique 62: 10-11.
70. Lameere A (1938) Les animaux de Belgique. Tome II. Vers Mollusques, Arachnomorphes, Crustacés, Myriapodes. Les Naturalistes belges 1938: 88-89.
71. Leclercq J (1957) Etude Biospéléologique. Fons de Forêts. Commission de Topographie et de Toponymie de la FSB 13: 2-6.
72. Lefevere S (1965) Le recouvrement biogène le long de la côte belge. Bulletin de I'Institut royal des Sciences naturelles de Belgique 26: 1-10.
73. Lefevere S, Leloup E, Van Meel L (1956) Observations biologiques dans le port d'Ostende. Mémoires de l'lnstitut royal des Sciences naturelles de Belgique 133: 1-110.
74. Leleup N (1948) Contribution à l'étude des arthropodes nidicoles et cavernicoles de Belgique. Mémoires de la Société royale d'Entomologie de Belgique 25: 1-56.
75. Leloup E (1957) Contributions à l'étude de la faune belge: XXV. Observations écologiques sur le fossé d'eau saumâtre entourant la "Demi-Lune" d'Ostende. Bulletin de I'Institut royal des Sciences naturelles de Belgique 33(11): 1-9.
76. Leloup E, Jacquemart S, Van Meel L (1954) Recherches hydrobiologiques sur trois mares d'eau douce des environs de Liège. Mémoires de l'lnstitut royal des Sciences naturelles de Belgique 131: 1-145.
77. Leloup E, Konietzko B (1956) Recherches biologiques sur les eaux saumâtres du Bas-Escaut. Mémoires de l'lnstitut royal des Sciences naturelles de Belgique 132: 1-100.
78. Leloup E, Miller G (1940) La flore et la faune du bassin de chasse d'Ostende (1937-1938). Mémoires de l'lnstitut royal des Sciences naturelles de Belgique 94: 1-122.
79. Leloup E, Polk Ph (1967) La flore et la faune du bassin de chasse d'Ostende (1960-1961) : III. étude zoologique. Mémoires de l'lnstitut royal des Sciences naturelles de Belgique 157: 1-114.
80. Leloup E, Van Meel L (1958) Quelques considerations hydrobiologiques sur un étang à Lombise. Bulletin de I'Institut royal des Sciences naturelles de Belgique 34(20): 1-16.
81. Leloup E, Van Meel L, Polk Ph, Halewyck R, Gryson A (1963) Recherches sur l'ostréiculture dans le bassin de chasse d'Ostende en 1962. Ministère de l'Agriculture. Commission TWOZ. Groupe de Travail Ostréiculture: Ostende, 58 pp.
82. Leruth R (1936a) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 25(3): 29-32.
83. Leruth R (1936b) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 25(5): 52-56.
84. Leruth R (1936c) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 25(6): 66-68.
85. Leruth R (1936d) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 25(8): 95-98.
86. Leruth R (1936e) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 25(11-12): 130.

87. Leruth R (1937a) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 26(1): 9-11.
88. Leruth R (1937b) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 26(2): 22-23.
89. Leruth R (1937c) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 26(9): 99-103.
90. Leruth R (1937d) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 26(11): 129-132.
91. Leruth R (1937e) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 26(12): 141-146.
92. Leruth R (1937f) Etudes biospéologiques. I. lsopoda (Crustacea). Bulletin du Musée royal d’histoire naturelle de Belgique 13(2): 1-25.
93. Leruth R (1939) La biologie du domaine souterrain et la faune cavernicole de la Belgique. Mémoires du Musée royal d’Histoire naturelle, Série 1 87: 1-506.
94. Lock K (2001) Trichoniscoides sarsi (Patience, 1908): a newspecies for the fauna of Belgium (Isopoda Trichoniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 137: 29-31.
95. Lock K (2007) Haplophthalmus montivagus Verhoeff, 1940: a new species for Belgium (Isopoda Trichoniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 143: 22-25.
96. Lock K, Durwael L (2000) Miktoniscus patiencei (Vandel, 1946): reported for the first time in Belgium (Isopoda Trichoniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 136: 21-23.
97. Lock K, Vanacker S (1999) Isopods on the gravelbanks of the Meuse (Isopoda). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 135: 193-196.
98. Loones J, Maelfait JP, Van Rhijn J, Dekoninck W, Adriaens T (2008) De rode bosmier in Vlaanderen: voorkomen, bedreigingen en herstelmaatregelen aan de hand van een detailstudie in de Sixtusbossen (Poperinge-Vleteren). Rapporten van het Instituut voor Natuur-en Bosonderzoek 2008 (INBOR200801). Instituut voor Natuur en Bosonderzoek, Brussel, 94 pp.
99. Mac Leod J (1880) Deux crustacés nouveaux pour la faune belge. Annales de la Société d’Entomologie de Belgique 23: 74-75.
100. Maelfait J-P, Bonte D, Grootaert P (2004) Annex 4: Terrestrische arthropoden. In: Speybroeck J, Bonte D, Courtens W, Gheskiere T, Grootaert P, Maelfait J-P, Mathys M, Provoost S, Sabbe K, Stienen E, Lancker VV, Vincx M, Degraer S (Eds) Studie over de impact van zandsuppleties op het ecosysteem Eindrapport Dossiernr 202165. Ministerie van de Vlaamse Gemeenschap, 201 pp.
101. Maitland RT (1897) Prodrome de la Faune des Pays-Bas et de la Belgique Flamande. Uitgave Boekhandel en Drukkerij voorheen Brill, Leiden, 62 pp.
102. Mares J (1994) Strandexcursie te Oostende (Opex) op 30 april 1994. De Strandvlo 14(3): 103-106.
103. Massart J (1912) Pour Ia protection de la nature en Belgique. H. Lamertin, Bruxelles, 308 pp.
104. Moniez R (1886) Comptes-rendus des séances. Assemblée mensuelle du 6 novembre 1886. Annales de la Société d’Entomologie de Belgique 30: 185.
105. Nijs G, Lambrechts J, Stassen E, Vanormelingen P, Lambeets K, Feys S (2016) De Grauwe klauwier in Vlaams-Brabant: inventarisatie, habitatpreferentie en voedselbeschikbaarheid. Rapport Natuurpunt Studie 2016/5, Mechelen, 160 pp.
106. Parmentier T, Vanderheyden A, Dekoninck W, Wenseleers T (2017) Body size in the ant-associated isopod Platyarthrus hoffmannseggii is host-dependent. Biological Journal of the Linnean Society 121(2): 305-311. doi:10.1093/biolinnean/blw052
107. Pelseneer P (1886) Note sur la présence de Caridina Desmaresti dans les eaux de la Meuse. Bulletin du Musée royal d’histoire naturelle de Belgique 4: 211-222.
108. Plateau F (1870) Matériaux pour la faune belge Crustacés lsopodes terrestres. Bulletin de I’Academie Belge, série 2 29: 112-121.
109. Plateau F (1886) Comptes-rendus des séances. Assemblée mensuelle du 4 décembre 1886. Annales de la Société d’Entomologie de Belgique 30: 190.

110. Plateau MF (1873) On the occurrence of Ligidium agile in Belgium. Annals and Magazine of Natural History 12: 75. doi:10.1080/00222937308680704
111. Polk Ph (1957) Studie der landisopoden van België. Biologisch Jaarboek Dodonaea 24: 157-181.
112. Polk Ph (1959a) De landpissebedden (lsopoda Oniscoidea) van Belgie en Nederland. Koninklijke Nederlandse Natuurhistorische Vereniging Tabel 31: 1-12.
113. Polk Ph (1959b) Notes sur la distribution et la bibliographie des Oniscoïdea de la Belgique. Biologisch Jaarboek Dodonaea 27: 452-460.
114. Polk Ph (1963) Bijdrage tot de kennis van de mariene fauna van de Belgische Kust. V. Some observations on the Crustacean fauna of the Sluice-dock (Bassin de Chasse) of Ostend. Bulletin de I'Institut royal des Sciences naturelles de Belgique 29(20): 1-8.
115. Polk Ph (1965) Oecologie van de Spuikom te Oostende in verband met de oestercultuur. PhD Thesis, Gent: Rijksuniversiteit Gent.
116. Polk Ph (1976) Inventarisatie plankton, fauna en flora. In: Nihoul JCJ, De Coninck L (Eds) Projekt Zee eindverslag: 7 Inventaris van de fauna en flora Projekt Zee eindverslag, 7. 233-311.
117. Polk Ph, Oye P (1956) Studie der Landisopoden in België : systematisch-oecologisch. Licenciaatsverhandeling, Gent: Universiteit Gent.
118. Preudhomme de Borre A (1886a) Comptes-rendus des séances. Assemblée mensuelle du 5 juin 1886. Annales de la Société d'Entomologie de Belgique 30: 125.
119. Preudhomme de Borre A (1886b) Note sur les Crustacés Isopodes de Belgique. Annales de la Société d'Entomologie de Belgique 30: 74-86.
120. Rappé G (1977) Verslag van het weekendje in Blankenberge op 25 en 26 september 1976. Tuimelaar 4(1): 7.
121. Rappé G (1989a) Annotated checklist of the marine and brackish water lsopoda (Crustacea, Malacostraca) of Belgium. In: Wouters K, Baert L (Eds) lnvertebraten van België - lnvertébrés de Belgique, Proceedings of the Symposium "Invertebrates of Belgium". Brussels, 165-168.
122. Rappé G (1989b) Haliclona xena De Weerdt, 1986 (Porifera, Desmospongiae), Petrobius maritimus (Leach) (Insecta, Thysanura) en enkele andere bijzondere waarnemingen van de oostelijke strekdam van Zeebrugge. De Strandvlo 9(4): 113-116.
123. Schollen K (1999) Evaluatie van de mogelijkheden van het bebossen van baggergronden aan de hand van enkele invertebratengroepen. Scriptie voorgelegd tot het behalen van de graad van Licentiaat in de Biologie (richting dierkunde). Academiejaar 2000, Gent: Universiteit Gent.
124. Schouteden H (1901) Résultat de ses chasses faites le 14 avril lors de l'excursion de la Société à Samson. Annales de la Société d'Entomologie de Belgique 45: 163-164.
125. Segers S (2015) Eenvoudig landpissebedden determineren [Zoekkaart]. Spinicornis, i.s.m. JNM vzw, Gent, 4 pp.
126. Senden L (1936) Bewoners van krotten en achterbuurten. Uitgeverij De Standaard, 89-102.
127. Swiecicka I, Mahillon J (2006) Diversity of commensal Bacillus cereus sensu lato isolated from the common sow bug (Porcellio scaber, Isopoda). FEMS microbiology ecology 56(1): 132-140.
128. Tavernier JM (1981) Isopoda. In: Guillemijn B, van den Bremt P (Eds) Het Honegemgebied te Erpe-Mere, Lede en Aalst Documentatiemap Landschapsonderzoek Rijksdienst voor Monumenten- en Landschapsonderzoek 3. 63-82.
129. Tavernier JM, Kerwyn Ch (1982) Een woordje over de fauna die omgewaaide populieren in elzenbroeken kunnen herbergen. 't Koninkje 11(1): 43-46.
130. Tavernier JM, Wouters K (1986) De havenpissebed Ligia oceanica (Linnaeus, 1758), in België. De Wielewaal 52: 100-102.
131. Tavernier JM, Wouters K (1989) Check-list of the terrestrial lsopoda (Crustacea) of Belgium. In: Wouters K, Baert L (Eds) lnvertebraten van België - lnvertébrés de Belgique, Proceedings of the Symposium "Invertebrates of Belgium". Brussels, 169-172.
132. Tavernier JM, Wouters K (1991) Check-list and distribution of terrestrial lsopoda (Crustacea) of Belgium. Biology of Terrestrial lsopods. Third International Symposium. Poitiers, 35-37 pp.

133. Troubleyn L, Kinnaer F, Ervynck A, Beeckmans L, Caluwé D, Cooremans B, De Buyser F, Deforce K, Desender K, Lentacker A (2009) Consumption patterns and living conditions inside Het Steen, the late medieval prison of Malines (Mechelen, Belgium). Journal of Archaeology in the Low Countries 1-2: 5-47.
134. Van Beneden PJ (1861) Recherches sur les crustacés du littoral de Belgique. Mémoires de l' Academie royale des Sciences, des Lettres et des Beaux-Arts 33: 1-174.
135. Van De Vyver E (2009) Populatie- en ecosysteemeffecten van metaalverontreiniging in baggergronden en enkele Kempische bossen. Gent: Universiteit Gent.
136. Van Gompel J, Rabaut K (1976) Golfbrekeronderzoek te Blankenberge. Tuimelaar 3(3): 7-8.
137. Vandekerckhove T, Watteyne S, Bonne W, Vanacker D, Devaere S, Rumes B, Maelfait JP, Gillis M, Swings J, Braig HR, Mertens J (2003) Evolutionary trends in feminization and intersexuality in woodlice (Crustacea, Isopoda) infected with Wolbachia pipientis (alpha-Proteobacteria). Belgian journal of zoology 133(1): 61-69.
138. Vandel A (1933) Liste des espèces de Trichoniscidae signalées jusqu'ici en France. Archives de zoologie expérimentale et générale 75: 35-54.
139. Vandel A (1952) Isopodes terrestres (Troisième série). Archives de zoologie expérimentale et générale 88: 232-262.
140. Vandepitte L, Decock W, Mees J (2010) Belgian Register of Marine Species, compiled and validated by the VLIZ Belgian Marine Species Consortium. Vlaams Instituut voor de Zee (VLIZ), Oostende, 78 pp.
141. Verhoeff KW (1937) Ueber eine angeblich neue Isopoden-Familie. Zoologischer Anzeiger 118: 173-176.
142. Wouters K, Tavernier JM, Meurisse L (2000) Distribution and bibliography of the terrestrial Isopoda (Crustacea) of Belgium. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 70: 193-205.

Oniscus asellus | Gert Arijs

Chapter 3

ARTHROPOD DETRITIVORES IN FOREST EDGES

Complementary distribution patterns of arthropod detritivores (woodlice and millipedes) along forest edge-to-interior gradients

Adapted from: De Smedt P, Wuyts K, Baeten L, De Schrijver A, Proesmans W, De Frenne P, Ampoorter E, Remy E, Gijbels M, Hermy M, Bonte D, Verheyen K (2016) Complementary distribution patterns of arthropod detritivores (woodlice and millipedes) along forest edge-to-interior gradients. Insect Conservation and Diversity 9: 456-469

Abstract

Worldwide, forest fragmentation induces edge effects, thereby strongly altering the forest microclimate and abiotic characteristics in the forest edge compared to the forest interior.

The impact of edge-to-interior gradients on abiotic parameters has been extensively studied, but we lack insights on how biodiversity, and soil communities in particular, are structured along these gradients.

Woodlice (*Isopoda*) and millipedes (*Diplopoda*) are dominant macro-detritivores in temperate forests with acidic sandy soils. We investigated the distribution of these macro-detritivores along forest edge-to-interior gradients in six different forest stands with sandy soils in Northern Belgium. Woodlouse abundance decreased exponentially with distance from the forest edge, while millipede abundance did not begin to decrease until seven meters inside the forest stands. Overall, these patterns were highly species specific and could be linked to the species' desiccation tolerance. While the observed abundance patterns were independent from forest stand and dominant tree species, tree species had a large effect on community structure.

Edge gradients in macro-detritivores may consequently have implications for nutrient cycling, especially in smaller forest fragments with a large edge-to-interior ratio.

Introduction

Forest habitats are profoundly fragmented around the world (Wade et al. 2003). Such fragmentation induces a reduction in forest fragment sizes and strengthens edge effects (Janzen 1986, Reed et al. 1996, Gascon et al. 2000, Harper et al. 2005, Fletcher et al. 2007, Echeverria et al. 2008). Forest edges are characterised by enhanced light availability (Delgado et al. 2007), higher wind speeds (Wuyts et al. 2008a), higher air and soil temperatures (Delgado et al. 2007, Heithecker & Halpern 2007), and lower relative humidity and soil moisture (Chen et al. 1995, Gehlhausen et al. 2000). They are also relative 'hotspots' for the deposition of eutrophying and acidifying atmospheric pollutants (Weathers et al. 2001, Wuyts et al. 2008b,c), compared to the forest interior. The magnitude and depth of influence of these edge effects are strongly affected by the structure and composition of the edge itself (Weathers et al. 2001, Wuyts et al. 2008b,c). These abiotic edge gradients then give rise to secondary effects on biotic effects at the edge of forest ecosystems (Murcia 1995, Harper et al. 2005).

Soil macro-invertebrates are dominant detritivores in temperate forests, which break down dead organic material (Lavelle 1997), thus affecting the physico-chemical characteristics of soil (Snyder & Hendrix 2008). By reducing the size of dead organic material on the forest floor (Anderson 1988, Grelle et al. 2000), they increase the accessible surface area for further decomposition by microbes (Harper et al. 2005). This results in a more stable soil organic matter layer (Wolters 2000). The transformation of fallen leaves into macro-detritivore faeces also has strong effects on the microbial response and consequently on the breakdown of the leaf material (Joly et al. 2015). Exclusion of these soil macro-arthropods slows down decomposition rates (Riutta et al. 2012, Slade & Riutta 2012), and their presence is therefore of vital importance for nutrient cycling in forest ecosystems. The distribution of macro-arthropods, such as woodlice and millipedes, within forests is highly scattered (Hornung 2011) and aggregated towards forest edges (Riutta et al. 2012). The occurrence of abiotic edge effects raises the question of whether the response from macro-arthropods also varies gradually as the forest edge is approached, and whether this is reflected in the accumulation of forest floor material. Yet our understanding of how biotic factors, such as different taxonomic groups of the soil fauna community, change along edge-to-interior gradients and how this could affect the litter decomposition process is extremely limited (Hättenschwiler et al. 2005). Temperature and humidity are important, and highly species specific, environmental triggers for survival and distribution of macro-detritivores (Warburg 1964, Haacker 1968, Meyer & Eisenbeis 1985, Dias et al. 2013). On the other hand, the spatial distribution of detritivores is also strongly influenced by soil acidity and exchangeable base cations (Kime 1992, Van Straalen & Verhoef 1997), as well as food quality (C/N-ratio) (Hassall et al. 2002, David & Handa 2010, Gerlach et al. 2014). These environmental parameters vary strongly along edge-to-interior gradients, and we would therefore expect species distribution patterns to be highly influenced by distance from the forest edge. However, detailed empirical data that could be used to investigate these patterns is, to our knowledge, very scarce.

In Northern Belgium, where forests are strongly fragmented, we investigated the distribution patterns of woodlice and millipedes in transects that stretched from the forest edge towards the forest interior, for several different forest stands (De Schrijver et al. 2007). On these acidic sandy forest soils, earthworms are very scarce or even absent (Muys & Lust 1992), and therefore woodlice and millipedes are the major macro-detritivore groups (Jeffery et al. 2010). Based on our knowledge of abiotic edge effects and macro-detritivore communities, we put forward the following hypotheses about the influence of edge effects on woodlouse and millipede distribution:

1. More favourable environmental conditions (higher temperatures and higher litter quality) at the forest edge will result in a higher abundance of macro-detritivores at this boundary, with abundance steadily declining towards interiors. If true, we expect the mass of the ectorganic horizon to show the inverse trend due to increasing rates of decomposition from the interior to the forest edge.
2. The response of macro-detritivores to edge proximity is species specific, since each species exhibits different temperature and humidity preferences.
3. Responses of detritivores to forest edge proximity can be related to changes in relevant abiotic parameters (i.e. food quality, cation content of the soil, etc.).

Methods

Site description

We selected six forest stands in the northern part of Belgium, located on poor, acidic, well-drained quartz-dominated sandy soils (Haplic podzols) of the Campine and Sandy region. The soils were quartz-dominated with a large share of relatively large particles (1.0-0.1 mm) and a well developed E-horizon (eluviated). This horizon has significantly been leached from minerals and organic content, leaving a poor and grey-coloured layer. All were recently created forests, formerly managed as heathlands until 80-90 years ago. This heathland management practice resulted in a significant depletion of soil nutrients through sheep grazing and turf cutting on these already naturally nutrient-poor soils. After some years of abandonment, the sites were afforested with monocultures of pedunculate oak (*Quercus robur* L.; stands Q1 and Q2), silver birch (*Betula pendula* Roth.; stands B1 and B2), Corsican pine (*Pinus nigra* ssp. *laricio* Maire; stand P1) or Austrian pine (*P. nigra* ssp. *nigra* Arnold; stand P2) (Table 3.1). The stands all had an abrupt forest edge, i.e. they lacked a gradual transition with the adjacent open land, and were always oriented towards the southwest, perpendicular to the prevailing wind direction. All were located in the periphery of forest complexes, within a fragmented landscape dominated by agriculture and intensive livestock breeding. Forest edges were bordered by grass pasture, extensively managed meadow (B1, Q1 and P2), or by arable land (B2, Q2 and P1). A road with roadside verges (~20 m in total) was present between the grassland or arable land and the forest edge of stands Q1 and Q2. The stands bordering arable land could have been exposed to drift of lime or fertilizer from agricultural applications. Understorey vegetation was absent in all stands except for (i) brambles (*Rubus fruticosus* agg.), which occurred in the first 20 m from the edge in Q1 and further than 50 m from the edge in P1 and (ii) creeping soft grass (*Holcus mollis* L.), which was present in the first 10 m from the edge in both P1 and P2. No significant quantity of coarse woody debris was present in the stands. The edge patterns of soil nitrogen leaching, soil acidification, litter and soil chemistry, stand structure, and the atmospheric deposition of nitrogen, acidifying ions and base cations in the studied forests were previously described by Wuyts et al. (2008b,c, 2011, 2013).

Table 3.1. *Overview of the forest interior characteristics of the six investigated forest stands. After the municipality also the province is presented: AN (Antwerp) and W-FL (West-Flanders).*

Stand	**Municipality**	**Dominant tree species**	**Other species***	**Age (y)**	**Soil pH(KCl)**
Q1	Ravels (AN)	*Quercus robur* L.	*Alnus glutinosa* L. *Sorbus aucuparia* L.	74	2.88
Q2	Waregem (W-FL)	*Quercus robur* L.	*Alnus glutinosa* L. *Prunus serotina* Erhr. *Sorbus aucuparia* L	96	3.35
B1	Ravels (AN)	*Betula pendula* Roth	*Pinus nigra* ssp. *laricio* Maire *Larix* spec. Mill.	35	3.40
B2	Zedelgem (W-FL)	*Betula pendula* Roth	*Quercus robur* L. *Sorbus aucuparia* L.	36-46	2.93
P1	Ravels (AN)	*Pinus nigra* ssp. *nigra* Arnold	*Sorbus aucuparia* L.	49	2.89
P2	Zedelgem (W-FL)	*Pinus nigra* ssp. *laricio* Maire	*Betula pendula* Roth *Quercus robur* L. *Sorbus aucuparia* L.	71	2.91

*subdominant, in the shrub layer.

Experimental set-up and sampling

In each of the forest stands, a transect was laid out perpendicular to the forest edge and heading towards the forest interior. Along each transect, samples were taken at 0, 2, 4, 8, 16, 32, 64 and 128 m from the forest edge. No samples could be taken at 128 m in the birch stands due to their smaller size. According to Murcia (1995) and De Schrijver et al. (2007), edge effects are negligible at distances greater than 50 m from the forest edge, so we assumed distances of 64 m and 128 m to be representative of the forest interior. At every distance, three samples of the ectorganic layer (including the litter, fermentation and humus layer) were taken, with a spacing of about 5 m from each other. Samples were collected in plastic bags. We used a wooden frame (25 cm x 25 cm) to cut out the ectorganic layer. All forests were sampled once between 12 July 2011 and 12 August 2011, before the peak litterfall period. While July 2011 was rather dry and cold, weather conditions in August 2011 were normal in the context of the previous ten years.

Dry mass of the ectorganic horizon was determined after removing the arthropods (see further) and drying the samples at 70°C for two days. No specific sampling was performed on decaying wood due to the lack of coarse woody debris. Fine woody debris was included in the ectorganic samples.

The samples were visually inspected for macro-arthropods in the lab within one day after collection, and the found organisms were removed and stored in 70% ethanol. Immediately following the visual inspection, an ectorganic horizon subsample was taken (± 500 cm^3) and transferred into a Berlese-Tullgren funnel for seven days to collect any remaining organisms. Once complete, collected arthropods were again stored in 70% ethanol, and the dry mass of the ectorganic horizon subsample was determined after drying as described previously. Afterwards, the abundance data of the Berlese-Tullgren subsamples were converted to sample level by multiplying arthropod abundance data with the total dry mass of the sample, divided by the dry mass of the subsample. The total abundance of woodlice and millipedes (numbers per square meter) was determined as the sum of both the visual counts and the converted data from the Berlese-Tullgren subsamples. The collected woodlice and millipedes were identified to the species level according to Berg & Wijnhoven (1997) and Andersson et al. (2005), respectively. We are aware that summer sampling is biased towards larger species since many small species retreat deeper into the soil during this period (Gregory 2009).

The fermentation and humus layer of the forest floor, as well as the upper 5 cm of the mineral soil, were sampled for chemical analyses in previous studies. This sampling campaign was carried out for all stands and at all sampling distances, and the pH(KCl) of the upper mineral soil is available at all of these locations (Wuyts et al. 2008b, 2013). In addition, the following data, described by Wuyts et al. (2011, 2013), is available for all stands except B1: (i) potassium (K), calcium (Ca), magnesium (Mg), carbon (C) and nitrogen (N) concentration in the ectorganic horizon; (ii) exchangeable amounts of K, Ca, Mg and aluminium (Al) (subsequent to a $BaCl_2$ extraction); and (iii) C and N concentration in the upper mineral soil (0-5 cm depth).For stand B1, only data on the C and N concentration of the forest floor were available (Wuyts et al. 2008b).

Late summer leaf area index (LAI) was measured at all sampling distances in previous studies (Wuyts et al. 2008b,c). LAI is used as a measure of light in the forest and is a crucial factor for woodlouse and millipede behaviour, since they are mostly night active and negative phototactic (they move away from light) (Sutton 1972, Hopkin & Read 1992). The LAI in stand B1 was determined using the LAI-2000 Plant Canopy Analyzer in August 2004. For all other stands, digital hemispherical photographs, taken in August-September 2006 and processed with Gap Light Analyzer 2.0, were used (www.caryinstitute.org). Although LAI measurements and chemical analyses were performed seven and five years prior to the arthropod collection, no major disturbances in the canopy (i.e. forest management, storm damage, insect damage, etc.) occurred, and therefore we considered the values as representative of the current situation in the studied forests.

Data analysis

Abundance patterns along forest edge-to-interior gradients were not expected to show linear relationships, and were therefore modelled with generalised additive models (GAM), using the *gam*-function in the *mgcv*-package in R 3.2.2 (Wood 2006, R Core Team 2015). Abundance values used in the models were calculated for each stand as the sum of the three samples taken at each sampling distance. By comparing three models of increasing complexity, we sequentially tested how the macro-detritivore abundances (dependent variable) were affected by taxonomic group, distance from the forest edge and taxonomic group-specific distance effects (predictor variables). First, a model with taxonomic group as the predictor variable tested differences in mean abundance between woodlice and millipedes. Second, log(distance+1) was added as a predictor variable to test how abundance changes from forest edge to interior. Because abundance does not change in a linear way along the edge-to-interior gradient, we modelled it using a smooth function of the distance predictor variable. Smooth functions are useful for this application because they can be used to model a wide range of trends. Finally, we allowed the distance effects to vary per taxonomic group (woodlice and millipedes); that is, each taxonomic group was allowed to have a different distribution pattern from edge to interior. The models were compared using an analysis of deviance table to successively test the significance of each of the predictor variables. An F test statistic was used to test the change in deviance across the three models. Tree species or stand may also have an influence on woodlouse and millipede abundance patterns from edge to interior. This was tested for each taxonomic group separately, by comparing (via change in deviance) models that allowed the distance effect to vary between the six stands or between the three tree species (oak, birch, pine; two stands each). We used the same methods to analyse differences in species richness of woodlice and millipedes as well as mass of the ectorganic horizon. Species-specific distance effects were tested for species with more than 50 individuals in the data set. Again, we used GAM-models with log(distance+1) as the main effect to test how species' abundances change from forest edge to interior. Although it would be interesting to further test whether species-specific abundance patterns differ between stands with different dominant tree species, individual macro-detritivore species did not generally occur in sufficient numbers in each of the stands to make this possible. The species-specific graphs for woodlice were ordered according to the desiccation resistance of the species, based on the experiments by Dias et al. (2013). For millipedes, this data has not yet been published, but the ordering was done after personal communication with M.P. Berg, who is measuring desiccation tolerance on millipedes using the same method as Dias et al. (2013).

In order to test the effect of distance from the forest edge, tree species and forest stand on the community structure of woodlice, millipedes and the two groups combined, we used the Bray-Curtis distance measure to calculate compositional dissimilarities between sampling locations with different distances from the forest edge, between different dominant tree species and between forest stands. This metric quantifies compositional variation driven by both compositional differences (i.e. different species are present) as well as differences in relative abundances (Anderson et al. 2006). A log(distance+1), tree species and stand effect was fitted using a permutational multivariate analysis of variance with 999 permutations (PERMANOVA; function *adonis* in the *vegan*-package) (Oksanen et al. 2015). We ran all models with only one explanatory variable at a time in order to have a proper comparison between the different variables. However, as PERMANOVA confounds location (compositional dissimilarities between groups) and dispersion effects (compositional dissimilarities within groups) (Anderson 2001, Warton et al. 2012), we tested separately for multivariate homogeneity of dispersions between groups using the function *betadisper* (*vegan*-package; centroid analysis). This is a multivariate analogue of Levene's test for homogeneity of variances (Anderson et al. 2006). If multivariate dispersion is significant, PERMANOVA results must be handled with care since we cannot distinguish between dissimilarities between and within groups.

Lastly, a principal component analysis was performed using the *vegan*-package (Oksanen et al. 2015), with woodlouse and millipede species abundances at different plots as response variables. Environmental variables significantly correlated with the ordination of the plots were afterwards plotted on the ordination diagram. The environmental variables used in the correlation analysis were LAI, mineral topsoil and ectorganic horizon variables. Environmental variables were retained after stepwise exclusion with variance inflation factors higher than 10. Four variables were retained and their relation to distance from the forest edge was analysed according to the same statistical methods used for the arthropod analyses.

Results

We found six woodlouse species belonging to five different families, and ten millipede species belonging to six different families (Table 3.2, on the right).The dominant woodlouse species were *Porcellio scaber* (56.7% of individuals) and *Philoscia muscorum* (22.1%). The dominant millipede species was *Proteroiulus fuscus* (32.7%).

Detritivore abundance patterns and trends in mass of the ectorganic horizon

The overall abundance of woodlice did not differ from that of millipedes (model with versus without effect of taxonomic group: t = 1.598, P = 0.111). However, the effect of distance was significant (model with versus without distance effect; F = 20.634, P < 0.001) and was also significantly different for the two taxonomic groups (with or without different distance effect per taxonomic group; F = 10.58, P < 0.01). Indeed, the total abundance of woodlice steeply decreased from the forest edge towards the forest interior, while the abundance of millipedes did not begin to decrease until about 7 meters inside the forest stands (Fig. 3.1). The abundance of woodlice (326 ind. m^{-2}) and millipedes (36 ind. m^{-2}) differed significantly at the forest edge (Intercept, t= 26.67, p<0.001), with higher abundances of woodlice compared to millipedes (Fig. 3.1a). The same patterns were found for species richness of woodlice and millipedes; that is, average species richness was the same (Intercept, t = 1.656, P = 0.099), but species richness of woodlice (1.96 ± 0.22) was higher at the forest edge compared to millipedes (1.14 ± 0.22) (Intercept, t= 9.901, p<0.001). Distance to the forest edge had a significant effect on species richness (F = 16.492, P < 0.001) and was also different for the two taxonomic groups (F = 5.5612, P = 0.019). As can be seen in Figure 3.1 (page 62), species richness (Fig. 3.1b) and abundance (Fig. 3.1a) show similar patterns with distance from the forest edge. We therefore focus further analysis on abundance patterns.

Table 3.2. *Species list, with their family, abbreviation (Abb.) and relative occurrence within their taxonomic group. Nomenclature follows Berg et al. (2008).*

Species	Family	Abb.	Rel. occurrence (%)
Woodlice			
Porcellio scaber Latreille, 1804	Porcellionidae	PORCSCAB	56.7
Philoscia muscorum (Scopoli, 1763)	Philosciidae	PHILMUSC	22.1
Oniscus asellus Linnaeus, 1758	Oniscidae	ONISASEL	8.2
Haplophthalmus danicus Budde-Lund, 1880	Trichoniscidae	HAPLDANI	6.9
Trichoniscus pusillus s.l.	Trichoniscidae	TRICPUSI	6.0
Ligidium hypnorum (Cuvier, 1792)	Ligiidae	LIGIHYPN	0.1
Millipedes			
Proteroiulus fuscus (Am Stein 1857)	Blaniulidae	PROTFUSC	32.7
Cylindroiulus punctatus (Leach 1815)	Julidae	CYLIPUNC	16.9
Glomeris marginata (Villers 1789)	Glomeridae	GLOMMARG	12.0
Polydesmus denticulatus C.L. Koch 1847	Polydesmidae	POLYDENT	11.1
Craspedosoma rawlinsii Leach 1814	Craspedosomatidae	CRASRAWL	4.0
Melogona spec.	Chordeumatidae	MELOSPEC	2.0
Julus scandinavius Latzel 1884	Julidae	JULUSCAN	1.9
Ommatoiulus sabulosus (Linnaeus 1758)	Julidae	OMMASABU	0.5
Chordeuma sylvestre C.L. Koch 1847	Chordeumatidae	CHORSYLV	0.3
Leptoiulus belgicus (Latzel 1884)	Julidae	LEPTBELG	0.1
Millipede spec. juvenile	/	MILLIJUV	18.5

Abundance patterns of both woodlice and millipedes varied considerably between stands (woodlice: F = 42.40, P <0.001; millipedes: F = 5.717, P < 0.01) (see also Appendix 3.1). In the case of woodlice, they varied in a consistent way between stands dominated by different tree species (F = 37.45, P < 0.001), but millipede abundance patterns were not consistent between the different tree species (F = 3.245, P = 0.072) (Fig. 3.2b). In fact, only three out of six stands showed patterns resembling the overall trend for millipedes (Fig. 3.1a).

However, it should be noted that the fitted lines were only significant for oak stands in the millipede data ($p<0.01$). For woodlice, fitted lines were significant for all forest stands ($p<0.001$) (Fig. 3.2a, p. 63).

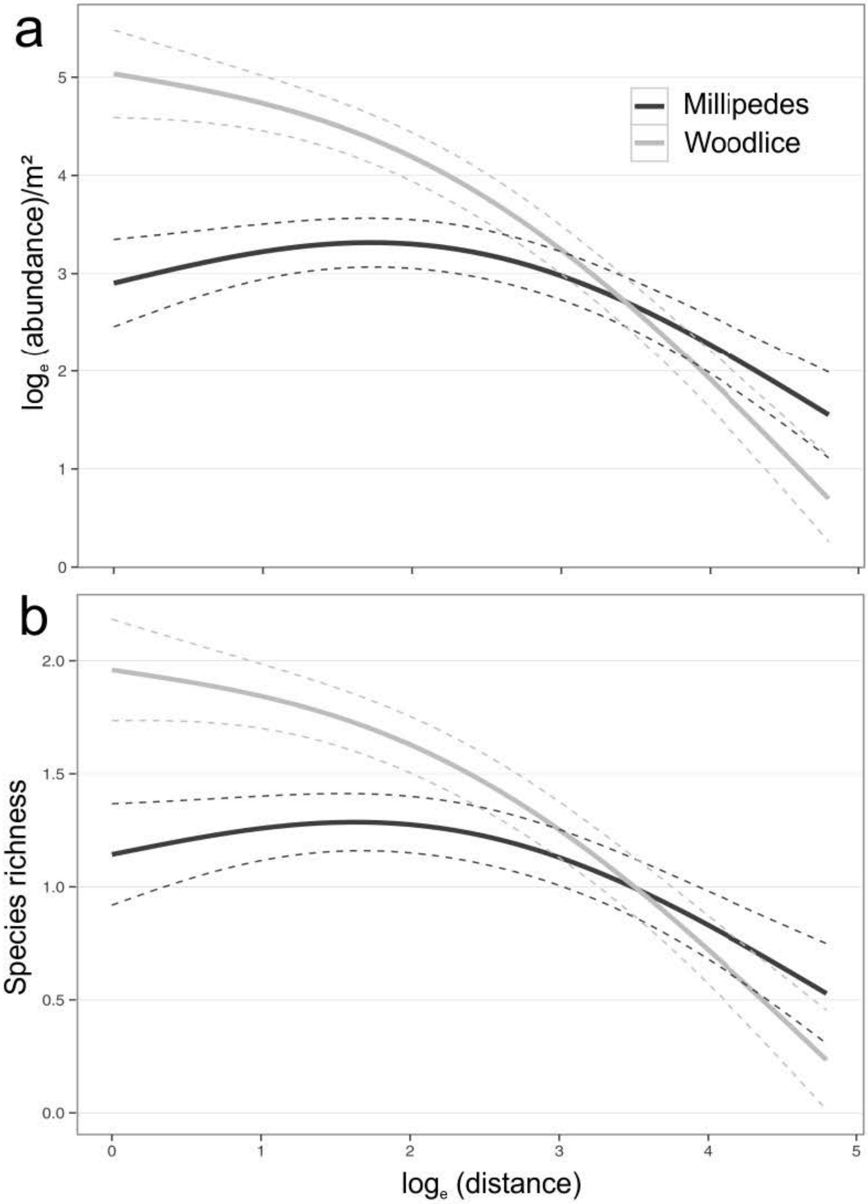


Figure 3.1. *Modelled abundance (ln-transformed) (a) and species richness (b) of woodlice and millipedes versus distance from the forest edge (ln-transformed) across all stands. Dotted lines denote ± 1*standard error.*

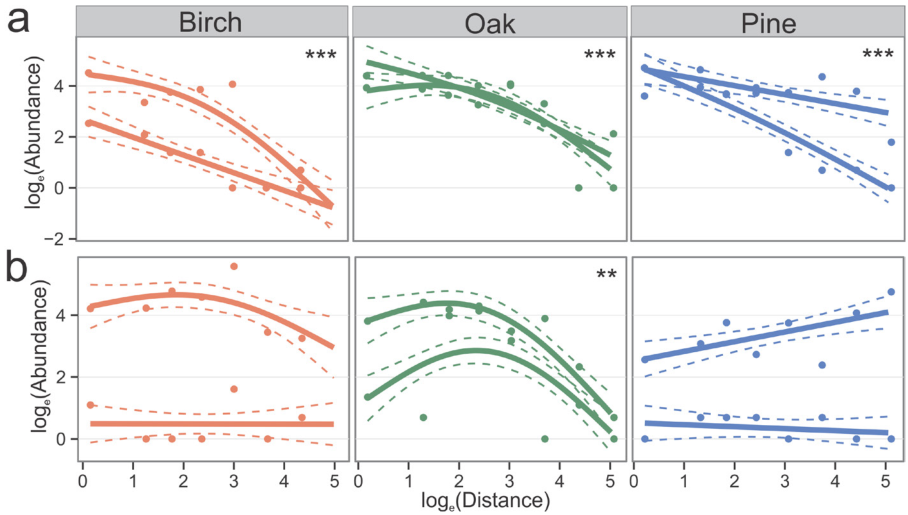


Figure 3.2. *Modelled abundance (ln-transformed) of woodlice (a) and millipedes (b) versus distance from the forest edge (ln-transformed) for six forest stands (solid lines, 2 per tree species) and three dominant tree species (Birch, Oak, Pine), with dots showing the actual data points. Dotted lines denote ± 1*standard error. Significant tree species effects are indicated with asterisks. Significance levels: **: $P < 0.01$, ***: $P < 0.001$.*

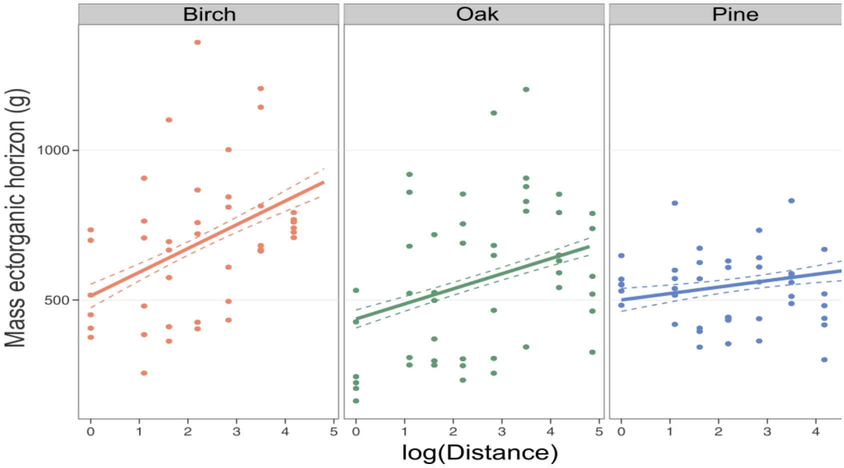


Figure 3.3. *Modelled mass of the ectorganic horizon versus distance from the forest edge (ln-transformed) for the tree dominant tree species (solid lines), with dots showing the actual data points. Dotted lines denote ± 1*standard error. All fitted lines contributed significantly to the model ($p<0.05$).*

The mass of the ectorganic horizon was significantly influenced by distance from the forest edge (F=6.333, p<0.05) and tree species (F=8.555, p<0.001) (Fig. 3.3), while no differences between stands (F=1.111, p>0.05) was found. For all stands, we found an increase in ectorganic horizon mass going from the forest edge towards the forest interior (Fig. 3.3).

Species-specific patterns

Species-specific distance-to-edge models were fitted for a total of five woodlouse species and five millipede species (Fig. 3.4). The fitted lines in this sequence reveal an interesting pattern for woodlice (Fig. 3.4a). Species such as *Haplophthalmus danicus*, or even *Trichoniscus pusillus* and *O. asellus*, which have low desiccation tolerances, are actually more abundant a certain distance away from the forest edge than they are at the edge itself, while species with high desiccation tolerance decrease exponentially with distance from the forest edge. The species with the highest desiccation tolerances show the strongest decreases. The same analysis was done for millipedes, but the observed patterns are less clear (Fig. 3.4b). In general, most millipedes show a slower decrease compared to woodlouse species, although the very drought tolerant millipede *Glomeris marginata* shows a very strong decrease after moving further than 16 m into the forest stand. While the trends for individual millipede species vary considerably, the significant trend for all millipedes (Fig. 3.1a) resembles the species-specific response of the most abundant millipede in the dataset: *P. fuscus*.

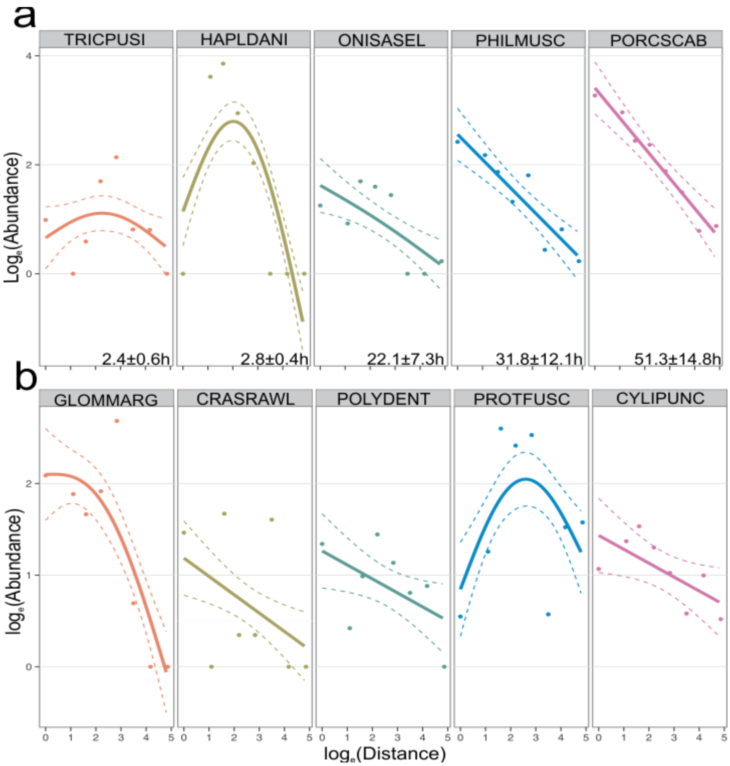


Figure 3.4 (previous page). *Abundance (ln-transformed) of woodlouse (a) and millipede (b) species versus distance from the forest edge (ln-transformed), showing modelled (solid lines) and actual data points (dots). Dotted lines denote ± 1*standard error. Species were ordered from left to right according to increasing desiccation resistance at 85% relative humidity (average survival time, in hours) (Dias et al. (2013)). Millipedes were ordered based on yet unpublished data, using the same methods as for woodlice (pers. comm. M.P. Berg).*

Community structure of species along edge-to-interior gradients

Community structure of woodlice and millipedes was most significantly affected by stand, with around 25% of the variation in community structure explained by stand alone (Table 3.3). For both taxa combined (woodlice + millipedes), the variance explained by stand was 22.5%. Tree species also explained a large percentage of the variation in community structure of woodlice (11.9%), millipedes (11.2%) and both groups combined (9.5%). Distance only explained a minor part of community variation, with 3.16% for woodlice and 3.64% for both groups combined. For millipedes, distance did not contribute significantly to the observed variation in community structure. However, the multivariate dispersion of some of the community data was significantly heterogeneous in relation to distance (woodlice + millipedes), tree species (millipedes and woodlice + millipedes) and stand (woodlice, millipedes and woodlice + millipedes) (Table 3.3). Hence, variation in community structure across stands results from both effective changes in community composition and dispersion (difference in average distance to group centre between tested groups).

Table 3.3. *Results of a permutational analysis of variance, relating the variation in community structure of woodlice and millipede communities to distance ($\log_e$), tree species and stand. Results show percentage of variance explained and p-values of the assumed location effect. P-value dispersion effect represents the p-value for the multivariate homogeneity of dispersions test. Significance levels: *: P < 0.05, **: P < 0.01, ***: P < 0.001, NS: P > 0.0.5.*

		% var. explained	*p-value location effect*	*p-value dispersion effect*
Woodlice	Distance	3.16	*	NS
	Tree species	11.9	***	NS
	Stand	24.5	***	**
Millipedes	Distance	2.48	NS	NS
	Tree species	11.2	***	**
	Stand	25.2	***	***
Woodlice + Millipedes	Distance	3.64	***	*
	Tree species	9.53	***	***
	Stand	22.5	***	*

In the principal component analysis (Fig. 3.5, below), variables with variance inflation factors higher than ten were excluded. The results showed that species of woodlice and millipedes have higher abundances at higher pH values, higher Mg content and lower C/N ratio of the forest floor litter (Fig. 3.5). They are less correlated to LAI, except for the woodlouse *P. scaber*, whose abundances are not highly correlated to any other species or environmental driver but are closely linked to LAI. In the lower part of the graph, species with low desiccation resistance, such as the woodlice *H. danicus* and *T. pusillus* and the millipede *Craspedosoma rawlinsii* , cluster together, but also the more drought tolerant *G. marginata* is found in this corner. Differences among tree species are mostly shown along the second axis, from higher to lower: Pine, Oak and Birch. This axis is also almost perfectly followed by the very common woodlouse *P. scaber*, which was the only abundant woodlouse in the pine stands, though the millipede *P. fuscus* was also very abundant there. Oak stands cover a wide range (Fig. 3.5) since all species (except the millipede *Leptoiulus belgicus*) were present in these stands (see also supplementary material 1).

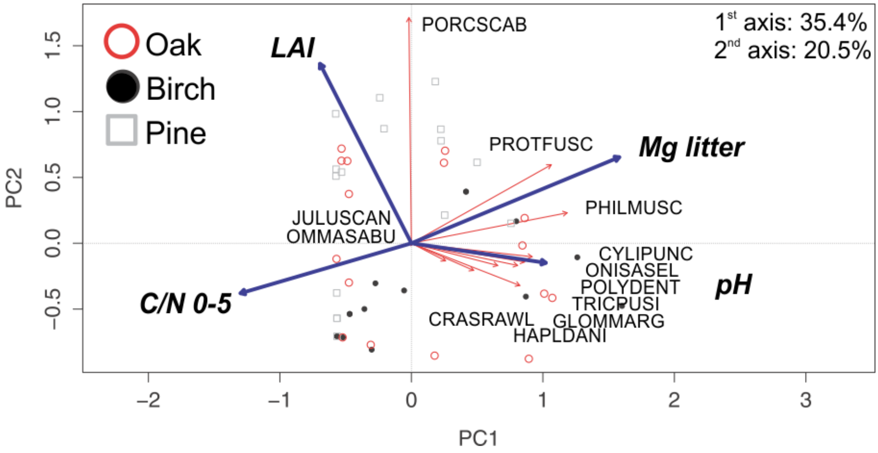


Figure 3.5. *PCA of arthropod detritivores distribution patterns and related variables along a forest edge-to-interior gradient. Symbols (further described in figure) represent dominant tree species. Normal arrows represent woodlouse and millipede species. Bold arrows represent environmental variables: pH: pH(KCl) of mineral topsoil, Mg litter: Mg-concentration of the ectorganic horizon, C/N 0-5: C/N-ratio of mineral topsoil, LAI: Leaf Area Index in August. Percentage of variation explained by the first and second axis is indicated in the figure. Only species occurring in at least 3 samples across all distances and stands are presented.*

Models of pH, C/N, Mg and LAI were all significantly influenced by distance from the forest edge ($p<0.05$): pH, Mg and LAI decreased with increasing distance, while C/N-ratio of the mineral top soil increased (Fig. 3.6, next page).

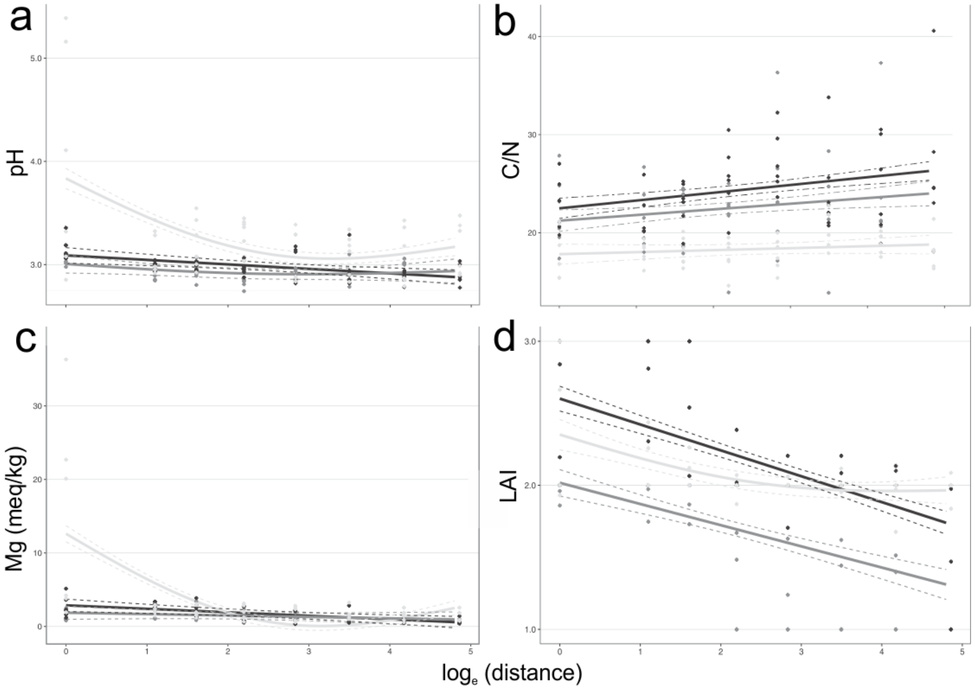


Figure 3.6. *Models of environmental variables (solid lines) significantly related to community composition, (as determined by PCA)versus distance (ln-transformed) from the forest edge, with dots showing the actual data points. Black lines and dots represent birch stands, light grey are oak stands and dark grey lines are pine stands. Subplots show (a) pHKCl of the mineral topsoil, (b) C/N-ratio of mineral topsoil, (c) Mg-concentration of the ectorganic horizon, (d) Leaf Area Index in August. For all four variables, distance contributed significantly to the model. Dotted lines denote ± 1*standard error. Data has already been published in previous studies by Wuyts et al. (2008b,c; 2011, 2013).*

Discussion

Arthropod detritivore abundances and species richness

Patterns of abundance of woodlice and millipedes differed as one moved from the edge to the interior of the forests. Woodlouse numbers were up to 40 times higher at the forest edge relative to the forest interior, while millipede numbers only began to decrease after a certain distance from the forest edge. Riutta et al. (2012) also found more woodlice in forest edges (7m) compared to forest interiors (107m) but did not find a difference in millipede abundance in woodlots in the UK. The community composition for woodlice was almost the same as in our study; however, millipede community composition was different, making it difficult to compare the results. Tajovský et al. (2012) found higher abundances of woodlice in smaller forest fragments (up to 0.8ha) compared to larger ones (>4.5 ha). The maximum distance to an edge in the small fragments was only 50 m, and therefore the observed relationship between woodlouse numbers and forest size could be attributed to a shorter distance to the forest edge.

While millipede species richness did not change along the studied gradient, the number of woodlouse species decreased towards the forest interior. While no such trend was found by Riutta et al. (2012) in the UK, the observed pattern is similar to the one found for total abundance and reaffirms that forest edges provide more optimal conditions for woodlice. A potential explanation is that higher productivity (i.e. higher growth rates of trees and understory; Harper et al. 2005), more niche diversity (through a more complex structure of the understory; Harper et al. 2005) and a higher herb species richness (especially in stands with fewer tree species; Normann et al. 2016) at the edge allows for the coexistence of more species, thereby resulting in larger total abundances. A higher litter production (Vasconcelos & Luizão 2004) and LAI (Beier & Gundersen 1989, Wuyts et al. 2008b) at the forest edge relative to the interior has also been reported but is not reflected in the dry mass of the ectorganic horizon in our study. So, although one would expect higher litter input where the LAI is higher, in deciduous forests (Jonckheere et al. 2004), at least, this effect does not seem to be translated into a larger litter build-up. We attribute this to the higher abundances and functionality of macro-detritivores in forest edges. Many studies indeed demonstrated a faster rate of decomposition when macro-detritivores are present (Wolters 2000, Vasconcelos & Luizão 2004, Hättenschwiler et al. 2005, Riutta et al. 2012, Slade & Riutta 2012).

Species-specific responses

Considering edge responses at the species level reveals highly species-specific patterns. In general, the abundance of species with high desiccation resistance declined more strongly along edge-to-interior gradients, and small species with very low desiccation resistance found optimal conditions deeper inside the forest, with some even showing what appears to be a maximum abundance a few meters inside the forest stand. Dias et al. (2013) also suggested that a negative relation between site moisture (lower at forest edges) and body size could reduce the relative abundance of smaller species (such as *H. danicus* and *T. pusillus*). However, these species are known to move deeper into the soil during summer because of drier conditions and thus show behavioural adaptive responses rather than physiological ones (own observations, Gregory 2009). Based on our sampling scheme, it is difficult to investigate whether the lower abundances at the forest edge are real or due to movement into the soil.

The maximum in the overall millipede abundance at intermediate distances from the edge can be attributed to the presence of *P. fuscus.* This typical forest species withstands acidic environments (Berg et al. 2008), which could explain why it was the most common species in our study on acidic sandy soils. Although *P. fuscus* seems to have a peak in abundance at about 14 m inside the forest (and thus resembles the pattern shown by woodlouse species with low drought tolerance), it has been reported to have a broad ecological amplitude towards humidity (Berg et al. 2008). The other millipede species showed an exponential decrease in abundance in moving towards the centre of the forests, similar to the responses observed for most woodlouse species. *G. marginata* was the exception, showing no changes in abundance at distances smaller than 15 m from the forest edge. This is likely the result of the species' ability to withstand very dry conditions by folding its body into a sphere to conserve moisture. The abundance of this drought tolerant species decreases strongly from 15 m onwards, similarly to the responses of the more drought tolerant woodlouse species. Drought tolerance thus appears to be an important trait in determining the distribution of arthropod detritivores along edge-to-interior gradients.

Soil moisture, temperature and leaf litter quality are of uttermost importance for the abundance and activity of woodlice and millipedes (Warburg 1964, Hopkin & Read 1992, David & Handa 2010, Hornung 2011). From forest edge to interior, soil moisture increases (Chen et al. 1995, Gehlhausen et al. 2000), while temperature and litter quality (C/N-ratio) tend to decrease (Matlack 1993, Chen et al. 1999, Vasconcelos & Luizão 2004, Harper et al. 2005, Wuyts et al. 2013). Although soil moisture and temperature measurements were not incorporated in the design of this study, Remy (pers. comm.) did record higher temperatures and lower soil moisture in the edges of the same forest stands. A warmer forest edge with higher litter quality could favour the overall abundance of macro-detritivores, while highly species-specific responses to soil moisture could explain differences in edge-to-interior patterns between the different woodlouse species. This pattern could not be detected for millipedes in our study, which may indicate different strategies to conserve moisture. A microcosm experiment by Collison et al. (2013) demonstrated that under low moisture conditions, litter decomposition was solely realised by two woodlouse species, *P. scaber* and *P. muscorum,* while the millipede species *G. marginata* was found to be rolled up and less active. However, *G. marginata* can survive around twelve times longer under dry circumstances than e.g. *P. scaber* (pers. comm. M.P. Berg). Therefore, behaviour may be an important factor in governing the distribution patterns of millipedes along forest edge-to-interior gradients. Although both woodlouse and millipede species contribute to litter decomposition under higher moisture conditions, under dry conditions millipedes burrow deeper into the soil and remain inactive for a longer period than woodlice (David & Handa 2010). Sterzynska et al. (2015) reported that woodlouse communities were more affected by changes in soil moisture than millipede communities. However, the woodlouse community that they investigated consisted mostly of species with low desiccation tolerance, such as trichoniscid and ligiid species. Overall, our results suggest that millipedes find a more favourable microclimate at a certain distance from the edge, where humidity is higher and temperature lower.

Effects on community structure

While individual species showed specific responses regarding forest edge effects, communities were overall less variable along the studied gradients. Moreover, specific stand effects, irrespective of forest typology, explained one fourth of all variation in community structure across all studied gradients. Other local factors are thus likely to be important for local arthropod detritivore community composition. We found a dominance of woodlice over millipedes in pine stands and the reverse pattern in birch stands. In oak stands, neither group was dominant over the other. Topp et al. (2006) also reported differences in woodlouse and millipede community composition in primeval oak forests (*Quercus polycarpa/cerris*) compared to beech/fir forests (*Fagus sylvatica/Abies alba*). For tropical forests in Puerto Rico, Richardson et al. (2005) also found significant effects of forest type on woodlouse and millipede abundances. They suggested that this effect was more important than direct effects of temperature and rainfall. The importance of tree species and stand in determining the community structure of macro-detritivores is supported by our data.

Soil acidity, C/N ratio of the mineral top soil, Mg content in the ectorganic layer and the LAI in late summer are all related to changes in macro-detritivore community composition among and within forests. Indeed, soil acidity and exchangeable base cation concentrations in the soil can strongly influence the spatial distribution of woodlice (Van Straalen & Verhoef 1997) and millipedes (Kime 1992). For both taxonomic groups, calcium and magnesium are required for the construction of the exoskeleton, and these macro-nutrients are (together with sodium and potassium) important cations in the hemolymph (Hopkin & Read 1992). Soil acidification causes base cation concentrations to decrease and exchangeable aluminium concentrations to increase (Bowman et al. 2008). Therefore, given that all studied forest types were found to have very acidic soils (pH(KCl) < 3.5), we would expect low exchangeable base cation concentrations and high availability of aluminium in the soil solution. Soejono Sastrodihardjo & Van Straalen (1993) studied pH preferences of woodlice and showed that most of our studied species preferred pH(H_2O) values ranging between 5 and 6 (equivalent to a pH(KCl) of about 4 to 5 in our study). Soil pH, as well as the exchangeable base cation concentration, was higher at the forest edge compared to the interior (Wuyts et al. 2013). More favourable chemical soil conditions at the forest edge could help to drive larger abundances of woodlice (and probably millipedes as well). Another important factor for woodlice and millipedes is the quality of available food sources. Organic matter with low C/N ratio is preferred (Hassall et al. 2002, David 2009, David & Handa 2010, Gerlach et al. 2014), since lower C/N ratios have been shown to result in higher woodlouse population stability (Kautz et al. 2000) and higher assimilation efficiency (Loureiro et al. 2006). Wuyts et al. (2011) previously reported lower C/N ratios of the ectorganic horizon and the mineral topsoil at the edge of the studied forests compared to the forest interiors. They suggested that this was a result of higher N deposition at the forest edge. Therefore, it is expected that litter at forest edges should be a better food source for woodlice and millipedes, resulting in larger populations. Surprisingly, no strong correlation was found between species abundance and LAI, except for *P. scaber*, which was the most abundant species in the forest edge. This could indicate that light availability is of minor importance for most species, or that its effect is overruled by other factors, such as the ones mentioned above. However, a more likely explanation is that the range in LAI is not big enough to detect effects on community composition. It remains very difficult to draw conclusions about the main abiotic factors driving macro-arthropod communities at forest edges, since most of these abiotic factors are related to distance from the forest edge and are therefore strongly inter-correlated.

Conclusion

Woodlice and millipedes showed clear differences in abundance with distance from the forest edge. While woodlouse numbers decreased exponentially with distance from the edge, millipede abundances only began to decline at distances greater than about 7 m from the edge. Similar patterns were found for species richness, showing that arthropod detritivores are rarer in the centre than at forest edges. The observed patterns were consistent within monocultures of different tree species and between forest stands for woodlice, but less for millipedes. Community composition was, however, predominantly determined by forest typology. Despite this general pattern, species-specific responses were found. For the five dominant species of woodlice in our study, we observed that species with a lower desiccation resistance retreated deeper into the forest and showed a different edge pattern than more drought tolerant species. The observed edge-to-interior gradients in arthropod detritivores, which are key in litter decomposition, are hypothesised to also give rise to edge gradients in nutrient mineralisation and nutrient turnover rates, thereby influencing nutrient cycling in fragmented forest landscapes. Small forest fragments with a large proportion of edge to interior area are thus expected to have a disproportional and stronger impact on this functioning relative to more continuous forests.

Acknowledgements

P.D.S. and W.P. each hold a doctoral fellowship of the Research Foundation-Flanders (FWO). A.D.S. and P.D.F. each hold a postdoctoral fellowship of the Research Foundation - Flanders (FWO). We would like to thank the Agency for Nature and Forest (ANB) and the private forest owners and their ground keepers for allowing access to their forests. L.B. and D.B. are funded by the FWO research network on the eco-evolutionary dynamics of biotic interactions. Special thanks to Luc Willems for technical support during the research.

Appendix 3.1. Detritivore abundance per forest type

Table A3.1.1. *Abundances of woodlice and millipedes per m^2 in the different forest types (mean ± standard error) averaged across all distances.*

Species group	*Species*	*Pine*	*Oak*	*Birch*
Woodlice		**212±35**	**208±32**	**110±40**
	P. scaber	171±33	107±22	16.6±7.5
	P. muscorum	32.8±10.7	22.9±7.2	66.1±27.8
	O. asellus	2.72±0.80	24.2±0.8	17.8±9.4
	H. danicus	0	35.7±14.6	0
	T. pusillus	5.92±4.16	16.6±6.4	9.44±6.72
	L. hypnorum	0	0.32±0.32	0
Millipedes		**106±40**	**165±29**	**257±80**
	P. fuscus	85.8±37.9	17.8±10.7	67.2±27.8
	C. punctatus	4.96±1.28	44.0±10.4	39.8±17.0
	G. marginata	0	53.3±14.1	6.88±6.56
	P. denticulatus	3.04±3.04	17.4±5.1	39.4±15.4
	C. rawlinsi	0	3.84±3.84	18.2±8.8
	Melogona spec.	0	3.2±3.2	7.36±7.36
	J. scandinavius	1.28±0.64	3.52±2.88	5.28±3.04
	O. sabulosus	0.96±0.64	1.60±1.28	0
	C. sylvestre	0	1.44±1.28	0
	L. belgicus	0	0	0.32±0.32
	Juvenile millipedes	9.44±4.64	19.0±8.0	72.3±37.6
All		**318±52**	**372±50**	**367±107**

Porcellio scaber | Gert Arijs

Chapter 4

DESICCATION RESISTANCE & WOODLICE DISTRIBUTION

Desiccation Resistance determines Distribution of Woodlice along Forest edge-to-interior Gradients

Adapted from: De Smedt P, Baeten L, Berg MP, Gallet-Moron E, Brunet J, Cousins SAO, Decocq G, Diekmann M, Giffard B, De Frenne P, Hermy M, Bonte D, Verheyen K (2018) Desiccation resistance determines distribution of woodlice along forest edge-to-interior gradients. European Journal of Soil Biology 85: 1-3.

Abstract

Forest edges show strong abiotic and biotic gradients potentially altering community composition and ecosystem processes such as nutrient cycling. While abiotic gradients are well studied, short-scale biotic gradients, like detritivore community composition and their associated trait distribution remains a poorly explored research-field. We sampled woodlice in 160 forest fragments across Western Europe at varying distances from the forest edge and discovered that species desiccation resistance determines distribution along forest edge-to-interior gradients. Forest edges are warmer and dryer compared to interiors and favour drought-tolerant species, while abundance and activity of drought-sensitive species is reduced at the edge. Key ecological factors for litter-dwelling detritivores (i.e. humidity) act as environmental filter, because of species-specific differences in desiccation resistance. Future research should focus on quantifying the consequences of a changing detritivore community and their associated functional traits for nutrient cycling.

Introduction

Habitat fragmentation affects forest around the world, inducing both abiotic and biotic edge-to-interior gradients (Wade et al. 2003). Such edge effects can alter forest community composition and ecosystem processes (Haddad et al. 2015). An important ecosystem process in forest ecosystems is nutrient cycling, which is mediated by the interaction between multiple abiotic drivers and decomposer and detritivore activity (Bradford et al. 2002, Hättenschwiler et al. 2005, Prescott 2010). Abiotic drivers, like moisture availability, show particularly strong edge-to-interior gradients (Chen et al. 1995, Gehlhausen et al. 2000), and are crucial for the distribution and activity of detritivores (David & Handa 2010, Hornung 2011, Purse et al. 2012). Although less well known, the distribution patterns of soil organisms are strongly influenced by the effects of forest edges (De Smedt et al. 2016c), but the importance of underlying mechanisms, such as soil moisture availability remains poorly studied (Tuff et al. 2016). In this context, species desiccation resistance (a key soil fauna functional trait) has been proposed as an important predictor for woodlice (Isopoda) distribution (De Smedt et al. 2016c, Dias et al. 2013), a dominant taxonomic group of leaf litter-dwelling macro-detritivores (Jeffery et al. 2010). Therefore, we assume that the effect of decreasing soil moisture along forest edge-to-interior gradients on woodlouse community composition can be predicted from values of desiccation resistance of the component species. We aim to investigate whether species' desiccation resistance predicts distribution patterns along forest edge-to-interior gradients.

Methods

The study was carried out using data of the smallFOREST-consortium (Valdés et al. 2015) from five regions across Western Europe, along a latitudinal gradient from Northern France to central Sweden. In each region, two 5x5 km landscapes were investigated who varied in land-use intensity. In every landscape, we selected 16 forest fragments, from diverse size and age classes, resulting in 160 fragments. Woodlice were sampled using pitfall traps (Ø 10 cm, depth 11 cm). Woodlice abundance in the pitfall traps was expressed as activity-density (see e.g. Woodcock 2004), since the magnitude of pitfall catches depends on how active woodlice are ("activity") and the amount of woodlice that are present ("density"). Therefore, these catches cannot be interpreted as true abundances but as a proxy. Activity-density has no unit and can only be used to compare data within the same study design or between studies with exactly the same research setup. The pitfall traps contained ethylene glycol and water (200 ml, 1/1 mixture). In each forest fragment, we sampled at two locations i.e. the forest centre and the south-oriented forest edge (between the first row of trees). At every location, we installed two sampling points spaced five meters from each other and parallel to the sampled forest edge. This resulted in four sampling points per forest fragment (two in the centre and two in the edge). A sampling point consisted of two coupled pitfall traps with a plastic barrier (originally designed to assess invertebrate predator fluxes) (see Appendix 4.1). This resulted in 640 sampling points with a total of 1280 pitfall traps. Pitfall traps were covered with an aluminium roof (leaving a gap of ± 3 cm) to prevent larger vertebrates from entering the traps. If the edge bordered manmade structures, like roads, ditches... respectively the east-, west- or north-oriented edge was used. Pitfall traps were emptied twice between April and August 2013 (based on the regional temperature sum[1], i.e. more northern regions were sampled later in the year to match phenology with more southern regions). The first sampling campaign was started at Growing Degree Hours values of ca. 10,000 and the second at 20,000 (based on data of local weather stations in 2008 and 2009). In both campaigns, traps were open for 14 consecutive days (see Lindsey & Newman 1956 for the calculation of Growing Degree Hours). All individuals were identified to the species level. Data on desiccation resistance (time (h) of survival at 15°C and 85% RH) of the species was based on Dias et al. (2013) complemented with own measurements using the same method. Desiccation resistance is a key functional trait and strongly correlates to other important species traits like water loss rate, body mass and length (see Dias et al. 2013 and Appendix 6.2).

We analysed the survey data in three steps. First (results presented in Fig. 4.1), we fitted a multilevel model with total activity-density totalled over all species per sampling point as a response (i.e. all species together) and distance to the forest edge, region and their interaction as predictors. To account for the paired nature of the sampling points within fragments, we added a group-level effect for forest fragment and allowed the activity-density at the forest edge (intercept) and its relationship with distance (slope) to vary between forest fragments. Second (results presented in Fig. 4.2), we fitted similar models for individual species distribution data, for the eleven most common species (52.4% of species and 99.8% of the individuals) represented with more than 150 collected individuals. The other ten species were excluded because they were only represented in very low numbers or in very few forest fragments (see Appendix 4.2). Both region and forest fragment were added as group-level effects and intercepts and slopes were again allowed to vary between fragments. Third (results presented in Fig. 4.3), the between-species variation in distribution along the forest edge-to-interior gradient (slopes of the individual species models) were related to the species-specific values of desiccation resistance in a multilevel meta-analytic model with a group-level effect for species and the standard error of the estimated slopes as a measurement error effect. Models were fitted in R 3.4.0 (R Core Team 2017) using the packages *lme4* (Bates et al. 2017) and *MCMCglmm* (Hadfield 2016) for the multilevel and meta-analytic models. Both the activity-density and distance were modelled on a log-scale.

---

[1] The regional temperature sum is calculated as the sum of hours when the temperature exceeds 5 degrees starting from Julian day 1 (1st of January). For example: if the temperature is 6 degrees for 5 hours on one day we add 5 Growing Degree Hours (GDH). If the temperature is 8 degrees for 2 hours (6 GDH), 7 degrees for 5 hours (10GDH) and 6 degrees for 6 hours (6 GDH) we add 22 GDH (see Lindsey & Newman 1956).

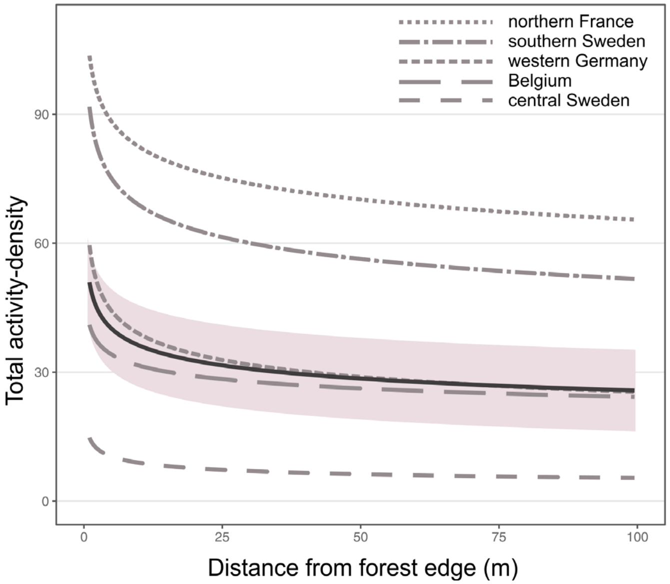


Figure 4.1. *Total activity-density of woodlice along forest edge-to-interior gradients per region (dotted lines). Displayed are data per sampling point summed for two trapping periods of fourteen days. The solid black line represents the average across all regions with 95% confidence interval (shaded area).*

Results

We sampled 75,486 woodlice from 21 species. While there were large differences in activity-density between the five regions ($F_{(4,152)}$=12.67, p<0.001), the edge-to-interior distribution patterns of woodlice were consistent across regions ($F_{(4,142)}$=0.74, p=0.56) (Fig. 4.1). In all regions, we found an exponential decrease in activity-density from the forest edge towards the forest interior, with effects diminishing after 25 to 50 meters from the forest edge ($F_{(1,142)}$=31.79, p<0.001). Species-specific patterns, however, were highly variable: activity-density of drought-resistant species (i.e. *Porcellio scaber*) strongly decreased from the forest edge towards the forest interior (Fig. 4.2a), while a reverse pattern was found for the drought-sensitive species *Ligidium hypnorum* (Fig. 4.2c). Species with an intermediate drought resistance, like *Oniscus asellus*, did not show a response (Fig. 4.2b). Comparing across the species, we found that the forest-edge-to-interior distribution (i.e. the slope of the species-specific regression) was negatively related to the species' desiccation resistance (pMCMC<0.05) (Fig. 4.3). High drought tolerance resulted in higher activity-densities in edges relative to forest interiors, while drought-sensitive species had lower activity-densities compared with forest interiors.

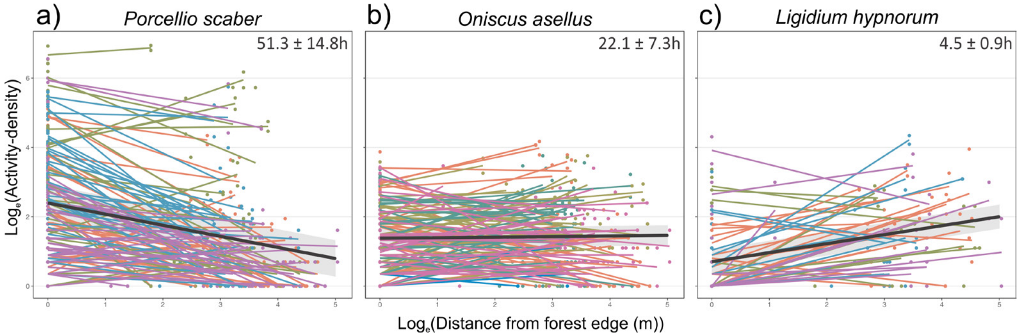


Figure 4.2. *Species-specific activity-density (log-transformed) in relation to the distance (log-transformed) from the forest edge towards the forest interior for a) Porcellio scaber, b) Oniscus asellus and c) Ligidium hypnorum. Displayed are data per sampling point summed for two trapping periods of fourteen days. The solid black line represents the global average across all regions and forest fragments with 95% confidence interval (grey shaded area). Coloured lines represent edge-to-interior patterns within individual forest fragments with dots being individual sampling points of forest fragments where the species was present. Values in the top right corner of each graph represent the mean desiccation resistance values (± SD) for the species (data from Dias et al. 2013).*

Discussion

Forest fragmentation and habitat loss strongly change thermal conditions along forest edge-to-interior gradients influencing soil moisture. These changes in abiotic conditions shape species morphology, distribution and activity patterns. However, to date, evidence from the field has been rather scarce (Tuff et al. 2016). Traits like desiccation resistance and water loss rate have been suggested to predict macro-detritivore and, more specifically, woodlice distribution (De Smedt et al. 2016c, Dias et al. 2013). Desiccation resistance is related to soil moisture availability (Dias et al. 2013), and studies have pointed out that moisture might be more important than temperature for soil arthropod performance (Dixie et al. 2015). We conclude that forest edges strongly shape woodlice distribution, with highly species-specific patterns that are significantly related to desiccation resistance of the species. This pattern is consistent across forest fragments on an almost continental scale. As most soil fauna groups are rather sensitive to drought we predict that our results will also hold for other soil fauna species. An important next step will be to evaluate whether the species that differ in desiccation resistance also differ in other traits that influence ecosystem functioning like nutrient cycling (via species effect traits). A first step has been taken by Remy et al. (2017), who interchanged edge and interior litter, mimicking edge microclimate in the forest interior (using experimental warming with open-top chambers), but without the presence of edge soil fauna. They confirmed a reduction in edge litter decomposition in the interior, in the absence of edge soil fauna. Similar experiments could be a good starting point for future experimental studies quantifying the variation in leaf litter breakdown caused by trait differences between drought-tolerant and drought-sensitive soil fauna species. This would be a valuable way forward to understand nutrient cycling in forest edges.

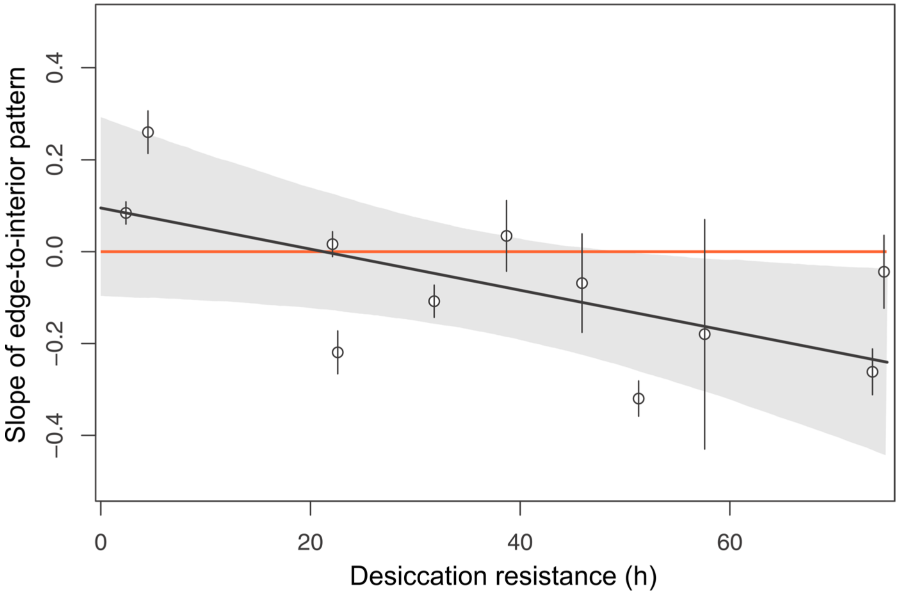


Figure 4.3. *Relationship between desiccation resistance of the eleven most common isopod species and the average slope of the regression between the species' activity-density and distance to the forest edge (cf. Fig. 4.2). The shaded area represents the 95% confidence interval of the relationship and the red line indicates the zero-slope, that is, when a species has the same activity-density across all distances. Points from left to right (increasing desiccation resistance) represent the species Trichoniscus pusillus s.s., Ligidium hypnorum, Oniscus asellus, Trachelipus rathkei, Philoscia muscorum, Porcellio gallicus, Armadillidium pulchellum, Porcellio scaber, Armadillidium opacum, Armadillidium vulgare and Armadillidium pictum. Error-bars on the points represent the standard error of the mean slope.*

Acknowledgements

P.D.S. holds a doctoral fellowship of the Research Foundation-Flanders (FWO). M.P.B was financed by the Uyttenboogaart-Eliasen Foundation. We thank Ludmilla Martin and Kent Hansson for help with the field work. The research was funded by the ERA-Net BiodivERsA project smallFOREST, with national funders ANR (France), MINECO (Spain), FORMAS (Sweden), ETAG (Estonia), DFG/DLR (Germany) and BELSPO (Belgium) part of the 2011 BiodivERsA call for research proposals.

Appendix 4.1. Sample setup

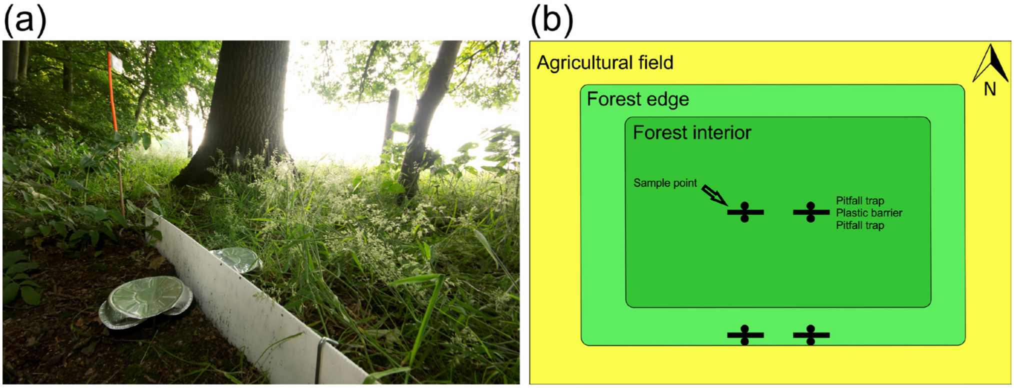


Figure A4.1.1. Sample setup. The design was originally used to assess invertebrate predator fluxes. Each sample point consisted of two pitfall traps separated by a plastic barrier (100cm X 30cm) (a), parallel to the forest edge (b). For this study, we pooled the two pitfall traps per sample unit since we do not investigate detritivore fluxes.

Appendix 4.2.
Species list and distribution

Table A4.2.1: *Woodlice species abundance per sampled region ordered according to their total abundance. Species in grey are represented with less than 150 individuals and were not used for the individual species models.*

Species	*Northern France*	*Belgium*	*Western Germany*	*Southern Sweden*	*Central Sweden*	*Total*
Philoscia muscorum (Scopoli, 1763)	7281	3948	4938	7616	0	23783
Armadillidium vulgare (Latreille, 1804)	19986	184	1	3027	0	23198
Porcellio scaber (Latreille, 1804)	10280	1838	3893	2710	0	18721
Oniscus asellus (Linnaeus, 1758)	1007	973	773	518	8	3279
Trachelipus rathkii (Brandt, 1833)	2	73	0	201	1772	2048
Ligidium hypnorum (Cuvier, 1792)	207	366	324	320	0	1217
Porcellio gallicus (Dollfus, 1904)	1024	0	0	0	0	1024
Armadillidium opacum (C. Koch, 1841)	0	174	0	237	333	744
Armadillidium pulchellum (Zenker, 1798)	0	0	394	0	312	706
Trichoniscus pusillus (Brandt, 1833)	68	142	9	105	112	436
Armadillidium pictim (Brandt, 1833)	0	0	29	0	136	165
Porcellio monticola (Lereboullet, 1853)	70	0	0	0	0	70
Philoscia affinis (Verhoeff, 1908)	0	0	60	0	0	60
Trichoniscoides albidus (Budde-Lund, 1880)	0	15	0	0	0	15
Porcellionides pruinosus (Brandt, 1833)	2	0	3	0	0	5
Trichoniscus provisorius (Racovitza, 1908)	0	5	0	0	0	5
Porcellio dilatatus (Brandt, 1833)	4	0	0	0	0	4
Porcellium conspersum (C. Koch, 1841)	0	0	3	0	0	3
Cylisticus convexus (De Geer, 1778)	1	0	0	0	0	1
Haplophthalmus mengii/montivagus	1	0	0	0	0	1
Trichoniscoides helveticus (Carl, 1908)	1	0	0	0	0	1
Total	**39934**	**7718**	**10427**	**14734**	**2673**	**75486**

Glomeris marginata | Theodoor Heijerman

Chapter 5

MACRO-DETRITIVORES, MICROCLIMATE & LITTER DECOMPOSITION

Macro-detritivore Identity and Biomass along with Moisture Availability control Forest Leaf Litter Breakdown in a Field Experiment

Adapted from: De Smedt P, Wasof S, Van de Weghe T, Hermy M, Bonte D, Verheyen K, Macro-detritivore identity and biomass along with moisture availability control forest leaf litter breakdown in a field experiment. Resubmitted, after major revisions, to Applied Soil Ecology

Abstract

Forests are structurally rich ecosystems with strong spatial variation in microclimate. Local temperature and soil moisture are important drivers of leaf litter breakdown, a key ecosystem process vital for forest functioning. Additionally, detritivore species composition and activity are equally dependent on microclimate, rendering changes in microclimate key to understand leaf litter breakdown. We investigated the interaction between microclimatic variables (i.e. temperature and moisture) and different combinations of macro-detritivores (drought sensitive vs. drought tolerant species) on litter breakdown of easily decomposable (high quality) Acer litter and decomposition resistant (low quality) Quercus litter in a full factorial microcosm field experiment in a temperate forest in Belgium. We hypothesize litter breakdown to be higher for high quality litter and macro-detritivore biomass and depended on macro-detritivore identity, mediated by forest microclimate.

We found high quality litter breakdown to be reduced by decreasing moisture availability, while it was not affected by temperature. There was no effect of moisture and temperature on litter breakdown of low quality litter. The effect of detritivore biomass on the breakdown of Quercus litter depended on detritivore identity: increasing millipede biomass increased litter breakdown of Quercus, which was not the case for woodlice. There was a positive effect of macro-detritivore biomass but not of macro-detritivore identity on leaf litter breakdown of high quality litter. In addition, the relative consumption rates were equal between the drought sensitive (woodlouse) and the drought tolerant (millipede) species for high quality litter, but different for low quality litter. The woodlouse species was more efficient in the breakdown of low quality litter compared to our tested millipede species. Relative consumption rate was not influenced by the moisture or temperature treatments. Combining to detritivores in a mixture had additive (non-synergistic) effects for litter breakdown, indicating that they are not complementary in their resource use. We conclude that mainly differences in moisture availability in forest ecosystems are important for litter breakdown and that detritivore identity is critical for the breakdown of especially low quality litter.

Introduction

Temperature and moisture determine global patterns in the breakdown of terrestrial leaf litter, with higher temperatures and moisture availability generally enhancing breakdown (Prescott, 2010). Similar variation in temperature and moisture can, however, be found at much smaller scales. For instance in forest, strong microclimatic gradients can be observed in relation to edge effects and other horizontal gradients in forest structure (Chen et al. 1999, Gehlhausen et al. 2000, Delgado et al. 2007, Arx et al. 2013, Loescher et al. 2014). This microclimatic variation is regarded as one of the main drivers of understory plant community composition (De Frenne et al. 2015, Normann et al. 2016). In parallel, the same drivers cause a strong shift in decomposer community composition (Riutta et al. 2012, De Smedt et al. 2016c, Remy et al. 2018), which depend on air and soil moisture and environmental temperature (Meyer & Eisenbeis 1985, Dias et al. 2013, Dixie et al. 2015). Microclimatic effects on litter breakdown are relatively well studied (Prescott 2010), however, the interaction of the microclimate with the decomposer community is poorly studied (cf. Sariyildiz 2008, David & Handa 2010, Prescott 2010). Investigating whether changes in forest microclimate regimes moderate leaf litter breakdown by decomposers is essential to understand the integral role that microclimate plays in ecosystem functioning, such as nutrient cycling.

Macro-detritivores are key components of the decomposer community because they increase breakdown by transforming leaf litter to a more readily accessible form for soil micro-organisms (such as micro-fauna, fungi and bacteria) (Bradford et al. 2002, Hättenschwiler et al. 2005). Macro-detritivore abundance, identity and diversity can strongly influence breakdown (Hättenschwiler et al. 2005, Vos et al. 2011). Macro-detritivore distribution in forests is highly species-specific, possibly resulting in contrasting decomposition rates in forest ecosystems (De Smedt et al. 2016c, 2018a). Although different taxonomic groups of macro-detritivores all dominantly feed on dead plant material, synergies between macro-detritivores have been reported in lab experiments (e.g. Zimmer et al. 2005, De Oliveira et al. 2010, Collison et al. 2013). Synergistic effects are positive non-additive effects, meaning that the litter decomposition rate by the different species together is higher than the sum of the decomposition rates by the individual species. In general, macro-detritivore species loss may jeopardise litter breakdown (Huhta et al. 1998, Handa et al. 2014) indicating the importance of complementarity between different groups in the decomposition process. This complementarity is expected to be caused by different feeding strategies of macro-detritivores or different nutritional requirements (Bardgett & Chan 1999, Zimmer et al. 2005).

Woodlice (Malacostraca, Isopoda, Oniscidea) and millipedes (Diplopoda) are dominant litter dwelling macro-detritivores in temperate regions (comprising about 30% of the macro-fauna individuals per square meter of forest soil) (Jeffery et al. 2010). Despite their taxonomically dissimilarity, woodlice and millipedes share similar ecological niches within the leaf litter and the upper soil layers of forests, in contrast to e.g. earthworms, which are dominant soil dwellers (David & Handa 2010). Despite their ecological similarity, they show different responses to environmental gradients, predicted by the among (De Smedt et al. 2016) and within (De Smedt et al. 2018a) taxa large differences in species desiccation resistance, with drought resistant species dominating in the drier and warmer microsites (De Smedt et al. 2018a). Therefore, we can expect an interaction between species identity and leaf litter breakdown with drought tolerant species performing better under higher temperatures and lower humidity compared to drought sensitive species.

Leaf litter quality is another important driver of litter breakdown. Although, macro-detritivores generally prefer high quality litter (i.e. litter containing a high amount of nitrogen relative to carbon and low concentrations of lignin) (Zimmer & Topp 2000, Zimmer 2002, Joly et al. 2015), the relative contribution to breakdown of different macro-detritivore species depends on litter quality. Certain species are more efficient for low or high quality litter compared to other macro-detritivore species (Vos et al. 2011). This could indicate that the effect of environmental variables like moisture availability and temperature on leaf litter breakdown by different assemblies of macro-detritivores might depend on litter quality as well. Additionally, litter quality may also influence complementarity between macro-detritivores (Zimmer et al. 2005).

To study the relative importance of microclimate, detritivore identity and litter quality on litter breakdown dynamics, we designed a full-factorial field experiment in autumn after the dominant litter fall period. We hypothesised that (1) forest leaf litter breakdown depends on macro-detritivore identity, mediated by the forest microclimate. Reduced moisture and increased temperature will less affect consumption of a drought tolerant species compared to a more drought sensitive species. (2) These effects will be more pronounced for high compared to low quality litter, because high quality litter is preferred by macro-detritivores. (3) Synergy (positive additive effects) between woodlice and millipedes for leaf litter breakdown will therefore depend on both microclimate and litter quality.

Methods

Study area and experimental set-up

This study was carried out in an ancient, mixed deciduous, temperate forest (39.5 ha), in the northern part of Belgium (Aelmoeseneie forest, Gontrode). Dominant tree species are Quercus robur L., Fagus sylvatica L., Larix kaempferi Carr., Fraxinus excelsior L., and Acer pseudoplatanus L. The soil developed in a quaternary layer of sandy loam on a shallow impermeable clay and sand complex of tertiary origin (FAO classification: Gleyic Cambisol). The pH-KCl of the topsoil layer (0-5 cm) averages about 3.53 (Vanhellemont et al. 2014).

We constructed 288 microcosms from PVC pipe (diameter 12 cm, depth 10 cm). The top and bottom were sealed with fiberglass gauze (1 x 2 mm mesh size; attached with cable ties disabling detritivores to escape) to allow transport of moisture, micro- and meso-fauna during the experiment. In each microcosm, we added 10 g of sycamore litter (*Acer pseudoplatanus* L.) and 2 g of oak litter (*Quercus robur* L.). Experimental leaf mass was based on the relative consumption of the different litter species by detritivores in a pilot study. 12 g was the maximum amount of litter that fitted in the microcosms without pressing litter together. The choice of the tree species was based on their differences in leaf chemical characteristics. *Acer pseudoplatanus* litter has for example higher Ca-content, lower lignin and C/N ratio compared to *Quercus robur* (Reich et al. 2005, Hantsch et al. 2014), making them respectively high and low quality litter as food for macro-detritivores in temperate regions (David & Handa 2010, Gerlach et al. 2014). The tree species will be further referred to by their genus names. We used freshly fallen litter from nearby sites, collected with nets in October 2015 and dried at 26 °C for three days. Drying the litter enables us to compare its mass before and after the experiment. The experiment was conducted from the end of October 2015 until the end of January 2016.

Four detritivore treatments were applied to the microcosms: a control treatment (no woodlice or millipedes; CO) (Fig. 5.1a), woodlouse monocultures (10 individuals; WL) (Fig. 5.1b), millipede monocultures (10 individuals; MP) (Fig. 5.1c) and mixed cultures (5 woodlice and 5 millipedes; MX) (Fig. 5.1d). All individuals were adults and pregnant females (with brood pouch) were not used to prevent a sudden increase of juveniles during the experiment. Sex was undetermined. Experimental density of the animals equaled 885 individuals per m^2, which is rather high for millipedes (Wolkers & Ekschmitt 1997; range 210-700 ind. m^2) but within normal ranges for woodlice (Wolkers & Ekschmitt 1997; range 96-1850 ind. m^2) in temperate forest. Woodlice and millipedes were weighed together per microcosm before they entered the microcosms to be able to assess macro-detritivore condition (mass loss/gain) after the experiment. We used the woodlouse *Oniscus asellus* L. and the millipede *Glomeris marginata* (Villers), two species that are common in ancient deciduous forests in Western Europe covering the same ecological niche (De Smedt et al. 2018b). However, both species differ strongly in their desiccation tolerance with *G. marginata* able to survive much longer under standardised dry conditions compared to *O. asellus* (Edney 1977, Dias et al. 2013, pers. comm. M. P. Berg). Animals were collected by hand during mid to late October 2015 around the study area. They were kept up to a maximum of one week in plastic containers with soil and leaf litter collected on site. The leaves in the microcosms were sprayed with a microbial wash before macro-detritivores were added, to restart microbial activity on the leaf litter after drying. The microbial wash was created by soaking ectorganic horizon of the study site in water for several days. Particles were then filtered out (0.02mm mesh size of the filter) and the solution was sprayed on the microcosms one day before and at the start of the experiment. This should mimic natural colonization of microbes immediately at the start of the experiment as microbial colonised litter is preferred by detritivores (Zimmer 2002).

The microcosms were installed on flat forest surface (with one side of fiberglass gauze touching the forest soil) under four different environmental treatments (Fig. 5.1e,f,g,h), based on realistic projected temperature changes (0.3-0.7 °C from 2016 to 2035) and precipitation changes (highly variable but more extreme) in the coming years in Western Europe (IPCC 2014). The treatments were in the realistic range of temperature and moisture changes in deciduous forest ecosystems (see Loescher et al. 2014). We installed a control treatment (Fig. 5.1e), a temperature treatment (Fig. 5.1f), rainfall treatment (Fig. 5.1g) and a combination of the two previous treatments (Fig. 5.1h). Rainfall was manipulated using plastic rainout shelters of $1m^2$ at a height of 1.20m above the forest floor. The shelters were removed and re-installed every two weeks. Temperature was manipulated using hexagonal open-top chambers (OTCs) from Plexiglas with inclined walls to passively heat the inside temperature (height 60 cm and covering a ground surface of 1.15 m^2).

In order to obtain a time series of litter breakdown, microcosms were taken out of the field in six time periods: respectively after 1, 2, 4, 6, 8 and 13 weeks (hereafter, time period). The experiment was replicated three times. The first microcosms were placed into the field on October 26th 2015, just after the dominant peak in litter fall, a second and third replicate were installed respectively one and three days later. This resulted in a total of 288 microcosms (4 fauna treatments x 2 temperature treatments x 2 moisture treatments x 6 time periods x 3 replicates).

The microcosms were placed on the forest floor in 30 groups, divided across the environmental treatments. Forest leaf litter was removed before installing the microcosms in the field to allow full contact with the soil. Small gaps between soil surface and OTC were closed with soil from the study side. We collected rainfall with a rain gauge on a weekly basis in every group (Fig. 5.1e). Temperature was measured every five minutes on the soil surface, just beneath the leaf litter layer in three OTCs and three control treatments using Type T miniature thermocouples (TC Direct, Nederweert, NL). Volumetric soil moisture content was measured immediately underneath the microcosm at a depth of about 3 cm when the microcosm was taken out of the field using a ML3 ThetaProbe (Delta-T Devices).

When a microcosm was collected from the field, soil fauna was removed, counted (number of living individuals to assess survival rate) and the total mass of all living individuals was weighed and divided over the number of living individuals to asses differences in detritivore mass. Leaf litter mass per tree species was determined after drying it for three days at 26°C.

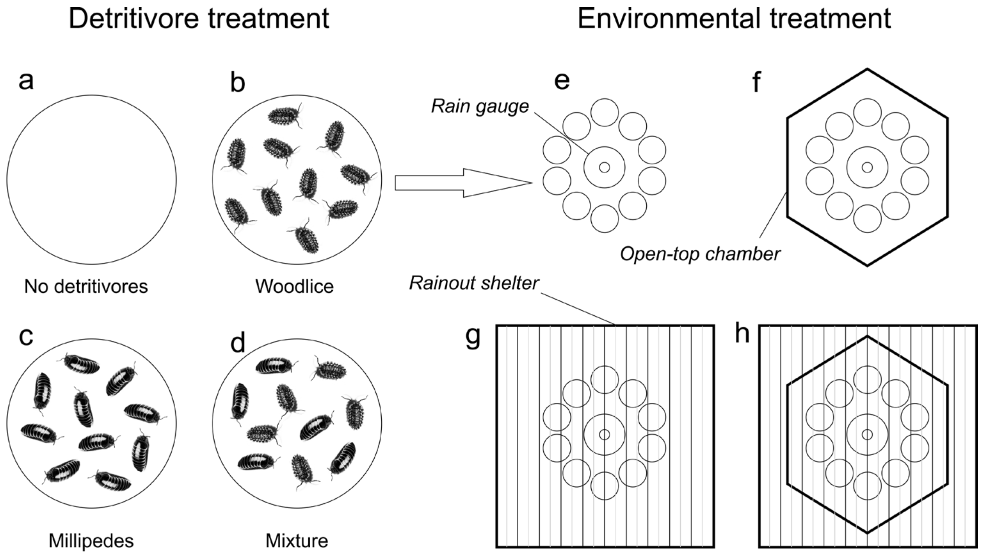


Figure 5.1. *Experimental setup for the different detritivore treatments and the different environmental treatments. Detritivore treatment: (a) control (no detritivores), (b) woodlice (ten individuals of Oniscus asellus), (c) millipedes (ten individuals of Glomeris marginata), (d) mixture (five individuals of Oniscus asellus and five individuals of Glomeris marginata). Environmental treatment: (e) control (no OTC or rainout shelter), (f) temperature treatment (OTC but without rainout shelter), (g) rainfall treatment (no OTC but with rainout shelter), (h) combined treatment (OTC and rainout shelter).*

Data analysis

Treatment effectiveness

In order to test the effectiveness of our treatments, i.e. to evaluate whether temperature was significantly increased using OTCs and whether rainfall and soil moisture decreased using rainout shelters, we used linear mixed-effects models with replicate nested in sampled week (i.e. 1, 2, 4, 6, 8 and 13) as a random factor. The dependent variable was the real quantitative measurement of either moisture, rainfall or temperature. Environmental treatments variable with rainfall (with or without rainout shelter), temperature (with or without OTC) and their interaction were used as fixed factor. We used the *lme*-function from the *nlme*-package (Pinheiro et al. 2017). Temperature was only measured in the three temperature treatments and three control treatments because of logistic constrains and subsequently only tested for temperature treatment, but this should give us confidence about the functioning of the OTCs.

Leaf litter mass loss

In order to investigate the interaction between microclimatic variables (i.e. temperature and moisture), macro-detritivores biomass and identity and time period (weeks after the start of the experiment) on the mass loss of Acer (easily decomposing) and Quercus (decomposition resistant), we used mixed effect models. Plot (cluster of microcosms in the field) was used as a random term using the *lme*-function from the *nlme*-package (Pinheiro et al. 2017). We tested the effect of detritivore identity (three levels), moisture treatment (two levels), temperature treatments (two levels), time period (six levels) and detritivore biomass (continuous and total per microcosm) on litter mass loss. Litter mass loss (g) (the response variable) was square-root-transformed to achieve normality. R-squared values were obtained using the *r.squaredGLMM*-function from the *MuMIn*-package (Bartoń 2015).

Relative consumption rate

In order to test the importance of macro-detritivore identity, environmental treatment and time period for leaf litter breakdown, we calculated the relative consumption rate (RCR) of the leaf litter by detritivores. We modelled litter mass loss of Acer and Quercus in the control treatments in order to calculate mass loss by microbes, micro-fauna etc. using linear models (*lm*-function) (Appendix 5.1). We used the modelled breakdown in the control plots to calculate the proportion of mass loss without the presence of macro-detritivores (D). Secondly, we calculated detritivore consumption (C_I), using the formula by Bocock (David 1998):

$$C_I = M_0 - M_0D - M_n \tag{1}$$

Where M_0 is the initial litter mass (dried at 26°C) and M_n is the final litter mass (dried at 26°C). RCR was calculated by dividing with detritivore mass after the experiment (M_{det}):

$$RCR = C_I/M_{det} \tag{2}$$

The effect of detritivore treatment (three levels; woodlice, millipedes and mixtures), moisture, temperature treatment, and time period on RCR of detritivores was tested using the *lme*-function as for leaf litter mass loss, with plot as a random effect term.

We tested the effect of different treatments (i.e. detritivore, temperature and moisture) and time period on detritivore weight difference (as a measure of animal condition) and detritivore survival (for survival using a binominal distribution). Animal condition (weight loss) and survival was tested to assess if our experimental set-up influenced detritivore condition or survival, which could confound effects on litter breakdown.

Synergy

Finally, the potential synergy (3) between woodlice and millipedes was calculated as the observed litter breakdown in mixtures ($M_{observed}$) minus the expected litter breakdown of woodlice and millipedes in monocultures based on detritivore mass (4).

$$Synergy = M_{observed} - M_{expected} \qquad (3)$$

$$M_{expected} = WL_{MX} * Mloss_{WLMO}/WL_{MO} + MP_{MX} * Mloss_{MPMO}/MP_{MO} \quad (4)$$

WL_{MX} is the total woodlouse weight in mixtures, $Mloss_{WLMO}$ is the average litter mass loss under woodlouse monocultures and WL_{MO} is the total woodlouse weight in monocultures. MP_{MX} is the total millipede weight in mixtures, is the average litter mass loss under millipede monocultures and MP_{MO} is the total millipede weight in monocultures.

A simple one-sample t-test was used to test if the observed values differed from zero. Linear mixed effect model with three-way interaction was used to test if synergy was influenced by moisture or temperature treatments or time period in the same way as above. All statistical analysis was done using R version 3.3.2 (R Core Team 2016).

Results

Treatment evaluation

Rainfall was significantly influenced by the use of a rainout shelter ($F_{(1,246)} = 605.26$; $p<0.001$) as well as OTCs ($F_{(1,246)} = 6.62$; $p<0.05$). Rainout shelters reduced rainfall with 26%. OTCs reduced rainfall with only 5%. OTCs significantly increased temperature with 0.54 °C, from 11.13 ± 0.08 °C outside OTCs to 11.67 ± 0.08 °C inside OTCs ($F_{(1,23)} = 11.19$; $p<0.01$) (Appendix 5.2). Soil moisture was significantly influenced by the use of a rainout shelter ($F_{(1,264)} = 82.51$; $p<0.001$) as well as OTCs ($F_{(1,246)} = 35.56$; $p<0.001$). Rainout shelters reduced soil moisture by 15% while OTCs reduced soil moisture by 10%.

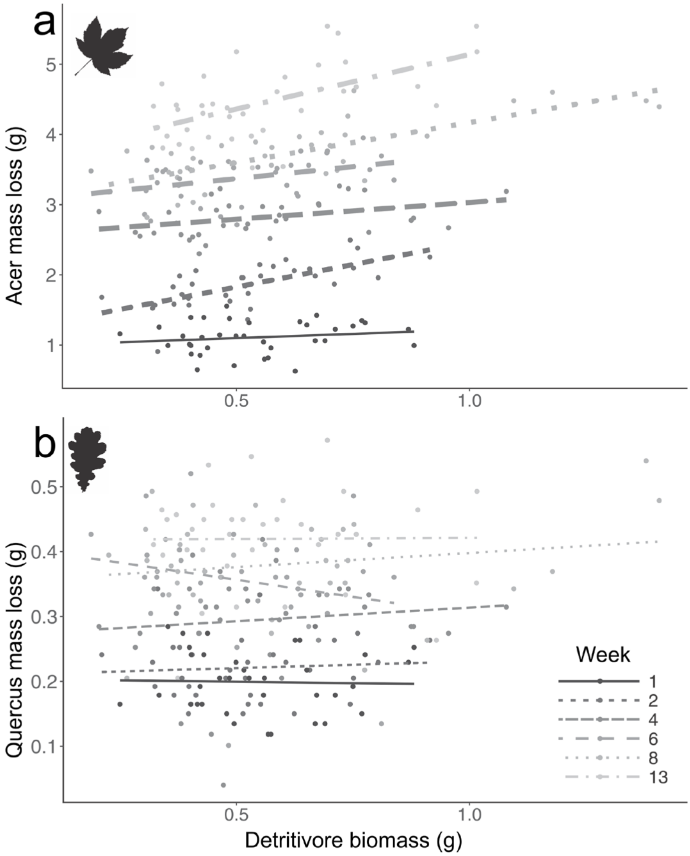


Figure 5.2. *Acer (a) and Quercus (b) mass loss according to detritivore biomass for the different weeks since the start of the experiment across all environmental treatments. Lines represent averages per week. Bold lines represent significant (p<0.05) regressions, based on the subsets per week but analyzed in the same way as the overall model (Table 5.1).*

Leaf litter mass loss

Litter mass loss of both *Acer* and *Quercus* was significantly influenced by time period (Table 5.1, Fig. 5.2). For *Acer* litter also the detritivore biomass and moisture treatment influenced litter mass loss, as well as the interaction between detritivore biomass and time period (Table 5.1). Increased detritivore biomass significantly increased Acer litter breakdown (Fig. 5.2a). Reduction in moisture availability caused a decrease in *Acer* litter breakdown of on average 6% (Fig. 5.3a). However, there was no significant effect of increasing temperature on the breakdown of *Acer* leaf litter (Fig. 5.3b). For *Quercus* litter, while there was no main effect of neither detritivore biomass, nor detritivore identity on the biomass loss, their interaction was significant (Fig. 5.2b, Table 5.1). Here, we see that *Quercus* mass loss increased with increasing millipede biomass in the monocultures (df=64, t=2.00, p<0.05), but *Quercus* mass loss was not influenced by detritivore biomass in woodlice monocultures (df=64, t=-0.93, p=0.36) or in mixtures (df=64, t=-1.43, p=0.16) (Fig. 5.4). After thirteen weeks, *Acer* litter mass loss was on average 39.26 ± 1.0% while it was only 18.63 ± 0.74% for *Quercus*.

Table 5.1. *Effect of significant factors explaining variation in mass loss of (a) Acer and (b) Quercus (sqrt-transformed). Results (F-values and degrees of freedom) of linear mixed effect models. Temperature effects did not contribute to any of the models. Significance levels: *: p<0.05, **: p < 0.01, ***: p < 0.001, NS: Not significant. The R-squared values for the fixed factors (marginal R-square) were high with 0.945 and 0.607 for the Acer and Quercus models, respectively. The addition of the random effect (i.e. group) was very limited resulting in a conditional R-square value of 0.949 and 0.607 for Acer and Quercus, indicating that our setup of random allocation of microcosms to groups did work.*

a		*Acer*	b		*Quercus*
Detritivore biomass (D)	$F_{(1,172)}$	164.81***	**Detritivore biomass (D)**	$F_{(1,173)}$	2.74 NS
Moisture treatment	$F_{(1,28)}$	14.87***	**Detritivore species (Pop)**	$F_{(2,173)}$	0.56 NS
Time period	$F_{(5,172)}$	661.00***	**Time period**	$F_{(5,173)}$	59.93***
D x Time period	$F_{(3,163)}$	4.11**	**D x Pop**	$F_{(2,173)}$	3.46*

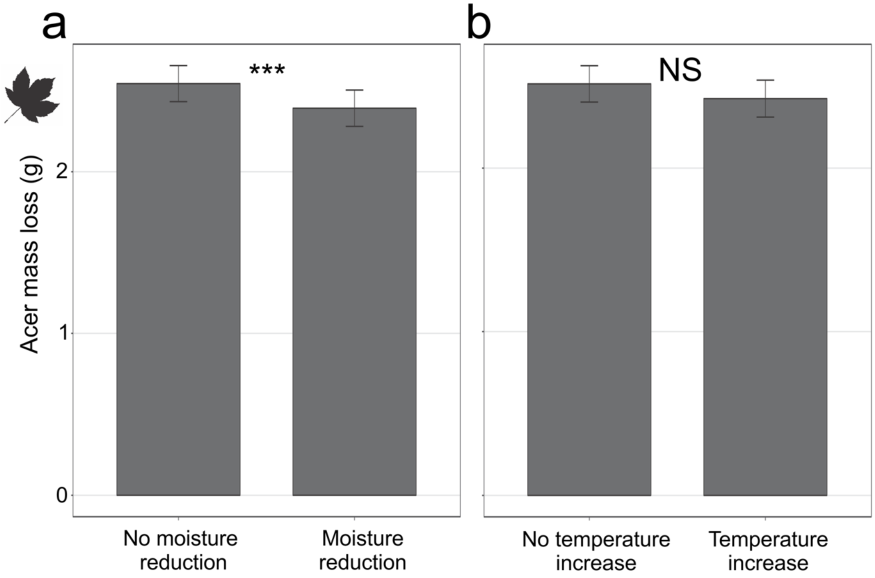


Figure 5.3. *Litter mass loss of Acer according to (a) moisture treatment and (b) temperature treatment (***: p < 0.001, NS: Not significant) across all sampled weeks. Error bars denote ± 1*standard error.*

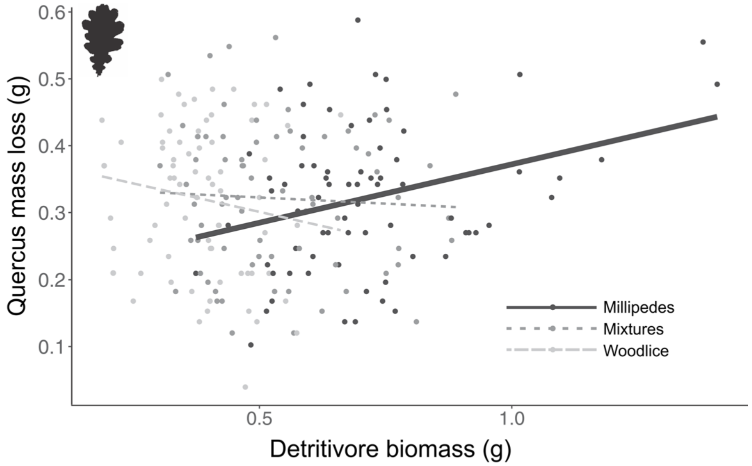


Figure 5.4. *Litter mass loss of Quercus according to detritivore biomass of the different detritivore treatments. Lines represent averages per detritivore treatment across all environmental treatments. Bold lines represent significant (p<0.05) regressions, based on the subsets per population but analyzed in the same way as the overall model (Table 5.1).*

Relative consumption rate

RCR of detritivores on *Acer* litter was only influenced by time period ($F_{(5,178)} = 16.64$; $p<0.001$), while the RCR on *Quercus* litter was influenced by time period ($F_{(5,176)} = 21.66$; $p<0.001$) and detritivore treatment ($F_{(3,176)} = 28.23$; $p<0.001$). RCR of *Acer* litter increased with time from 0.24±0.04 g/g detritivore after one week to 1.39±0.22 g/g detritivore after thirteen weeks (Fig. 5a). Consumption on Quercus litter was lower and ranged from 0.23±0.02 g/g detritivore after one week to 0.59±0.04 g/g detritivore after thirteen weeks. Overall, consumption of *Acer* was about two times higher compared to *Quercus* for woodlice and four times higher for millipedes. At week thirteen, RCR of *Quercus by* woodlice was higher (0.77±0.05 g/g detritivore) than by mixtures (0.59±0.07 g/g detritivore), which in turn was higher than by millipedes (0.43±0.06 g/g detritivore) (Fig. 5.5b).

Average weight of individual woodlice and millipedes was 41.3 ± 11.6 mg and 72.1 ± 24.9 mg (both with N = 1065), respectively. Woodlouse and millipede weight loss and survival were not influenced by time period or any of the treatments or their interactions (all p-values of the lme's > 0.05). We can therefore assume that the effects cannot be attributed to a decreasing macro-detritivore condition or population (Appendix 5.3).

Synergy

Synergy values (observed minus expected breakdown by detritivores in mixtures) of *Acer* and *Quercus* were not influenced by time period or any of the treatments (moisture and temperature) or their interactions (all p-values of the lme's > 0.05). Synergy values did not differ from zero for *Acer* (t=-1.65, df=70, p=0.103) (Fig. 5.6a) or *Quercus* (t=-1.39, df=70, p=0.170) (Fig. 5.6b).

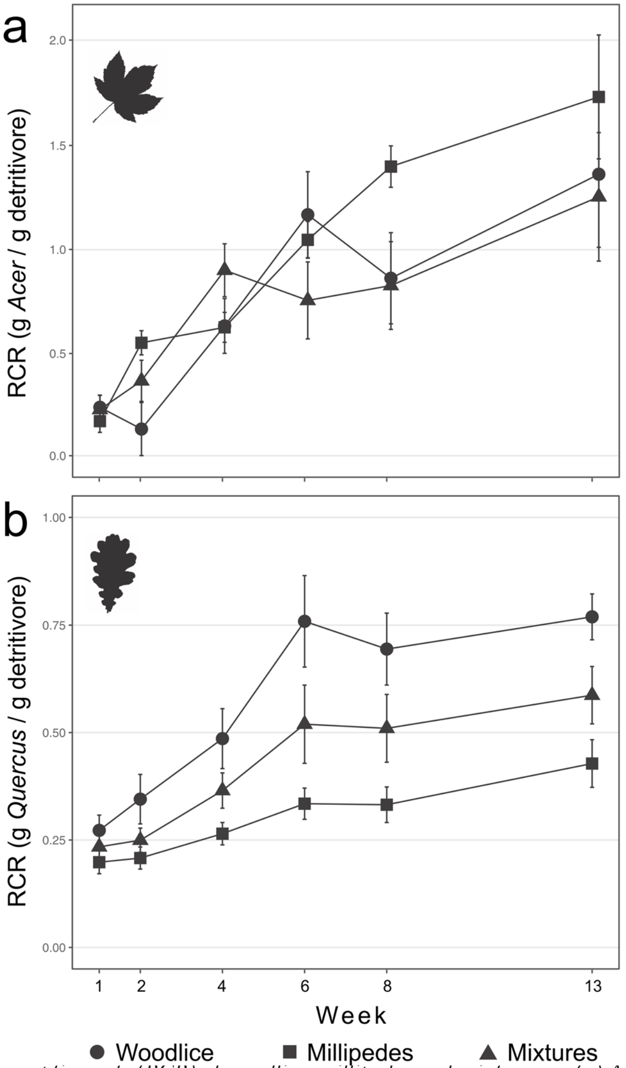
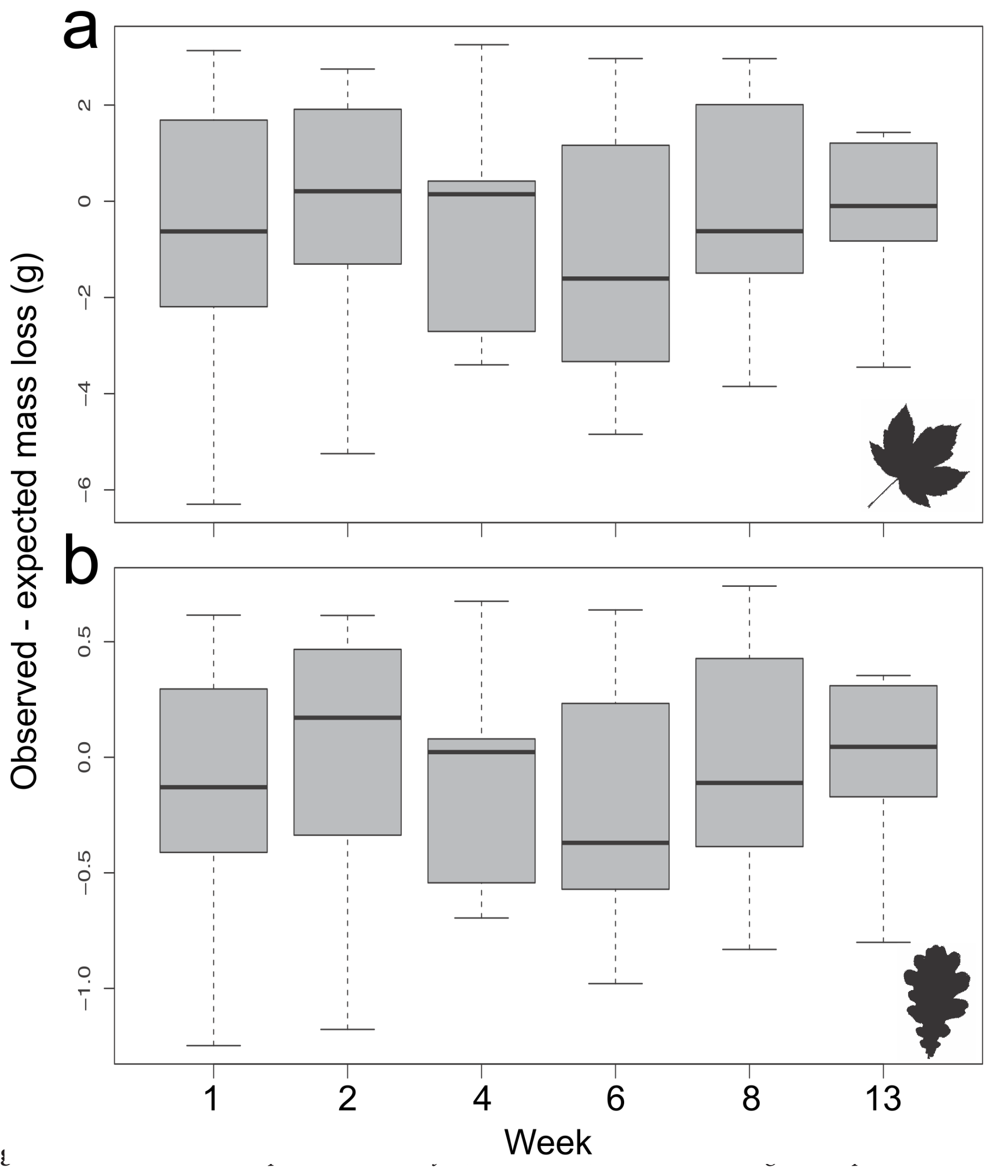


Figure 5.5. *Relative consumption rate (RCR) of woodlice, millipedes and mixtures on (a) Acer litter and (b) Quercus litter. Error bars denote ± 1*standard error.*



Fi

since the start of the experiment). Observed mass loss is the observed mass loss in mixtures with woodlice and millipedes. Expected mass loss is calculated based on mass loss in monocultures of woodlice and millipedes and their biomass in mixtures. Boxes represent upper and lower quartile with the mean as solid black line in between; whiskers represent 95% confidence interval.

Discussion

Leaf litter mass loss

Soil moisture availability affected leaf litter mass loss of high quality litter, but not of low quality litter, which is supported under laboratory conditions (Collison et al. 2013). Also in the field, soil moisture was a limiting factor for litter breakdown (Riutta et al. 2012) and we show that this does not interact with detritivore identity or biomass. This is unexpected since under high moisture conditions, macro-detritivores can remain active for longer periods (Dias et al. 2012, Broly et al. 2013, Dixie et al. 2015) increasing their feeding time and subsequently increasing leaf litter breakdown. While this interaction was found under laboratory conditions (Collison et al. 2013) we could not detect this under field conditions (see also Riutta et al. 2012). This stresses the limitations of experimental lab microcosm studies which could possibly not mimic field conditions (Rouifed et al. 2010). Furthermore, the effect of moisture on leaf litter breakdown depended on litter type. Again unexpected, but caution is required since the breakdown of low quality litter is slower and longer study periods might be necessary to detect effects.

Increased temperature did not affect leaf litter mass loss, yet temperature is supposed to have a positive effect on leaf litter breakdown (Prescott 2010) and positively influences many life history traits of macro-detritivores (e.g. development time, relative growth rate, and fertility (David & Handa 2010, Dixie et al. 2015)). Of course, these positive effects act within sharply defined boundaries depending on the species (see e.g. Warburg 1968). In addition, also macro-detritivore behaviour (like running speed and activity) is influenced by higher temperatures (Dailey et al. 2009) enhancing their ability to search for food. However, increased temperatures in forests accord with decreased moisture availability (Chen et al. 1993) and the positive temperature effects on macro-detritivore activity might be compensated for by decreased moisture availability. By studying different life history traits of macro-detritivores, Dixie et al. (2015) concluded that temperature effects were less important for macro-arthropod biology compared to moisture availability. This can be confirmed by our study. Alternatively, in our study, temperature increase (0.68°C on average) might be too small to actually detect differences in the field although it are realistic estimates of small-scale horizontal temperature variation (Loescher et al. 2014) and future warming effects in forests (De Frenne et al. 2010). However, it is important to notice that also in our field experiment an increase in temperature coincided with a decrease in soil moisture using OTCs. The observed soil moisture reduction contradicts with the expectation that OTCs have little influence on soil moisture (De Frenne et al. 2010). Therefore, it remains important to assess both temperature and moisture differences when using OTCs in experimental studies on ecosystem functioning.

Interestingly, although, no influence of detritivore biomass and detritivore identity on leaf litter breakdown of Quercus leaves were detected, their interaction was significant. We found that increasing millipede biomass will increase Quercus consumption, whereas a neutral pattern has been found for woodlice and the mixtures. This neutral (week negative) relationship between woodlice biomass and Quercus breakdown is hard to explain. However, we know that the biofilm (thin layer of micro-organism surrounding leaf litter) is an important secondary food source for woodlice (Zimmer 2002, Horváthová et al. 2016), and suggested to be less important for millipedes (despite some specialised species; Hopkin & Reed 1992). This biofilm is key towards the microbial breakdown of dead organic material. Detritivores, like woodlice, influence the composition of this biofilm by grazing on it (Ihnen & Zimmer 2008, Moghadam & Zimmer 2014). Our study was carried out with relatively high amounts of woodlice biomass, with numbers comparable to areas with high amount of coarse woody debris (Topp et al. 2006). It sounds plausible that high amounts of woodlice “overgraze” the biofilm on lower quality litter and therefore reduce microbial breakdown. This could indicate that leaf litter breakdown is slowed down at places with high woodlice biomass like areas with large amounts of dead wood in forest. No effect was found on Acer litter breakdown, but could be owed to the nature of the biofilm, which can be highly variable on different substrates (Hantsch et al. 2014, Li et al. 2014) i.e. Quercus leaves have higher fungus pathogen load compared to Acer possibly resulting in a higher grazing pressure of the Quercus biofilm (Hantsch et al. 2014). The positive effects on the physical breakdown of Quercus leaves could be counteracted by grazing on the biofilm when woodlouse biomass is high. Humidity and temperature are considered important drivers in biofilm formation (Else et al. 2003), although this could not be detected in our field experiment.

Relative consumption rate

Macro-detritivores prefer leaf litter low in carbon relative to nitrogen (Zimmer 2002), and therefore it is not surprising that relative consumption rates (RCR) of Acer litter are higher compared to Quercus litter. RCR of detritivores was unaffected by temperature or moisture availability opposing our hypothesis that the RCR of a drought resistance species is less affected by reduced moisture and elevated temperatures compared to a drought sensitive species. Future research with larger temperature and moisture ranges and with more macro-detritivore species might be needed to shed some light on the validation of our hypothesis. However, strong differences in RCR were observed for Quercus litter between the different detritivore treatments, while no difference was found for Acer litter. The contribution of macro-detritivores to litter breakdown has shown to be especially important in recalcitrant litter types (Hättenschwiler & Gasser 2005, Jacob et al. 2009, Riutta et al. 2012), supporting our results.

The millipede G. marginata seems to be less functionally efficient in comparison to the woodlouse Oniscus asellus for the breakdown of Quercus litter. This adds to studies indicating that mainly woodlice are important for the breakdown of recalcitrant litter types (Jacob et al. 2009, Vos et al. 2011, Collison et al. 2013). Even stronger, the presence of low quality litter (Fagus) in litter mixtures induced a selection effect of woodlice causing the other litter species in the mixture to lose more mass (Vos et al. 2011). We provided litter always as a mixture of low and high quality, projecting the selection effect (Vos et al. 2011) to our study would indicate that consumption of woodlice monocultures on Acer litter would be lower if Acer would be offered as single species litter. Detritivores may alternate their consumption between litter species to fulfil their dietary requirements in an efficient way. They could adapt their consumption and growth rates based on the available food source, with overall consumption and growth being higher in more diverse litter (Hättenschwiler & Gasser 2005). This demonstrates the importance of detritivore identity to leaf litter breakdown. However, due to the huge variety in available food sources and the different nutritional requirements of species, the underlying mechanisms remain an open question.

Synergy

Effects of mixing two detritivores had additive, non-synergistic effects on the leaf litter breakdown of both Acer and Quercus. Indicating that the consumption by the two detritivore species in mixtures is not different from the sum (additive) of consumption per gram detritivore of the two species as predicted in monocultures. This contradicts with our expectation that synergy occurs between macro-detritivores (see e.g. Zimmer et al. 2005, De Oliveira et al. 2010, Collison et al. 2013). However, the mentioned studies are lab experiments, which could explain the contradictory nature of our results. Litter quality has been recorded to be important in detecting synergistic effects (synergy for high quality litter see Zimmer et al. 2005) as well as moisture conditions (synergy for low moisture conditions see Collison et al. 2013). We did not detect an effect of litter quality, moisture or temperature on synergy values between woodlice and millipedes. The use of microcosm experiments are very useful to disentangle the influence of different (a)biotic drivers, however they have limitation for scaling up to ecosystem processes (Rouifed et al. 2010, Collison et al. 2013). We think that field experiments with microcosms can be a valued addition to lab experiments because they are a step closer in incorporating the complexity of (forest) ecosystems.

Conclusion

We performed an experiment disentangling the effects of forest microclimate, detritivore biomass and identity on leaf litter breakdown of high and low quality litter. The field conditions make this experiment unique considering all other factors of forest ecosystem complexity. We have shown that changes in rainfall and associated soil moisture have the potential to alter leaf litter breakdown in temperate forests by macro-detritivores. Direct effects of changes in temperature are expected to be of minor importance and is probably an indirect driver of breakdown due to its effect on soil moisture. Changes in forest microclimate resulting in reduced moisture availability e.g. in forest edges (Chen et al. 1995, Gehlhausen et al. 2000) has therefore the potential to result in lower litter breakdown. However, macro-detritivore abundance and activity is higher in forest edges (De Smedt et al. 2016c, 2018b), which implies that mainly macro-detritivore relative consumption rate will go down but not absolute consumption. Macro-detritivore distribution in forests is highly species-specific (De Smedt et al. 2018a) and species identity has proven to be an important determinant for the breakdown of low quality litter. Therefore, the effects of altered species distributions can be expected to be stronger for the breakdown of low quality litter. The use of microcosms along forest transect (e.g. across forest stands, along forest edge-to-interior gradients) can be seen as a valuable tool to strengthen our understanding of the observed patterns and grasping the complexity of forest ecosystems.

Acknowledgements

P.D.S. holds a doctoral fellowship of the Research Foundation-Flanders (FWO). Many thanks to Gert Arijs, Daan Mertens and Willem Proesmans for their help with the collections of woodlice and millipedes and to Matty P. Berg for the useful discussions. We thank two anonymous reviewers for their valuable comments on an earlier version of the manuscript.

Appendix 5.1. Litter mass loss without detritivores

In order to calculate the relative consumption rate (RCR) by the different monocultures, we first modelled litter mass loss in the absence of detritivores. First, using only the control treatment data, we tested the influence of four-way interactions effect between soil moisture, temperature, detritivore treatment and time period on the mass loss of both *Acer* and *Quercus*. Then, the non-significant interaction terms dropped from the model until the minimal adequate model was obtained. *Acer* litter mass loss was significantly influenced by additive effects of time period (F = 121.59; df=5; p<0.001) and the moisture treatment (F = 11.49; df=1; p<0.001) and these two variables were then kept to model breakdown in the absence of detritivores. Litter mass loss of *Quercus* was only influenced by time period (F = 20.72; df=1; p<0.001) and only this variable was kept to model breakdown in the absence of detritivores. Then, we extracted the prediction of the retained model and used it to calculate the D index: .

is the mass loss in the control treatment (without the presence of detritivores) and is the initial mass.

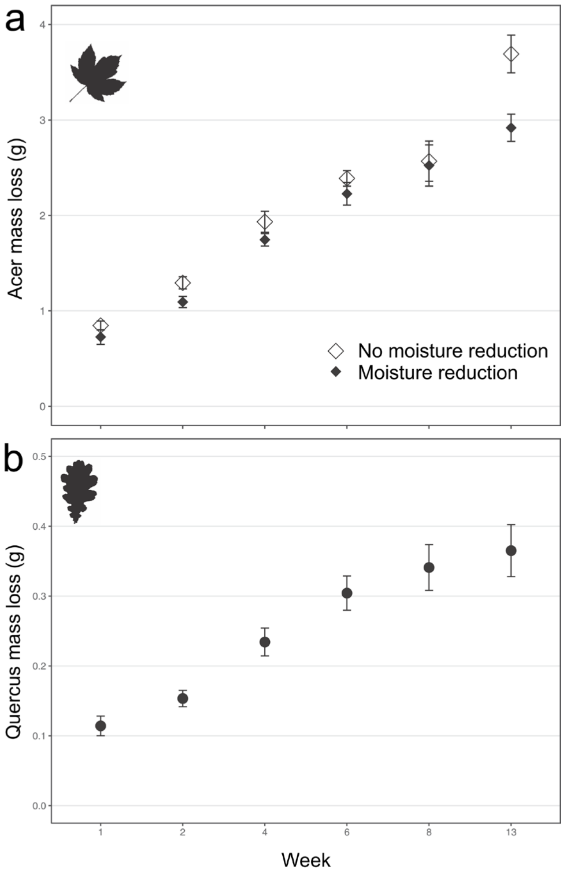


Figure A5.1.1 (previous page): *Litter mass loss of (a) Acer and (b) Quercus litter without the presence of macro-detritivores (woodlice and millipedes). Only significant predictor variables were modelled, i.e. sampled week and moisture treatment for Acer and sampled week for Quercus. These values are used to calculate relative consumption rates (RCR) of detritivores added to the microcosms.*

Appendix 5.2. Environmental treatments

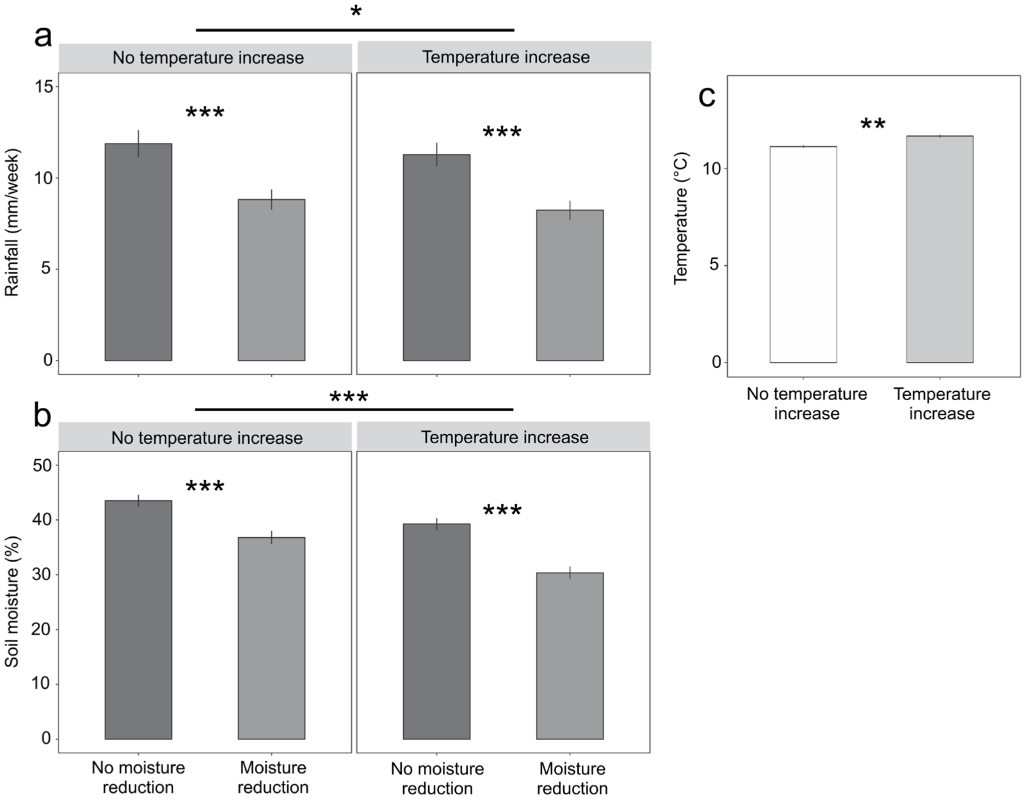


Figure A5.2.1: *Average rainfall (a), soil moisture (b) and temperature (c) under the different environmental treatments. *: p<0.05, **: p < 0.01, ***: p < 0.001. Error bars denote ± 1*standard error.*

Appendix 5.3. Survival and detritivore condition

Survival and detritivore condition (weight loss) was tested to assess if our experimental set-up influenced detritivore condition or survival, which could confound effects of other variables on litter breakdown.

In order to investigate the interaction between microclimatic variables (i.e. temperature and moisture), macrodetritivores treatment and time period (weeks after start of the experiment) on macrodetritivore survival and macrodetritivore weight difference before and after the experiment, we used mixed effect models with plot (cluster of microcosms in the field) as a random term. We have split up the analysis for millipedes and woodlice. We tested for four-way interactions with detritivore treatment (two levels being mixture or monoculture), moisture treatment (two levels), temperature treatment (two levels) and time period (six levels) on detritivore survival (Figure A5.3.1a,b) and change in detritivore biomass (Figure A5.3.1c,d). We used a binominal distribution for the survival analyses, while detritivore biomass was normally distributed. We used the *lmer*-function form the *lme4*-package (Bates et al. 2015) in the statistical software of R (R Core Team 2017).

Millipede and woodlouse survival and weight loss were not influenced by time period, any of the treatments or their interactions (all p-values of the lmer's > 0.05). We can therefore assume that the effects on leaf litter mass loss cannot be attributed to a decreasing macro-detritivore condition or population size. The below results incorporate all studied microcosms.

Of course, the death of a very large or very small detritivore could highly bias the weight difference results, therefore, we ran the analysis a second time only incorporating microcosms of which all individuals survived (i.e. 59 (82%) monoculture microcosms and 64 (89%) mixture microcosms for millipedes and 35 (49%) monocultures and 48 (67%) mixtures for woodlice). The outcomes were the same (all -values of the lmer's > 0.05).

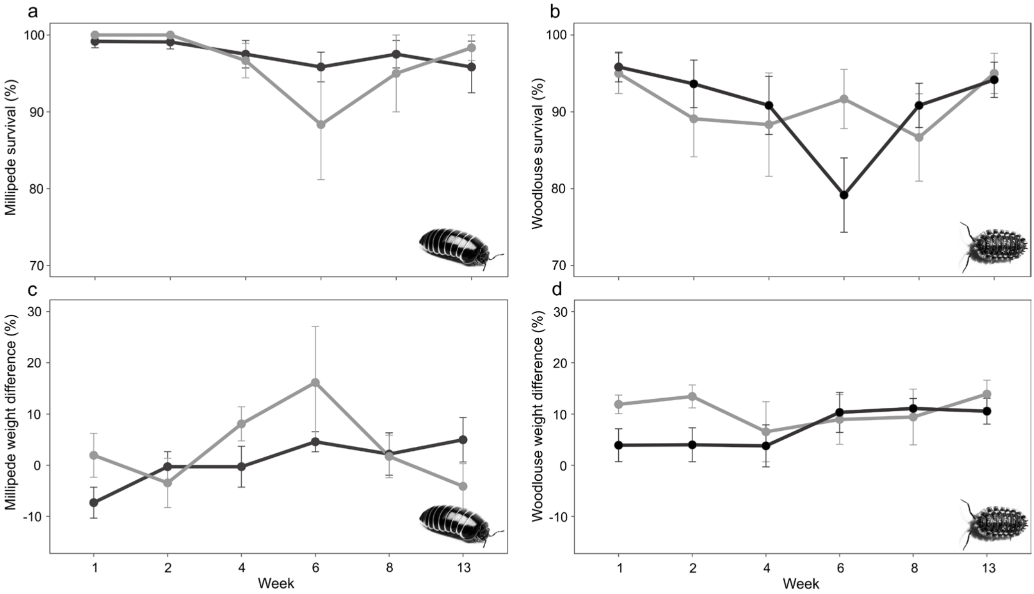


Figure A5.3.1: *Survival of (a) millipedes and (b) woodlice (%) and weight loss (%) of (c) millipedes and (d) woodlice per sampled week. Black lines represent individuals from monocultures; grey lines represent individuals from mixtures. Error bars denote ± 1*standard error.*

Porcellio monticola | Gert Arijs

Chapter 6

ARTHROPOD DETRITIVORES IN EUROPEAN FOREST FRAGMENTS

Linking macro-detritivore distribution to desiccation resistance in small forest fragments embedded in agricultural landscapes in Europe

Adapted from: De Smedt P, Baeten L, Proesmans W, Berg MP, Brunet J, Cousins SAO, Decocq G, Deconchat M, Diekmann M, Gallet-Moron E, Giffard B, Liira J, Martin L, Ooms A, Valdés A, Wulf M, Hermy M, Bonte D, Verheyen K (2018) Linking macrodetritivore distribution to desiccation resistance in small forest fragments embedded in agricultural landscapes in Europe. Landscape Ecology 33: 407-421.

Abstract

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 macro-detritivore community, which is however, poorly studied. We investigated macro-detritivore distribution patterns at local and landscape-level and used a key functional trait (desiccation resistance) to gain mechanistic insights of the putative drivers.

Macro-detritivores 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 community composition. Secondly, we tested if desiccation resistance of macro-detritivores varied across communities at different spatial scales using linear mixed effect models.

Forest edge-centre and landscape-use intensity determined activity-density and community composition of macro-detritivores in forest fragments, while fragment characteristics like size and continuity were relatively unimportant. Forest edges and higher land-use intensity landscapes supported higher activity-density of macro-detritivores and determined community composition. Forest edges sustained woodlouse communities dominated by more drought tolerant species.

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

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 spillover 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, because 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 & 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 macro-detritivores, at least in terms of their biomass (Jeffery et al. 2010), but poorly studied in a landscape context (David & 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 (Deconinck et al. 2005, Topp et al. 2006, Tajovský et al. 2012, De Smedt et al. 2016c). Within forest fragments, there are large differences in macro-detritivore distribution between forest edges and forest interiors (Riutta et al. 2012, Bogyó et al. 2015, De Smedt et al. 2016c). 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 & Handa 2010, Martins da Silva et al. 2015). Therefore, we studied distribution of macro-detritivores 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 macro-detritivore 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. 2008). 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. Macro-detritivores show strong responses to changes in soil moisture levels, which has been proposed a key factor in their distribution (David & 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 macro-detritivore patterns in small forest fragments using community weighted desiccation resistance of the species. Significant trait-patterns could therefore indicate drivers of macro-detritivore biodiversity in these landscapes and give insights about the potential effects on ecosystem functioning.

We intend to investigate the following hypotheses (1) macro-detritivore distribution differs at different spatial scales across Western Europe; (i) between landscapes, (ii) forest fragments and (iii) locations within forest fragments; (2) community weighted mean macro-detritivore 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 2,000 km (Fig. 6.1a). In every region, we selected two 5 x 5 km landscape windows: one higher land-use intensity landscape and one lower land-use intensity landscape (n = 14 landscape 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 and a more stable hydrology allowing agricultural intensification (see e.g. Fig. 6.1b and Table 6.1). 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 hydrology and lower soil fertility (see e.g. Fig. 6.1c and Table 6.1). We expect these landscapes to be more permeable for species to move across the landscape.

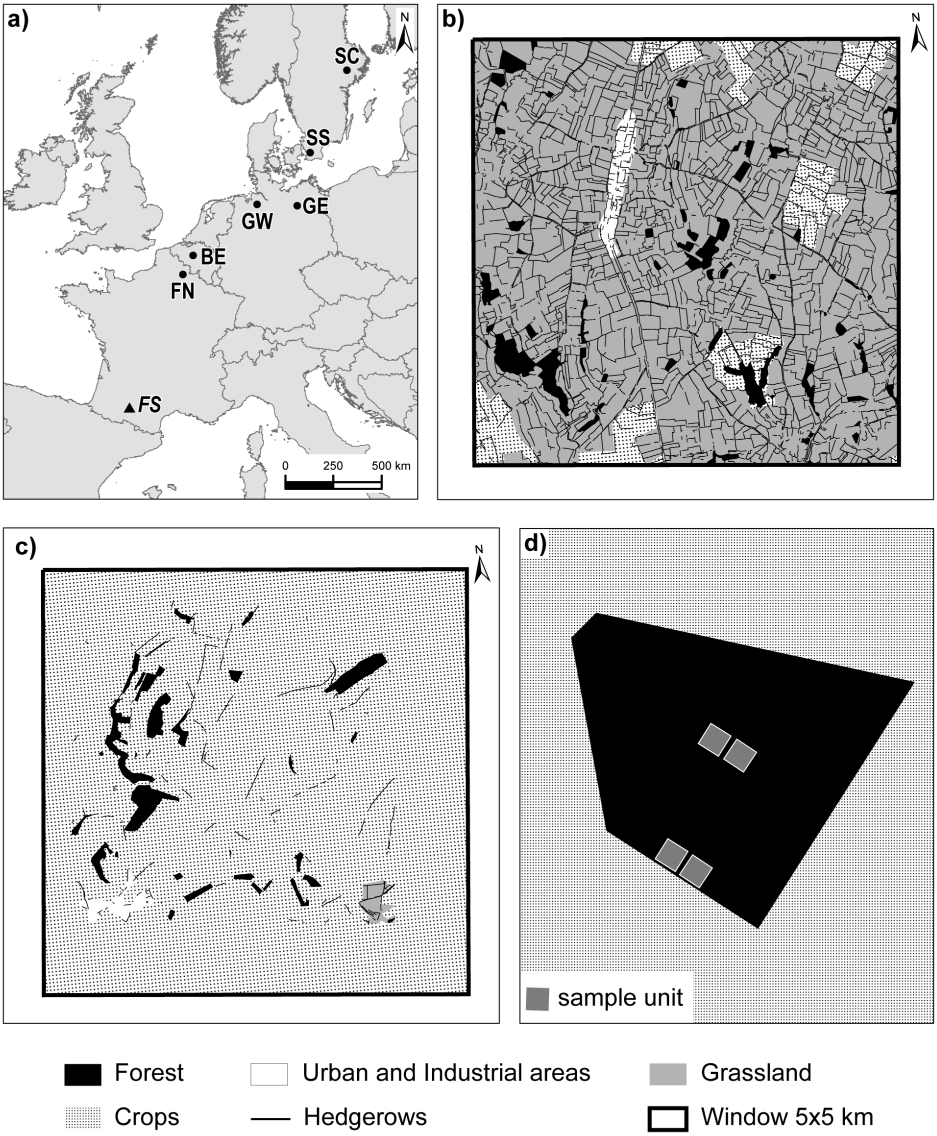


Figure 6.1. *Study area and experimental set-up. a) Study area with all regions sampled for woodlice and millipedes; FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, GE: Eastern Germany, SS: Southern Sweden and SC: central Sweden. All regions represented by a dot are incorporated in the trait study as well. b) lower land-use intensity landscape window (5 x 5 km) of Northern France. c) higher land-use intensity landscape window (5 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.*

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 digitised 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 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 landscape window. Four fragments per category and per landscape window were retained for field sampling: hence, 16 fragments per landscape window and 224 fragments across Western 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 0.08ha to 44.12ha with a median of 1.39ha. Forest continuity ranged from 12 years to 269 years with a median of 51 years.

Table 6.1. *Characteristics of the landscape windows in the different regions according to landscape-use intensity (LUI). Percentage of forest cover, annual crops, pastures and the amount of hedgerows per hectare. Total represent the average value across landscape windows ± 1* standard deviation.*

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

Macro-detritivore 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. Community composition has also been reported as not being reflected by pitfall traps (Topping & 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-oriented 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. 6.1d and Chapter4: Appendix 6.1). If the south-oriented edge was not suitable e.g. bordered by a ditch, road or other physical barrier (38% of the edges), we used the east- (16% of the edges), west- (18%) or north-oriented edge (4%). Macro-detritivores were sampled twice between April and August 2013. 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. 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 (Appendix 6.1). This database consists of standardised laboratory measurements on wild caught individuals from the Netherlands. 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 database, 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. Animals were placed in a “desiccation chamber” with the bottom-side made of mesh (to allow gas-exchange) and a glycerol solution underneath. This solution keeps the air humidity at a constant of 85% while temperature was kept at 15°C. This temperature does not impose temperature stress on the animals (for more details on the methods see Moretti et al. 2017). The average survival time (h) under constant relative humidity was used as an estimate of *desiccation resistance* (h) (Moretti et al. 2017). 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, Appendix 6.2). *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 & Hill 2007, Qian & 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, landscape 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:

$$y_i = \beta^0 + \beta^{region}_{j(i)} + \beta^{window}_{k(i)} + \beta^{fragment}_{l(i)} + \beta^{LUI}_{m(i)} + \beta^{loc}_{n(i)} +$$

$$\beta^{window\ x\ loc}_{k(i),n(i)} + \beta^{size}_{k(i)}.\,size_i + \beta^{cont}_{k(i)}.\,cont_i + \varepsilon_i$$

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, $\beta^{region}_{j(i)}$ is an effect of region (j = 1, …,7), $\beta^{window}_{k(i)}$ is an effect of landscape window (k = 1, …,14), $\beta^{fragment}_{l(i)}$ is an effect of forest fragment (l = 1, …, 224), $\beta^{LUI}_{m(i)}$ is an effect of landscape-use intensity (m = 1[lower intensity] or 2[higher intensity]), $\beta^{loc}_{n(i)}$ is an effect of location in the forest (n = 1[edge] or 2[centre]), $\beta^{window\ x\ loc}_{k(i),n(i)}$ is an effect of the interaction between landscape window and location in the forest, $\beta^{size}_{k(i)}.\ size_i$ is the effect when we allow the slope of size to differ between landscape windows, $\beta^{cont}_{k(i)}.\ cont_i$ is the effect when we allow the slope of continuity to differ between landscape windows. Residual error was modelled from a normal distribution ($\varepsilon_i \sim N(O,\sigma^2)$) and's β's were modelled from separate zero mean normal distributions (e.g. $\beta^{region}_{j(i)} \sim N(O,\sigma^2_{region})$, with σ^2_{region} the between-region "biogeographic" variance). Prior distribution of β^0 was modelled around zero with a variance around 100. Prior distribution of the other β's were modelled around zero with a variance around 1. Variance components were calculated as finite-population standard deviations of the effects β (e.g. s_{region}), with 95% and 68% credibility intervals (Gelman & Hill 2007). 10,000 Markov chain Monte Carlo (MCMC) sampling iterations were used of which 5,000 as warmup (number of iterations divided by two) and posterior distributions were derived from the remaining 5,000 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 visualised using a graphical ANOVA table (Gelman & 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 community 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 community 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). This is the weighted mean of trait values based on individual species abundances at each sample point. 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 (Appendix 6.3). 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 (at region level, i.e. the two windows per region combined) are included in the data set (Fig. 6.2). Woodlice regional (γ-diversity) species richness followed a latitudinal gradient (Fig. 6.2a) 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. 6.2b), which showed the highest species richness in the centre regions (Belgium and Northern France) and lower species richness in the other regions.

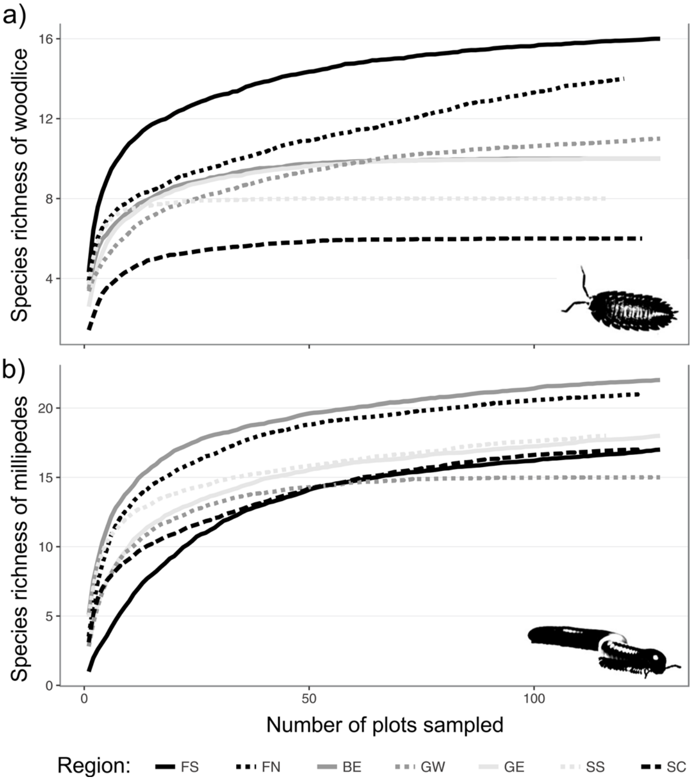


Figure 6.2. *Regional species accumulation curves for woodlice (a) and millipedes (b) for the different regions; FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, GE: Eastern Germany, SS: Southern Sweden and SC: central Sweden. Curves are based on random sampling of the different sampling units (100 permutations).*

Distribution patterns

Region, landscape window and fragment explained about the same amount of variation compared with the unexplained residual variation for the activity-density, indicating that region, landscape 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. 6.3). Landscape-use intensity and location were important design variables in explaining variation in the activity-density, with landscape-use intensity explaining the same amount of variation as interregional variation and location explaining more than half of the interregional variation for woodlice (Fig. 6.3a). This means, for instance, that the variation in total activity-density between the higher- versus lower land-use intensity landscapes was more important than variation between the regions along this >2,000 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. 6.3b,d). The location effect seemed to be consistent over the different landscape windows for woodlouse activity-density (low interaction effect), but depended on landscape 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 landscape 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. 6.4). The effects are by far the most extreme in Northern France (Appendix 6.4). 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 (Appendix 6.5).

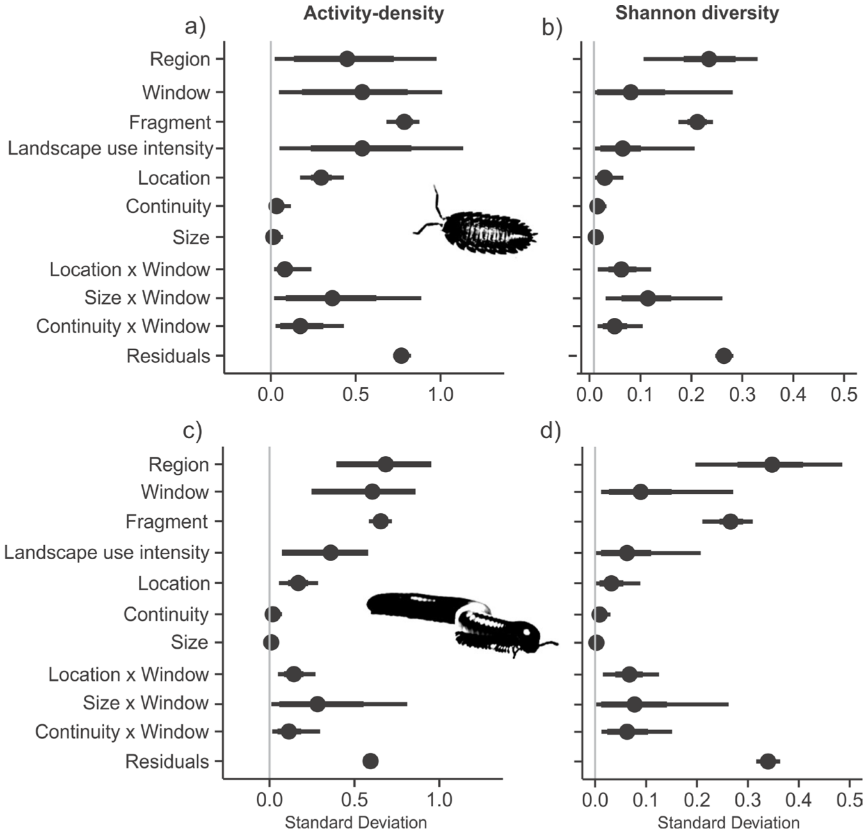


Figure 6.3. (previous page) *Variance components based on a multilevel analysis of variance presented as a graphical ANOVA. (a) Woodlouse activity-density, (b) woodlouse Shannon-diversity, (c) millipede activity-density and (d) millipede Shannon-diversity. Point estimates show posterior means, wide lines are the 68% posterior credible intervals and thin lines are the 95% posterior credible intervals.*

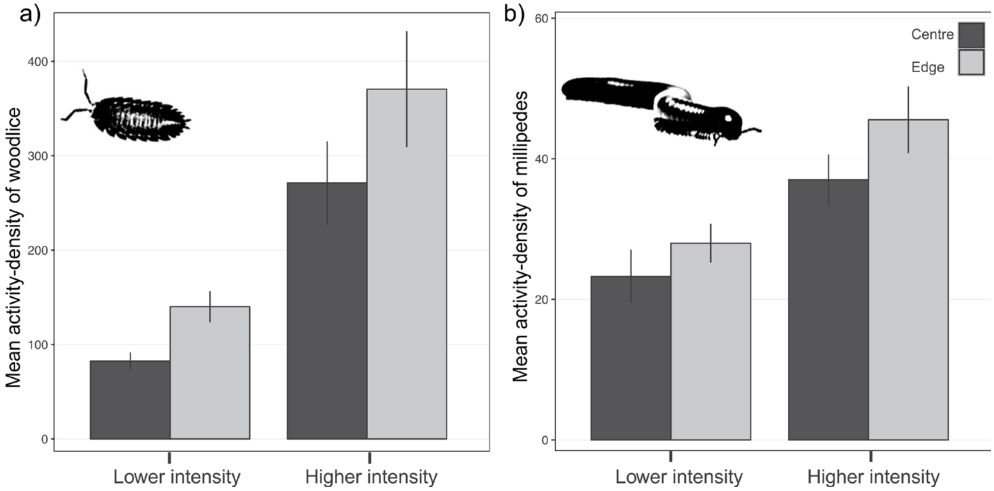


Figure 6.4. *Mean activity-density of (a) woodlice and (b) millipedes in forest edges and forest centres at the sample unit level in lower land-use intensity (LUI) landscapes and higher land-use intensity (LUI) landscapes. Error bars represent ± 1 standard error.*

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. 6.5). 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, the importance of landscape-use intensity diminished and was only significant for two regions for woodlice and in two regions for millipedes (Fig. 6.5). 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).

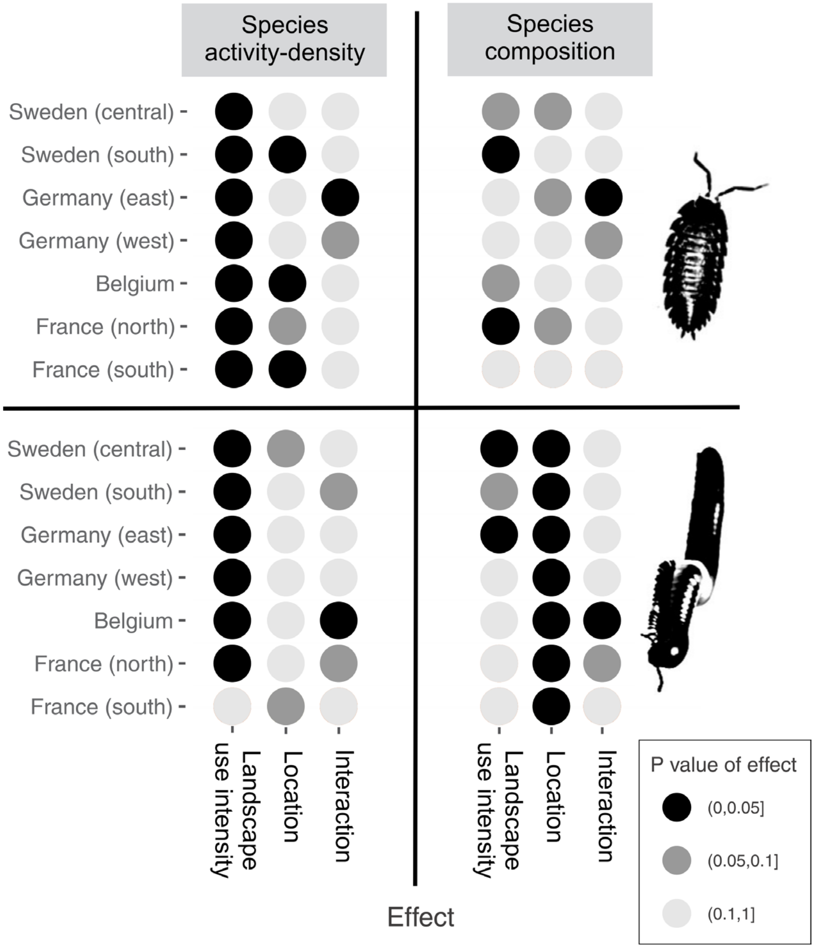


Figure 6.5. *Effects on landscape-use intensity (lower vs. higher land-use intensity landscapes), location (edge vs. centre) and their interaction on the community structure of woodlice and millipedes in fragmented forests. We tested which factors are associated with variation in the multivariate species activity-densities of the communities (left part) or the community composition (relative species activity-densities; right part).*

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. 6.6). No significant differences in desiccation resistance (lme, df=5, F=1.88, p>0.05) were found between landscapes differing in landscape-use intensity. The interaction between landscape-use intensity and location was not significant for desiccation resistance (lme, df=187, F=0.87, p>0.05).

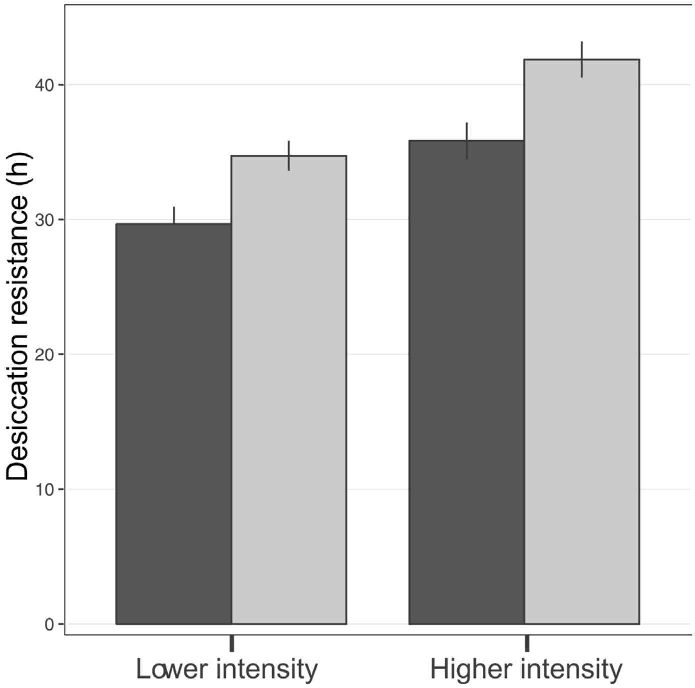


Figure 6.6. *Average community weighted mean desiccation resistance of woodlice as survival time (in hours) under constant relative humidity of 85% for lower land-use intensity landscapes and higher land-use intensity landscapes. Dark grey bars represent forest centres; light grey bars represent forest edges. Error bars represent ± 1 standard error.*

Discussion

Macro-detritivore distribution

We performed a large scale study on the distribution patterns of macro-detritivores in forest fragments embedded in agricultural landscapes across Western 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 community 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 & 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 results are supported by earlier research from Riutta et al. (2012) and De Smedt et al. (2016c), showing that forest edges have a higher abundance of macro-detritivores. 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. 2016c) 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. 2016c). 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 (Heithecker & Halpern 2007, Delgado et al. 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 macro-detritivore distribution and functioning (David & 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 & Handa 2010, Hornung 2011, Gerlach et al. 2014). The altered microclimate at forest edges also causes a more abundant and species rich herb layer (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). This is underpinned by the extreme high activity-density of detritivores in the highly managed landscape window in Northern France (Appendix 6.4). A landscape that has more than 92% annual crops, less than 6% forest and few semi-natural elements like hedgerows harbours more than a fivefold of woodlice activity-densities in its small forest fragments compared to other landscape windows. 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 spillover of nutrients, there could also be a spillover of organisms from one system to the other (Tscharntke et al. 2012, Boetzl et al. 2016, Madeira et al. 2016). This spillover can be strongly dependent on the neighbouring landscape (Madeira et al. 2016). Few data are available for macro-detritivores, but low abundances of woodlice in intensively cultivated agricultural fields (Paoletti & Hassall 1999) makes it unlikely that a spillover 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 fragments embedded in higher land-use intensity landscapes compared to lower intensity landscapes (See Appendix 6.3: Table A6.3.2). We can therefore assume a spillover of these millipede species from agricultural fields to forest fragments, 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 (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 macro-detritivore 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 macro-detritivore 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 & 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 & 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. Additionally, many of the sampled forest patches are leftovers of former continuous forest and have an elongated shape, because they border small streams or consist of forest trips between two landowners. Therefore, the correlation between size and the distance of the forest interior to the nearest forest edge is weak and size does not inform on amount of forest edge and forest interior (De Smedt et al. unpublished data). The average size of a forest fragment in Chapter 4 (Regions FN, BE, GW, SS and SC) is 3.45±5.56 ha. If these forest fragments would be perfectly circular, the average distance between the forest interior and the forest edge is 105 m, while in our sampled forests the average distance from the forest interior to the forest edge is only 33 m. In Chapter 4, we found very strong correlations between arthropod abundance and distance from the forest edge. This indicated that probably the size of interior area is more important than total forest size for arthropod detritivore abundance and species composition.

We quantified forest continuity as a weighted average of the different stand ages; and the weak effect that we found could raise the question if we used a good measure to quantify forest continuity. Alternatively, Kolb & Diekman (2004) for example quantified forest continuity as the period when at least a part of the forest meets the condition of temporal continuity and tested the effect on forest plant species. However, they found only a relatively weak effect on community 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. Arthropod detritivores show strong differences in abundance at small spatial scale, possibly also continuity is important on these small scales. Therefore, large forest patches of which only a small part remains forested for a long period might be enough to sustain detritivore population of certain species through time.

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 (Heithecker & Halpern 2007, Delgado et al. 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 6.2). 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 & Gundersen 1989, Wuyts et al. 2008b)) 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 macro-detritivore abundance and community composition is strongly altered by landscape use intensity and forest edges. Indicating the importance of both landscape context and within forest-fragment gradients for macro-detritivore distribution. Although fragment characteristics are important for macro-detritivore 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 macro-detritivore 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 mimicking 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.

Acknowledgements

This research was funded by the ERA-Net BiodivERsA project smallFOREST, with the national funders ANR (France), MINECO (Spain), FORMAS (Sweden), ETAG (Estonia), DFG (Germany), BELSPO (Belgium) and DFG (Germany) part of the 2011 BiodivERsA call for research proposals. P.D.S. and W.P. each hold a doctoral fellowship of the Research Foundation-Flanders (FWO). The research of K.V. is supported by the ERC Consolidator Grant 614839 – PASTFORWARD. D.B. and L.B. are supported by the FWO research network EVENET. Many thanks to Gert Arijs, Kent Hansson, Marco Langer, Vincent Le Roux, Jessica Lindgren, Mathias Reiche, Sabine Sigfridsson and Rieneke Vanhulle for help during field sampling.

Appendix 6.1. Raw data for trait analysis

An existing trait database from the Netherlands (Berg et al., unpublished data) was complemented with trait data measured on living individuals of of *Porcellio monticola* and *Philoscia affinis* caught in Belgium (Viroinval, Hainaut) and individuals of *Porcellio gallicus* in Northern France (Landifay-et-Bertaignemont, Aisne). The animals (captured in January 2016) were kept outside in plastic boxes with soil and litter from the place where they were captured until measurements at the Vrije Universiteit, Amsterdam, The Netherlands in February 2016.

Table A6.1.1 *Woodlouse family, length, desiccation resistance and abundance of the studied species used in the trait analysis. NA indicates that the data is not available for a certain trait.*

	Family	**Length (mm)**	**Desiccation resistance (h)**	**Abun-dance**
Armadillidium opacum (C. Koch, 1841)	Armadillidae	8.43	57.6	937
Armadillidium pictim (Brandt, 1833)	Armadillidae	5.92	74.7	167
Armadillidium pulchellum (Zenker, 1798)	Armadillidae	4.77	45.9	1099
Armadillidium vulgare (Latreille, 1804)	Armadillidae	8.33	73.6	23238
Cylisticus convexus (De Geer, 1778)	Cylisticidae	13.5	NA	1
Ligidium hypnorum (Cuvier, 1792)	Ligiidae	5.56	4.5	1339
Oniscus asellus (Linnaeus, 1758)	Oniscidae	9.68	22.1	3477
Philoscia affinis (Verhoeff, 1908)	Philosciidae	6.90	26.4	60
Philoscia muscorum (Scopoli, 1763)	Philosciidae	6.45	31.8	28728
Porcellio dilatatus (Brandt, 1833)	Porcellionidae	16.5	NA	4
Porcellio gallicus (Dollfus, 1904)	Porcellionidae	9.00	38.7	1024
Porcellio monticola (Lereboullet, 1853)	Porcellionidae	9.70	99.9	70
Porcellio scaber (Latreille, 1804)	Porcellionidae	7.86	51.3	23501
Porcellionides pruinosus (Brandt, 1833)	Porcellionidae	7.38	NA	5
Porcellium conspersum (C. Koch, 1841)	Trachelipodidae	5.54	18.1	431
Trachelipus rathkii (Brandt, 1833)	Trachelipodidae	7.21	22.6	2122
Trichoniscoides albidus (Budde-Lund, 1880)	Trichiniscidae	2.85	2.2	15
Haplophthalmus (Schöbel, 1860) mengii/montivagus	Trichiniscidae	1.86	2.8	1
Trichoniscoides helveticus (Carl, 1908)	Trichiniscidae	2.23	2.6	1
Trichoniscus provisorius (Racovitza, 1908)	Trichiniscidae	2.94	2.4	5
Trichoniscus pusillus (Brandt, 1833)	Trichiniscidae	2.94	2.4	520

Appendix 6.2.
Traits related to desiccation resistance

This appendix describes the methods and correlations of some traits related to desiccation resistance. Since both body length, body mass and water loss rate are strongly correlated to desiccation resistance they were excluded from further analysis in the manuscript itself.

Methods

Desiccation resistance and *water loss rate* were calculated by exposing specimens to 85% relative humidity. The average survival time (hours) under constant relative humidity of 85% was used as an estimate of desiccation resistance (Dias et al. 2013). *Desiccation resistance* (h) is used as a measure for the capacity of the species to withstand dry conditions. *Water loss rate* (mg/mg fw/h) was calculated by the slope of the linear regression between water mass of the species and time and was expressed as the proportion of initial water content that was lost per hour (for detailed methods see Dias et al. 2013). *Length* (mm) was measured on fresh individuals from the tip of the head until the end of the telson (posterior-most division of the woodlouse body). *Mass* was measured as the average dry weight (mg) after drying specimens at 60 °C. The above traits were measured on 5-35 adult specimens per species for each trait.

We used a linear model (from the *stats* package) to assess the relation between desiccation resistance, body length, body mass and water loss rate across the 19 woodlouse species.

Results

Woodlouse species desiccation resistance increases with increasing length and mass of the species, and decreases with increasing water loss rate (Table A6.2.1). Woodlouse species water loss rate decreases with increasing species length and mass. Woodlouse species mass increases with increasing woodlouse length.

Table A6.2.1 *Linear relationship between different woodlouse traits. Values represent t-values of linear models. Significance levels: **: P < 0.01, ***: P < 0.001*

	Length	Mass	Water loss rate
Desiccation resistance	3.55 **	3.30 **	-3.87 **
Water loss rate	-5.28 ***	-3.73 **	
Mass	9.44 ***		

Appendix 6.3. Species lists

A) Millipedes according to location in the forest

Table A6.3.1. *Species list with total abundances of the collected millipedes per region. Species numbers are divided according to sample location in the forest with individuals caught in the forest centre (CE) before the slash and individuals caught in forest edges (ED) after the slash. All individuals were identified to the species level if possible. Female millipedes of the Julidae family, which cannot be identified morphologically to species level with 100% certainty, were identified as Julidae spp. FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, GE: Eastern Germany, SS: Southern Sweden and SC: central Sweden.*

Amount CE/ amount ED	**FS**	**FN**	**BE**	**GW**	**GE**	**SS**	**SC**	**Total**
Allajulus nitidus (Verhoeff 1891)	2/11	50/53	14/16	1/6	3/0	4/6	23/4	193
Blaniulus guttulatus (Fabricius 1798)		1/1	0/1				1/1	5
Brachydesmus superus Latzel 1884	4/7	6/9	16/48	17/8	2/31	44/46	25/92	355
Brachyiulus pusillus (Leach 1814)	0/7	7/14	118/68			0/1		215
Choneiulus palmatus (Nemec 1895)							0/4	4
Chordeuma sylvestre C.L. Koch 1847		2/3						5
Craspedosoma rawlinsi Leach 1814		0/6	6/6	5/2		48/41	1/1	116
Craspedosoma spec.	3/2							5
Cylindroiulus caeruleocinctus (Wood 1864)	1/1	261/179	25/55		33/33	131/213	783/906	2621
Cylindroiulus latestriatus (Curtis 1845)			0/1		0/1	1/0		3
Cylindroiulus londinensis (Leach 1814)	16/19							35
Cylindroiulus punctatus (Leach 1815)	5/3	8/16	76/84	18/15	20/24	18/10	3/2	302
Glomeris intermedia Latzel 1884		55/49	57/26					187
Glomeris marginata (Villers 1789)	99/174	1/2	92/125	75/157	32/55	59/83		954
Hirudisoma latum (Ribaut 1908)	1/0							1
Julidae spec.	2/5	37/19	46/39	53/86	233/225	363/354	137/218	1817
Julus scandinavius Latzel 1884		17/9	37/29	62/84	168/208	69/121	83/99	986
Julus scanicus Latzel 1884					1/0			1
Julus terrestris Linnaeus 1758							0/21	21
Leptoiulus belgicus (Latzel 1884)			0/5					5
Leptoiulus kervillei (Brolemann 1896)		65/68	132/155					420

Leptoiulus proximus (Nemec 1896)					7/6			13
Melogona gallica (Latzel 1884)		19/28	30/40					117
Melogona voigtii (Verhoeff 1899)						0/1		1
Mycogona sp.				2/2				4
Nemasoma varicorne C.L. Koch 1847			1/2		1/3		2/1	10
Ommatoiulus rutilans (C.L. Koch 1847)	1/31							32
Ommatoiulus sabulosus (Linnaeus 1758)	0/1	2/2	0/3	75/110	111/159	5/9	139/134	750
Ophiodesmus albonanus (Latzel 1895)		1/1						2
Ophyiulus pilosus (Nemport 1842)				8/3	1/0	214/91	38/87	442
Orthochordeumella pallida (Rothenbuhler 1899)		3/4						7
Polydesmus angustus Latzel 1884	3/2	79/123	18/13	97/101				436
Polydesmus complanatus (Linaeus 1761)					48/24	18/3	1/1	95
Polydesmus coriaceus Porat 1871	13/31		156/253					453
Polydesmus denticulatus C.L. Koch 1847	0/9	8/16	9/16	33/10	19/17	0/2	206/364	709
Polyzonium germanicum Brandt 1837					25/18	195/140		378
Polydesmus inconstans Latzel 1884	2/17	10/8	16/27	8/21	35/28	236/176	64/168	816
Propolydesmus testaceus (C.L. Koch 1847)		21/32						53
Proteroiulus fuscus (Am Stein 1857)	1/0		2/2	11/7	10/4	164/17	4/11	233
Tachypodoiulus niger (Leach 1814)		267/633	282/427	8/25				1642
Unciger foetidus (C.L. Koch 1838)				1/2	41/48	239/214	12/0	557
All species	**153/320**	**920/ 1275**	**1133/ 1441**	**474/639**	**790/884**	**1808/ 1528**	**1522/ 2114**	**15001**

B) Millipedes according to landscape-use intensity

Table A6.3.2. *Species list with total abundances of the collected millipedes per region. Species numbers are divided according to landscape-use intensity with individuals caught in lower land-use intensity landscapes (L-LUI) before the slash and individuals caught in higher land-use intensity landscapes (H-LUI) after the slash. All individuals were identified to the species level if possible. Female millipedes of the Julidae family, which cannot be identified morphologically to species level with 100% certainty, were identified as Julidae spp. FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, GE: Eastern Germany, SS: Southern Sweden and SC: central Sweden.*

Amount L-LUI/ amount H-LUI	**FS**	**FN**	**BE**	**GW**	**GE**	**SS**	**SC**	**Total**
Allajulus nitidus (Verhoeff 1891)	3/10	10/93	17/13	5/2	1/2	0/10	0/27	193

Blaniulus guttulatus (Fabricius 1798)		0/2	1/0				0/2	5
Brachydesmus superus Latzel 1884	2/9	11/4	38/26	18/7	31/2	49/41	6/111	355
Brachyiulus pusillus (Leach 1814)	2/5	0/21	42/144			0/1		215
Choneiulus palmatus (Nemec 1895)							1/3	4
Chordeuma sylvestre C.L. Koch 1847		4/1						5
Craspedosoma rawlinsi Leach 1814		6/0	8/4	0/7		64/25	2/0	116
Craspedosoma spec.	4/1							5
Cylindroiulus caeruleocinctus (Wood 1864)	2/0	22/418	0/80		53/13	7/337	0/1689	2621
Cylindroiulus latestriatus (Curtis 1845)			1/0		0/1	1/0		3
Cylindroiulus londinensis (Leach 1814)	28/7							35
Cylindroiulus punctatus (Leach 1815)	4/4	13/11	58/102	9/24	30/14	16/12	2/3	302
Glomeris intermedia Latzel 1884		51/53	83/0					187
Glomeris marginata (Villers 1789)	132/141	3/0	204/13	69/163	0/87	142/0		954
Hirudisoma latum (Ribaut 1908)	1/0							1
Julidae spec.	2/5	6/50	48/37	76/63	155/303	386/331	148/207	1817
Julus scandinavius Latzel 1884		8/18	43/23	85/61	189/187	99/91	59/123	986
Julus scanicus Latzel 1884					1/0			1
Julus terrestris Linnaeus 1758							0/21	21
Leptoiulus belgicus (Latzel 1884)			0/5					5
Leptoiulus kervillei (Brolemann 1896)		60/73	153/134					420
Leptoiulus proximus (Nemec 1896)					12/1			13
Melogona gallica (Latzel 1884)		3/44	16/54					117
Melogona voigtii (Verhoeff 1899)						0/1		1
Mycogona sp.				4/0				4
Nemasoma varicorne C.L. Koch 1847			3/0		3/1		0/3	10
Ommatoiulus rutilans (C.L. Koch 1847)	11/21							32
Ommatoiulus sabulosus (Linnaeus 1758)	1/0	0/4	0/3	28/157	148/122	8/6	45/228	750
Ophiodesmus albonanus (Latzel 1895)		2/0						2
Ophyiulus pilosus (Nemport 1842)				9/2	1/0	130/175	28/97	442
Orthochordeumella pallida (Rothenbuhler 1899)		5/2						7
Polydesmus angustus Latzel 1884	0/5	15/187	15/16	138/60				436
Polydesmus complanatus (Linaeus 1761)					50/22	16/5	1/1	95

Polydesmus coriaceus Porat 1871	23/21		79/330					453
Polydesmus denticulatus C.L. Koch 1847	0/9	3/21	10/15	15/28	16/20	2/0	125/445	709
Polyzonium germanicum Brandt 1837					35/8	321/14		378
Polydesmus inconstans Latzel 1884	1/18	18/0	2/41	9/20	59/4	195/217	1/232	816
Propolydesmus testaceus (C.L. Koch 1847)		1/52						53
Proteroiulus fuscus (Am Stein 1857)	0/1		3/1	11/7	12/2	174/7	4/11	233
Tachypodoiulus niger (Leach 1814)		478/422	299/410	33/0				1642
Unciger foetidus (C.L. Koch 1838)				2/1	49/40	350/103	0/12	557
All species	**216/257**	**719/ 1476**	**1123/ 1451**	**511/602**	**845/829**	**1960/ 1376**	**422/ 3214**	**15001**

C) Woodlice according to location in the forest

Table A6.3.3. *Species list with total abundances of the collected woodlice per region. Species numbers are divided according to sample location in the forest with individuals caught in the forest centre (CE) before the slash and individuals caught in forest edges (ED) after the slash. FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, GE: Eastern Germany, SS: Southern Sweden and SC: central Sweden.*

Amount CE/ amount ED	**FS**	**FN**	**BE**	**GW**	**GE**	**SS**	**SC**	**Total**
Armadillidium nasatum (Budde-Lund, 1885)	11/60							71
Armadillidium opacum (C. Koch, 1841)			17/157		127/66	99/138	31/302	937
Armadillidium pictim (Brandt, 1833)				8/21			52/86	167
Armadillidium pulchellum (Zenker, 1798)				252/142	248/145		154/158	1099
Armadillidium vulgare (Latreille, 1804)	348/ 3348	6516/ 13470	56/128	1/0	5/35	412/ 2615		26934
Chaetophiloscia elongata (Dollus, 1884)	669/720							1389
Cylisticus convexus (De Geer, 1778)		0/1						1
Haplophthalmus (Schöbel, 1860) *mengii/montivagus*		1/0						1
Ligidium hypnorum (Cuvier, 1792)		111/96	308/58	266/58	96/26	175/145		1339
Lucasius pallidus (Budde-Lund, 1885)	0/5							5
Oniscus asellus (Linnaeus, 1758)	2/1	620/387	524/449	428/345	123/75	238/280	5/3	3480
Oniscus simonii (Budde-Lund, 1885)	2/1							3
Orthometopon planum (Budde-Lund, 1885)	64/12							76

Philoscia affinis (Verhoeff, 1908)	1154/469			32/28				1683
Philoscia muscorum (Scopoli, 1763)	1226/997	3916/3365	1823/2125	2286/2652	2394/2551	3710/3906		30951
Porcellio dilatatus (Brandt, 1833)	0/4	4/0						8
Porcellio gallicus (Dollfus, 1904)	299/155	553/471						1478
Porcellio monticola (Lereboullet, 1853)	284/113	54/16						467
Porcellio scaber (Latreille, 1804)	5/13	5003/5277	327/1511	879/3014	1428/3352	687/2023		23519
Porcellionides pruinosus (Brandt, 1833)	0/1	0/2		0/3				6
Porcellium conspersum (C. Koch, 1841)				3/0	320/108			431
Sphaerobathytropa ribauti (Verhoeff, 1908)	170/45							215
Trachelipus rathkii (Brandt, 1833)		1/1	50/23		16/58	23/178	578/1194	2122
Trichoniscoides albidus (Budde-Lund, 1880)			13/2					15
Trichoniscoides helveticus (Carl, 1908)		1/0						1
Trichoniscus provisorius (Racovitza, 1908)			0/5					5
Trichoniscus pusillus (Brandt, 1833)	68/35	49/19	82/60	7/2	39/45	83/22	82/30	623
All species	**4302/5979**	**16829/23105**	**3200/4518**	**4162/6265**	**4796/6461**	**5427/9307**	**902/1773**	**97026**

D) Woodlice according to landscape-use intensity

Table A6.3.4. *Species list with total abundances of the collected woodlice per region. Species numbers are divided according to landscape-use intensity with individuals caught in lower land-use intensity landscapes (L-LUI) before the slash and individuals caught in higher land-use intensity landscapes (H-LUI) after the slash. FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, GE: Eastern Germany, SS: Southern Sweden and SC: central Sweden.*

Amount L-LUI/ amount H-LUI	**FS**	**FN**	**BE**	**GW**	**GE**	**SS**	**SC**	**Total**
Armadillidium nasatum (Budde-Lund, 1885)	28/43							71
Armadillidium opacum (C. Koch, 1841)			174/0		0/193	237/0	333/0	937
Armadillidium pictim (Brandt, 1833)				29/0			138/0	167
Armadillidium pulchellum (Zenker, 1798)				123/271	0/393		0/312	1099

Armadillidium vulgare (Latreille, 1804)	2106/1590	17/19969	12/172	1/0	40/0	1/3026		26934
Chaetophiloscia elongata (Dollus, 1884)	14/1375							1389
Cylisticus convexus (De Geer, 1778)		0/1						1
Haplophthalmus (Schöbel, 1860) *mengii/ montivagus*		0/1						1
Ligidium hypnorum (Cuvier, 1792)		198/9	250/116	100/224	33/89	320/0		1339
Lucasius pallidus (Budde-Lund, 1885)	0/5							5
Oniscus asellus (Linnaeus, 1758)	0/3	367/640	261/712	273/500	117/81	246/272	1/7	3480
Oniscus simonii (Budde-Lund, 1885)	1/2							3
Orthometopon planum (Budde-Lund, 1885)	1/75							76
Philoscia affinis (Verhoeff, 1908)	535/1088			0/60				1683
Philoscia muscorum (Scopoli, 1763)	673/1550	825/6456	1873/2075	2074/2864	1463/3482	4211/3405		30951
Porcellio dilatatus (Brandt, 1833)	0/4	0/4						8
Porcellio gallicus (Dollfus, 1904)	300/154	0/1024						1478
Porcellio monticola (Lereboullet, 1853)	385/12	1/69						467
Porcellio scaber (Latreille, 1804)	5/13	5003/5277	327/1511	879/3014	1428/3352	687/2023		23519
Porcellionides pruinosus (Brandt, 1833)	0/1	1/1		2/1				6
Porcellium conspersum (C. Koch, 1841)				0/3	316/112			431
Sphaerobathytropa ribauti (Verhoeff, 1908)	215/0							215
Trachelipus rathkii (Brandt, 1833)		0/2	16/57		73/1	29/172	497/1275	2122
Trichoniscoides albidus (Budde-Lund, 1880)			15/0					15
Trichoniscoides helveticus (Carl, 1908)		0/1						1
Trichoniscus provisorius (Racovitza, 1908)			4/1					5
Trichoniscus pusillus (Brandt, 1833)	76/27	37/31	102/40	2/7	68/16	77/28	19/93	623
All species	**4350/5931**	**1688/38246**	**3489/4229**	**5007/5420**	**3365/7892**	**5304/9430**	**988/1687**	**97026**

Appendix 6.4. Activity-density of woodlice and millipedes per region

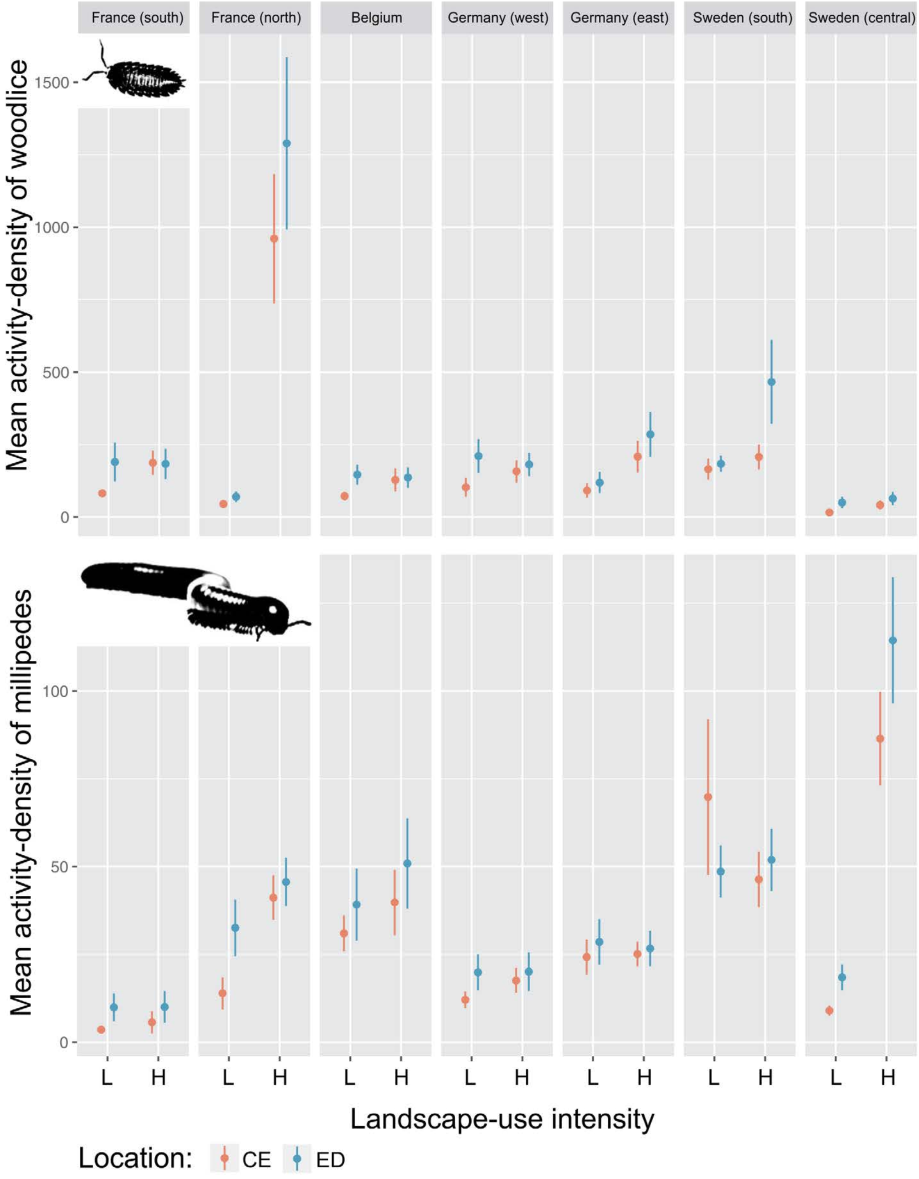


Figure A6.4.1. *Mean activity-density at sample unit level of woodlice and millipedes in forest edges (ED) and forest centres (CE) in lower land-use intensity (L) and higher land-use intensity (H) landscapes for the different regions. Error bars represent ± 1 standard error*

Appendix 6.5. Diversity of woodlice and millipedes per region

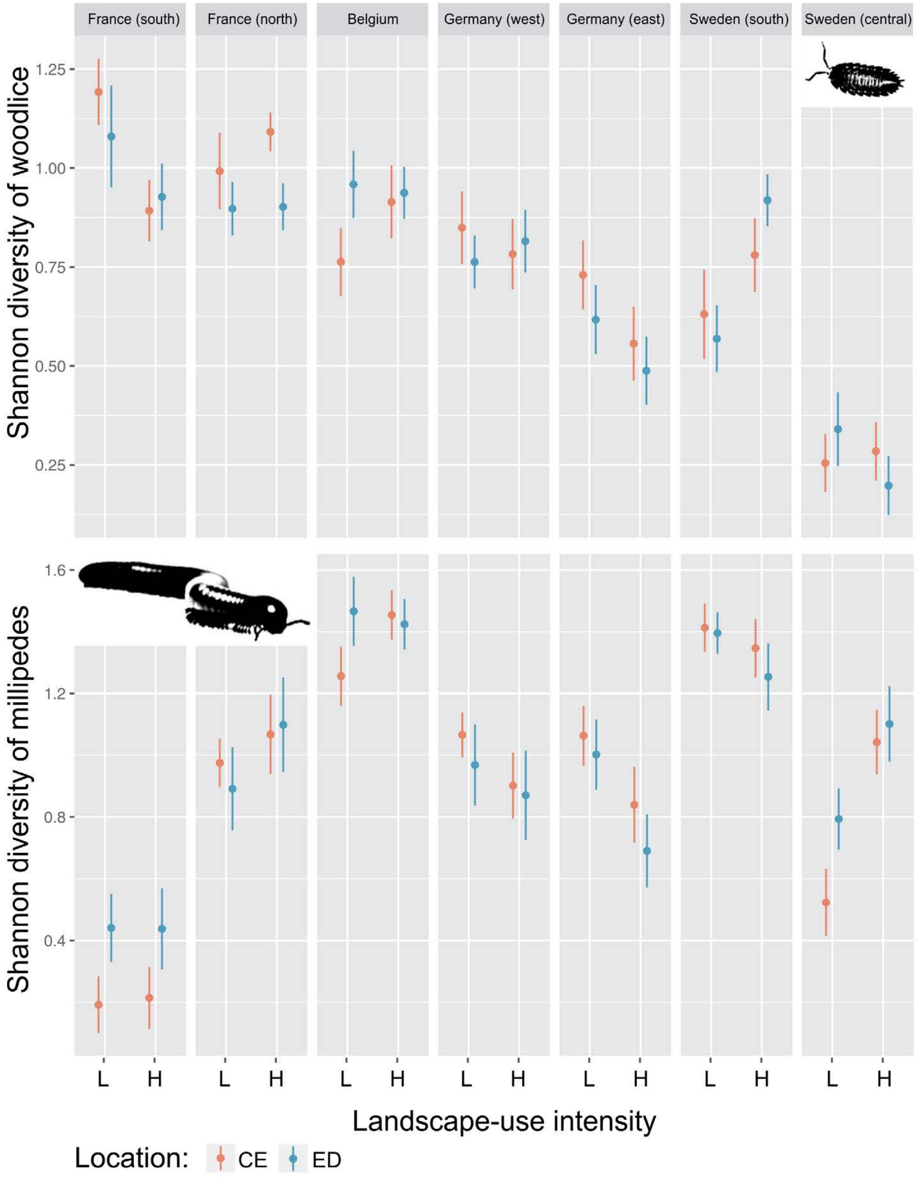


Figure A6.5.1. *Mean Shannon-diversity of woodlice and millipedes in forest edges (ED) and forest centres (CE) in lower land-use intensity (L) and higher land-use intensity (H) landscapes for the different regions. Error bars represent ± 1 standard error.*

Nemostoma bimaculatum | Jinze Noordijk

Chapter 7

LITTER-DWELLING MACRO-ARTHROPODS IN SMALL FOREST FRAGMENTS

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

Adapted from: De Smedt P, Baeten L, Proesmans W, Van de Poel S, Van Keer J, Giffard B, Martin L, Rieneke Vanhulle R, Brunet J, Cousins SAO, Decocq G, Deconchat M, Diekmann M, Gallet-Moron E, Le Roux V, Liira J, Valdés A., Wulf M, Andrieu E., Hermy M, Bonte D, Verheyen K. Strength of forest edge effects on litter-dwelling macro-arthropods across Europe is influenced by forest age and edge properties. In Preparation for Ecography.

Abstract

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.

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 across Western Europe. 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).

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 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.

These ecological effects are anticipated to feedback on important ecosystem services like nutrient cycling, carbon sequestration and natural pest control in small forest fragments.

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 (Wade et al. 2003, Ibisch et al. 2016). In Western Europe, this fragmentation has led to scattered small forest fragments within an agricultural matrix (Kolb & Diekmann 2004, Decocq et al. 2016) putting severe pressure on forests' biodiversity and the multiple ecosystem services it can provide (Krauss et al. 2010, Haddad et al. 2015). 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 e.g. higher temperature, litter input… (Matlack 1993, Gehlhausen et al. 2000, Delgado et al. 2007) generally favouring biotic activity (De Smedt et al. 2016c, Remy et al. 2018) and therefore we can expect strong changes in community compositions and ecosystem processes along forest edge-to-interior gradients (De Smedt et al. 2018a). Furthermore, forest edges are ecotones on the brink of forest and the adjacent land-use where species from both habitats can co-occur (Boetzl et al. 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 larger 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 (Matlack 1993, Chen et al. 1995). The shaded north-oriented edges more closely resemble forest interior resulting in a stronger 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) (Reino et al. 2009, Peyras et al. 2013, Yekwayo et al. 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 et al. 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 (Jeffery et al. 2010, de Vries et al. 2013, Costanza et al. 2017). However, beside natural pest control agents (see e.g. Rand et al. 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 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 larger with increasing distance from the forest edge as well as increased dissimilarity in community composition between edge and interior (H2). Furthermore, we hypothesise that this distance effect is modulated by forest age and edge properties (edge orientation and edge contrast with the adjacent land-use) (H3).

Methods

Study area and selected forest fragments

The study was carried out in six regions across the temperate forest biome of Western Europe, along a latitudinal gradient spanning more than 2,000 km. In every region, we selected two 5 x 5 km landscape windows of different land-use intensity (n = 12 landscape windows) (see Chapter 6 Fig. 6.1 and Valdes et al. 2015) for more information about landscape characteristics). 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 digitised 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.

Litter fauna sampling

Litter-dwelling arthropods were sampled using pitfall traps (Ø 10 cm, depth 11 cm). 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 meters apart, resulting in four sample units per forest fragment (see De Smedt et al. 2018b for more details on trap setup and Chapter 4 Fig. A4.1.1). 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 and fertilizers, 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.

Data analysis

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 et al. 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 if the taxa specific edge significantly differed from zero. Secondly, 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 (as random effect). Individual taxa were tested according to the same procedure (Appendix 7.1).

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 et al. 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, i.e. SØrensen dissimilarity index (referred to as compositional variation), species turnover and nestedness, we used a linear multilevel model (*lmer*-function) to test for significant differences between taxa. We used landscape window nested in region as a random effect to account for significant 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). Secondly, we tested if 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 (Appendix 7.3). All analysis were performed within the statistical software of R (R Core Team 2017).

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 Appendix 7.4 for complete species lists).

Edge effect on activity-density

The edge effect on activity-density differed significantly between taxa ($F_{(6,141)}$=15.12, p<0.001) (Fig. 7.1). 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) was not significantly different 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 7.1) but only in older forest, not in recent forest (Fig. 7.2). 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 (Table A7.1.1). However, the 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 (Fig. A7.1.1). The edge effect on activity-density for spiders increased when distances between forest edges and interiors became larger (Fig. A7.1.2). 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 (Fig. A7.1.3). Edge effect on millipede activity-density increased with increasing distance from the forest edge (Fig. A7.1.4). Edge effects on woodlice activity-density showed a similar pattern as the overall trend (Fig. A7.1.5). No significant trends were observed for harvestmen and centipedes (Table A7.1.1).

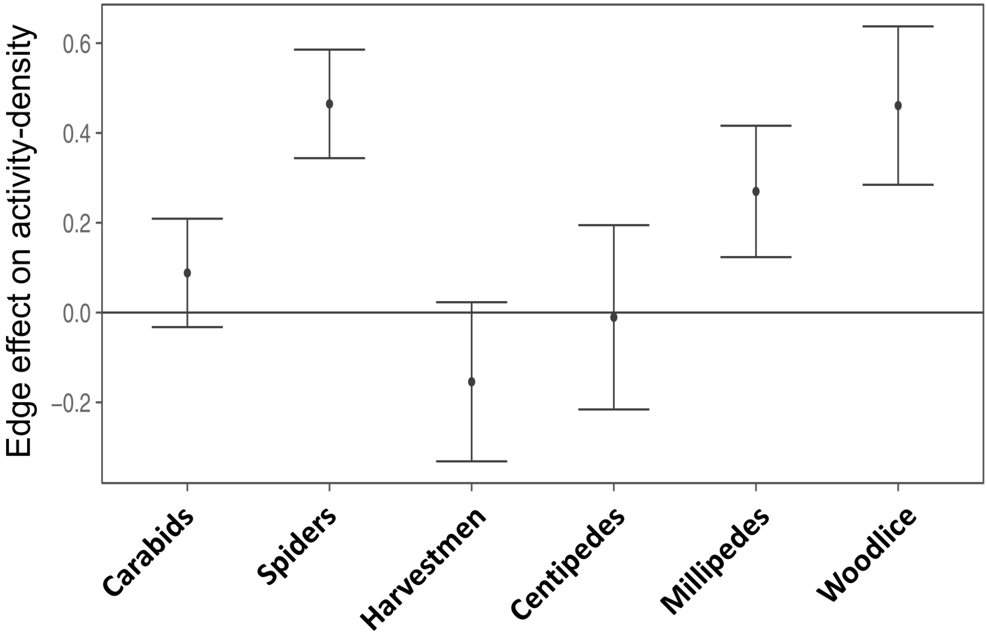


Figure 7.1. *Edge effect on activity-density, calculated as a log response ratio effect size, on six taxa of litter-dwelling macro-arthropods. A response ratio of zero indicates equal activity-density in forest edges and forest interiors and positive (negative) values higher (lower) activity-density at the forest edge. Points and error bars represent mean effects ± 1 SE.*

Table 7.1. *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 across six taxa. Results (F-values and degrees of freedom) of linear multilevel models. *: p<0.05, ***: p<0.001*

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 X Age	**$F_{(1,861)}$**	**11.40 *****
Dist x Cont	$F_{(1,754)}$	0.03
Dist x Or	$F_{(1,719)}$	0.75

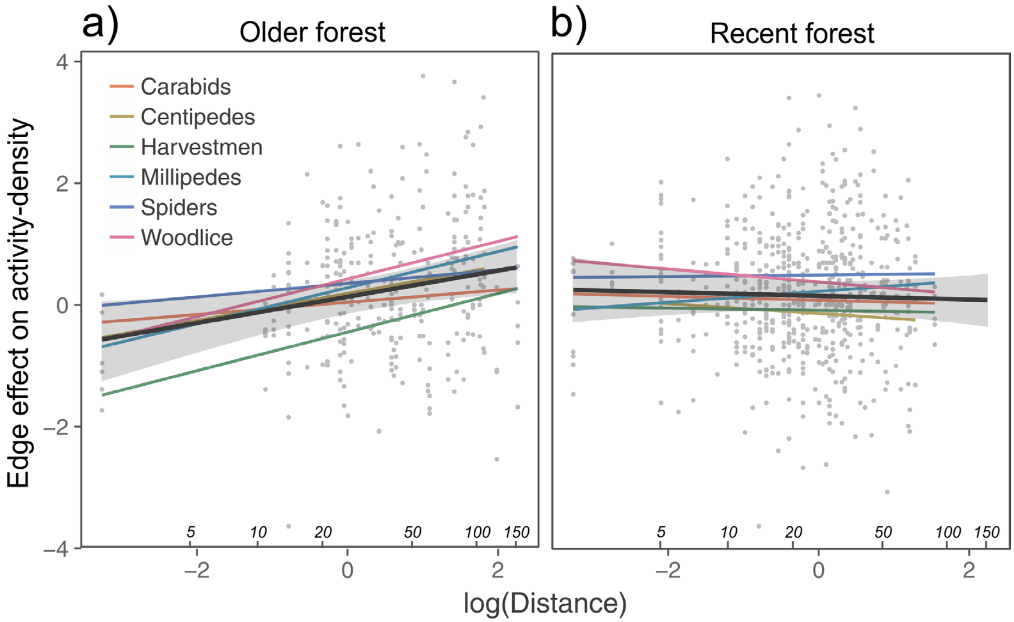


Figure 7.2. *Edge effect on activity-density, calculated as a log response ratio effect size, according to distance of the forest interior from the forest edge for a) older forest fragments and b) recent forest fragments. Different colours represent the six taxa of litter-dwelling macro-arthropods. Data 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.*

Edge effect on community composition

Edge effects on community composition (compositional variation) within forest fragments significantly differed between taxa ($F_{(5,822)}$=108.84, p<0.001), with spiders showing the highest overall compositional variation, followed by carabid beetles (Fig. 7.3a). Centipedes and millipedes had a lower overall compositional variation, but higher compared to harvestmen and woodlice (Fig. 7.3a) (see Appendix 7.2). 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 (Fig. 7.3). Species turnover patterns were similar compared with overall compositional variation (Fig. 7.3b). Nestedness was lower for spiders compared to all other taxa, except woodlice (Fig. 7.3c) and lower for woodlice compared to millipedes (Fig. 7.3c) (Appendix 7.2).

Across all taxa, compositional variation and turnover was influenced by the actual distance between forest edge and interior (Table 7.2) in older forest (Fig. 7.4a) and south-oriented forest edges (Fig. 7.4d), not in recent forest (Fig. 7.4b) or in north-oriented forest edges (Fig. 7.4c). 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 (Fig. A7.3.1). 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) (Fig. A7.3.2).

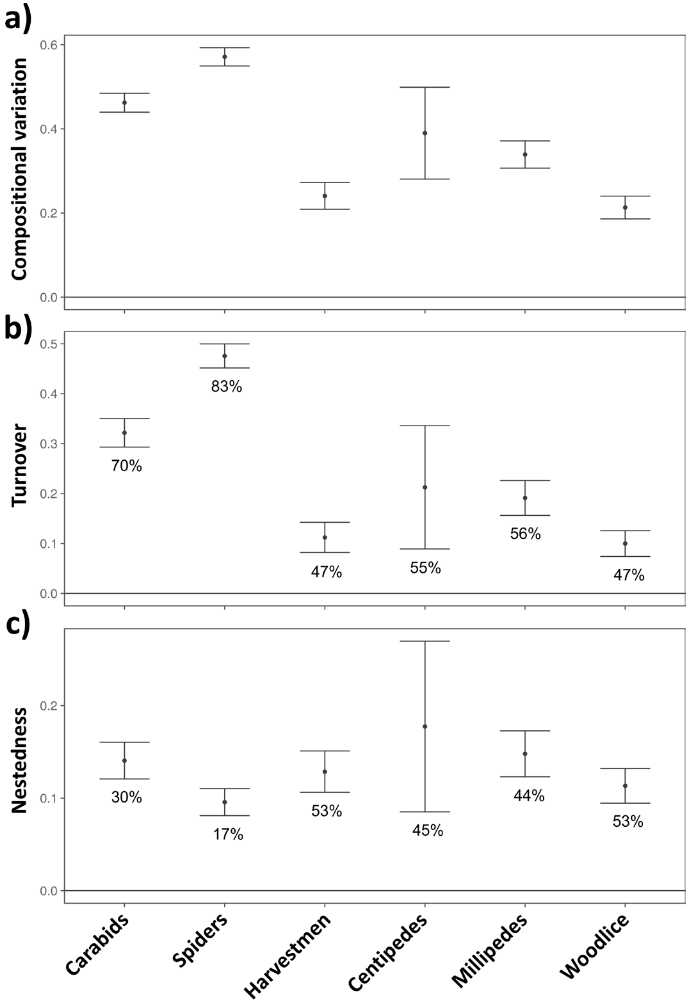


Figure 7.3. *Mean compositional variation (±1 SE) between the interior and edge community within forest fragments for six taxa of litter-dwelling macro-arthropods for (a) compositional variation (SØrensen dissimilarity index) and its two additive components: (b) turnover (Simpson Index) and (c) nestedness. Percentages report the proportion of community variation that is attributed to turnover or nestedness. Significance values between taxa can be found in Appendix 7.3.*

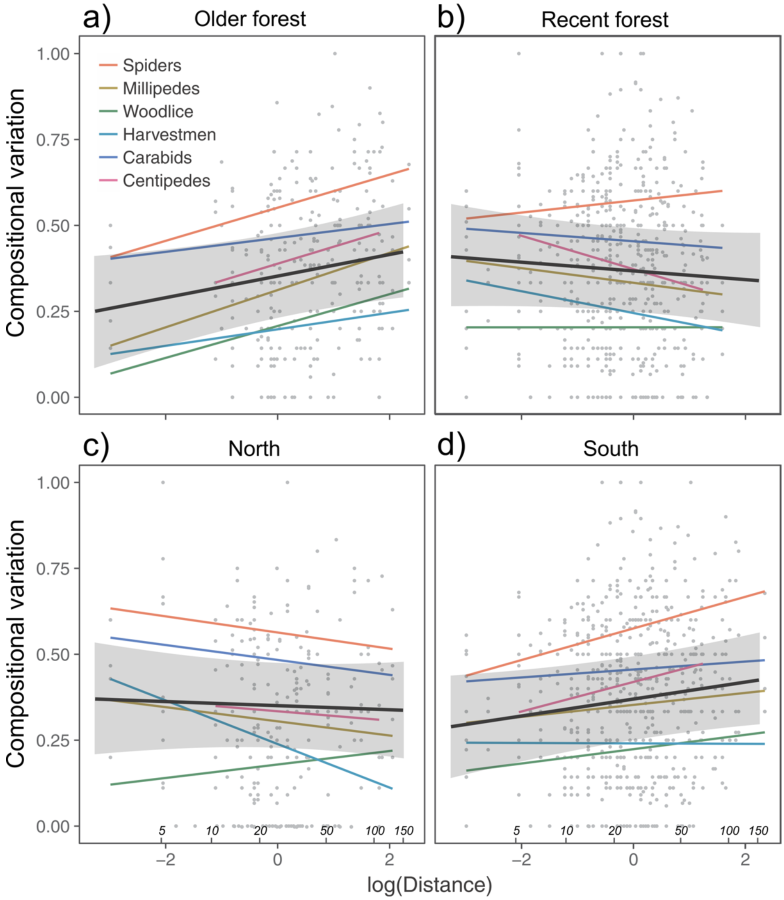


Figure 7.4. *Edge effect on the compositional variation between interior and edge communities of six taxa of litter-dwelling macro-arthropods according to distance between forest edge and interior for a) older and b) recent fragments according and c) north- or d) south-oriented edges. Different colours 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.*

Table 7.2 (next page). *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 across six taxa. Results (F-values and degrees of freedom) of linear multilevel models. . : p<0.1, **: p<0.01, ***: p<0.001*

	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 X Age	**$F_{(1,812)}$**	**11.55^{***}**
	Dist x Cont	$F_{(1,750)}$	1.73
	Dist x 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 X Age	**$F_{(1,812)}$**	**13.49^{***}**
	Dist x Cont	$F_{(1,746)}$	1.29
	Dist x 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 X Age	$F_{(1,815)}$	0.58
	Dist x Cont	$F_{(1,765)}$	0.04
	Dist x Or	$F_{(1,806)}$	0.33

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 i.e. with grassland on the outside.

Activity-density in forest edges vs interiors

The higher activity-density of different litter-dwelling taxa suggest that the habitat conditions in forest edges are more favourable for arthropods compared to forest interiors. Forest edges have higher temperatures (Heithecker & Halpern 2007; Delgado et al. 2007), which increases arthropod activity, metabolic rate and results in a shorter reproduction time (Gillooly et al. 2001). Additionally, edge leaf litter has a lower C/N-ratio (De Smedt et al. 2016c) 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 (Pearce & Venier 2006, David & Handa 2010, Hornung 2011, Bogyó et al. 2015), 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 et al. (2018a) 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 are also the species, which have the lowest number of eggs in their brood pouch and can be considered as woodlice K-strategists (Warburg et al. 1984). The drought resistant species from the forest edge on the contrary have larger number of eggs (r-strategists) enabling them to built-up large populations in a short time-period (Warburg et al. 1984). The r/K strategy theory has also been established for plants in forest edges (Chabrerie et al. 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.

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 larger local site-to-site variation (Baselga et al. 2010). Species-poor taxa had low relative turnover rates, this could be explained by (1) interior communities being largely a subset of edge communities due to lower densities and therefore lower capture rates or (2) edge communities becoming more species rich because of spillover from adjacent agricultural land. De Smedt et al. (2018a) 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 been found for millipedes (De Smedt et al. 2018b) and centipedes (Lacasella et al. 2015). A species-rich taxon, like carabid beetles, showed a higher degree of typical interior species (Soga et al. 2013, Tóthmérész et al. 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 larger compositional variation between forest edge and interiors for carabid beetles and spiders.

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 et al. 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. Next to the role of abiotic differences between young and older forest in explaining compositional variation between forest edges and interior, stochastic variables might play an important role. It is well known that low dispersive woodland species are absent in young forest, but still present in older forest. This might result in a larger compositional variation in older forest. Recent forests lack for example characteristic older forest vegetation (Verheyen et al. 2003; Flinn & Vellend 2005) and differ from older forest in microbial and micro-fauna community (De la Peña et al. 2016).

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 (Matlack 1993, Chen et al. 1995). 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) e.g. in forest edges (Baldissera et al. 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; Honnnay et al. 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.

Carabid beetles and spiders are abundant predators with great potential for natural pest control (Marc & Canard 1997, Holland & Luff 2000, Symondson et al. 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). Arthropod predators like spiders and carabid beetles can hardly 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 et al. 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 et al. 2005). However, the observed patterns might be explained by the fact that meadows and croplands have different arthropod communities (Samu & Szinetár 2002; Jeanneret et al. 2003), and species-specific responses might govern distributional patterns (Niemelä et al. 1993, Magura 2002).

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 mineralisation, water purification, natural pest control) in small forest fragments in agricultural landscapes.

Acknowledgements

This research was funded by the ERA-Net BiodivERsA project smallFOREST, with the national funders ANR (France), MINECO (Spain), FORMAS (Sweden), ETAG (Estonia), DFG (Germany), BELSPO (Belgium) and DFG (Germany) part of the 2011 BiodivERsA call for research proposals. P.D.S. and W.P. each hold a doctoral fellowship of the Research Foundation-Flanders (FWO). The research of K.V. is supported by the ERC Consolidator Grant 614839 – PASTFORWARD. L.B. and D.B. are supported by the FWO research network EVENET. Many thanks to Kent Hansson, Jessica Lindgren and Sabine Sigfridsson for help during field sampling.

Appendix 7.1. Taxon-specific activity-density analysis

Table A7.1.1. *Results of the multilevel model testing the effect of distance (log-transformed), forest age, adjacent field type and edge orientation on log-ratio activity-density of forest edge versus forest interior for the six taxa separately. Results (F-values and degrees of freedom) of linear multilevel models.* “.”: $p<0.1$, “*”: $p<0.05$, “**”: $p<0.01$, “***”: $p<0.001$

Taxon	*Explanatory variable*	*F-value*	
Carabid beetles	Distance (Dist)	F(1,174)	0.30
	Forest age (Age)	F(1.166)	0.06
	Edge contrast (Cont)	**F(1,107)**	**5.02***
	Orientation (Or)	F(1,174)	0.10
	Dist X Age	F(1,172)	0.74
	Dist x Cont	**F(1,174)**	**4.07***
	Dist x Or	F(1,174)	0.22
Spiders	Distance (Dist)	F(1,174)	1.45
	Forest age (Age)	F(1.171)	0.65
	Edge contrast (Cont)	F(1,118)	1.87
	Orientation (Or)	F(1,175)	2.49
	Dist X Age	F(1,172)	0.92
	Dist x Cont	**F(1,174)**	**6.51***
	Dist x Or	**F(1,174)**	**4.49***
Harvestmen	Distance (Dist)	F(1,136)	2.19
	Forest age (Age)	F(1,112)	3.15.
	Edge contrast (Cont)	F(1,42)	2.28
	Orientation (Or)	F(1,130)	0.12
	Dist X Age	F(1.135)	2.84.
	Dist x Cont	F(1,136)	0.00
	Dist x Or	F(1.134)	0.98
Centipedes	Distance (Dist)	F(1,64)	0.40
	Forest age (Age)	F(1,64)	2.19
	Edge contrast (Cont)	F(1,64)	0.03
	Orientation (Or)	F(1,64)	0.17
	Dist X Age	F(1,64)	0.88
	Dist x Cont	F(1,64)	2.15
	Dist x Or	F(1,64)	0.27

Millipedes	**Distance (Dist)**	**F(1,160)**	**4.07***
	Forest age (Age)	F(1,138)	0.25
	Edge contrast (Cont)	F(1,69)	3.39.
	Orientation (Or)	F(1,160)	1.78
	Dist X Age	F(1,158)	1.61
	Dist x Cont	F(1,160)	0.81
	Dist x Or	F(1,160)	1.71
Woodlice	Distance (Dist)	F(1,175)	1.30
	Forest age (Age)	F(1,175)	0.08
	Edge contrast (Cont)	F(1,175)	1.17
	Orientation (Or)	F(1,175)	0.32
	Dist X Age	**F(1,175)**	**4.44***
	Dist x Cont	F(1,175)	0.01
	Dist x Or	F(1,175)	0.54

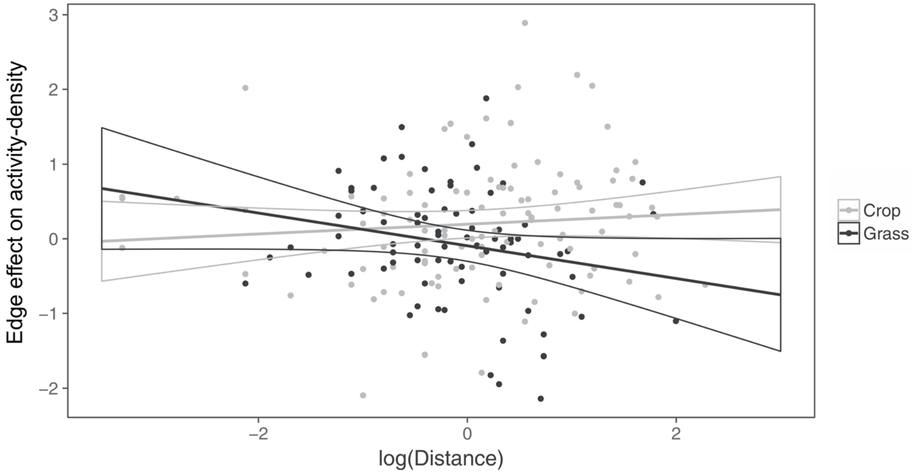


Figure A7.1.1. *Edge effect on activity-density of carabid beetles, calculated as a log response ratio effect size, according to distance of the forest interior from the forest edge for different edge contrasts (grass: lower contrast, crop: higher contrast). Distance was log-transformed and centred to average to zero across all regions. Bold lines represent modelled average ± 1 SE (thin lines).*

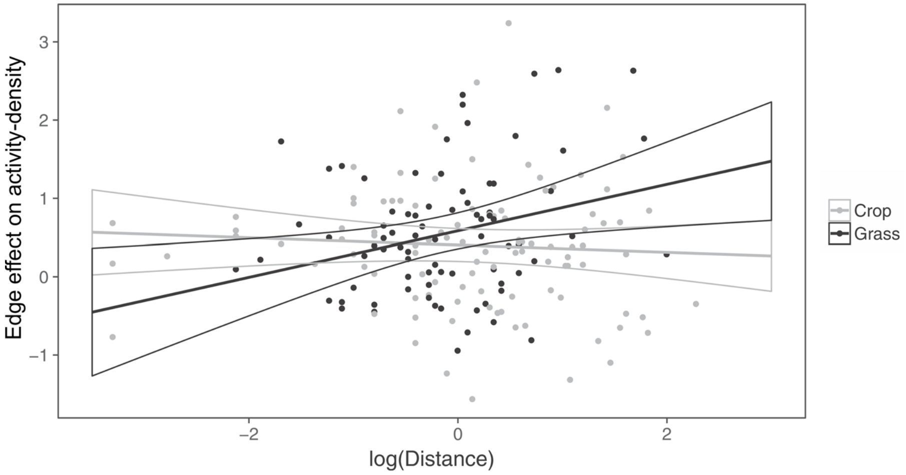


Figure A7.1.2. *Edge effect on activity-density of spiders, calculated as a log response ratio effect size, according to distance of the forest interior from the forest edge for different edge contrasts (grass: lower contrast, crop: higher contrast). Distance was log-transformed and centred to average to zero across all regions. Bold lines represent modelled average ± 1 SE (thin lines).*

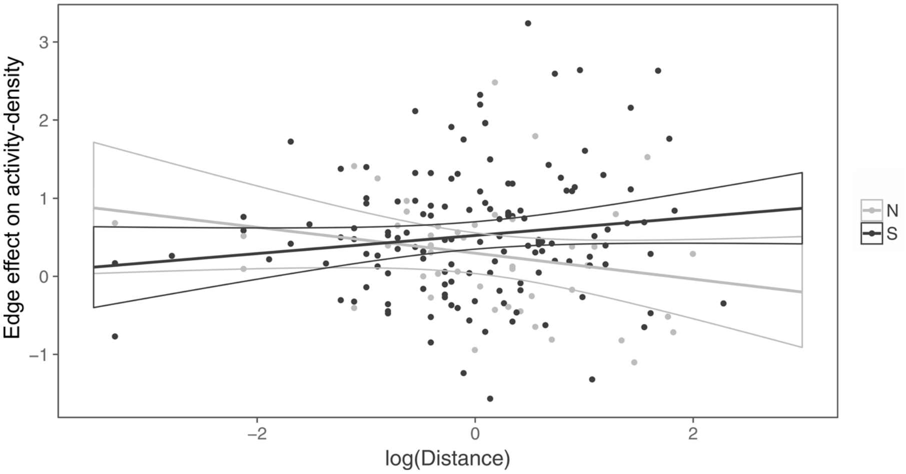


Figure A7.1.3. *Edge effect on activity-density of spiders, calculated as a log response ratio effect size, according to distance of the forest interior from the forest edge for different edge orientations (N: North, S: South). Distance was log-transformed and centred to average to zero across all regions. Bold lines represent modelled average ± 1 SE (thin lines).*

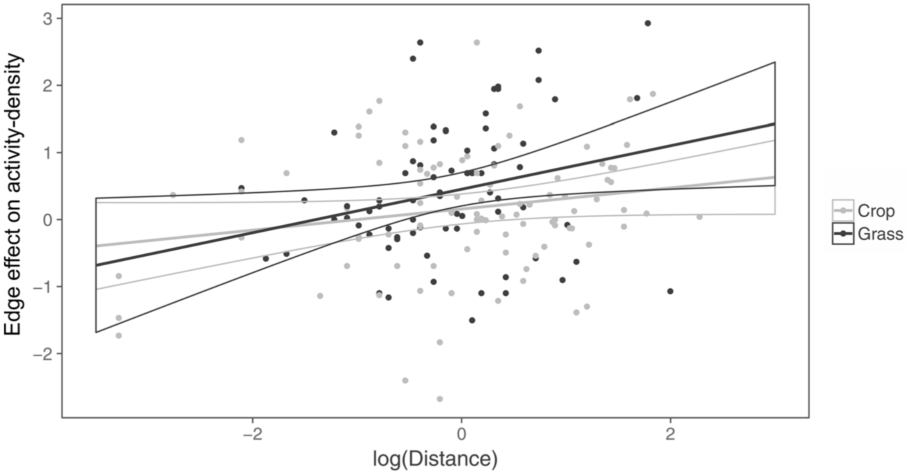


Figure A7.1.4. *Edge effect on activity-density of millipedes, calculated as a log response ratio effect size, according to distance of the forest interior from the forest edge for different edge contrasts (grass: lower contrast, crop: higher contrast). Distance was log-transformed and centred to average to zero across all regions. Bold lines represent modelled average ± 1 SE (thin lines).*

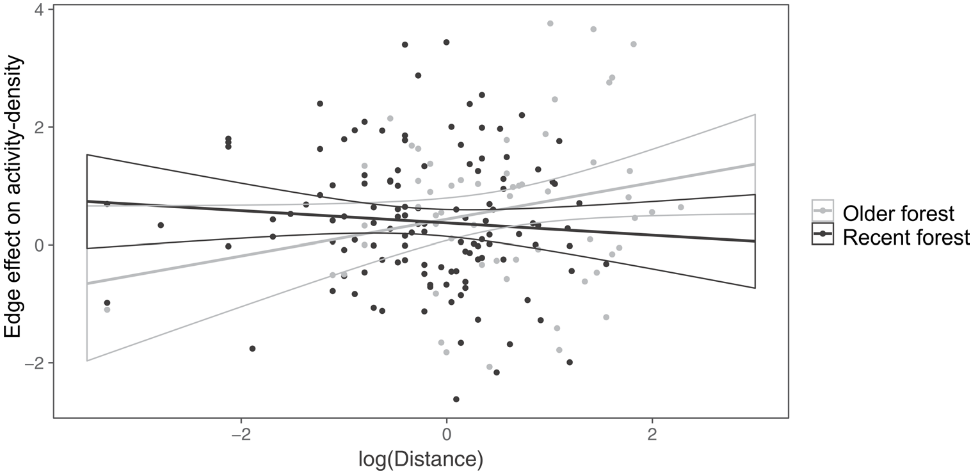
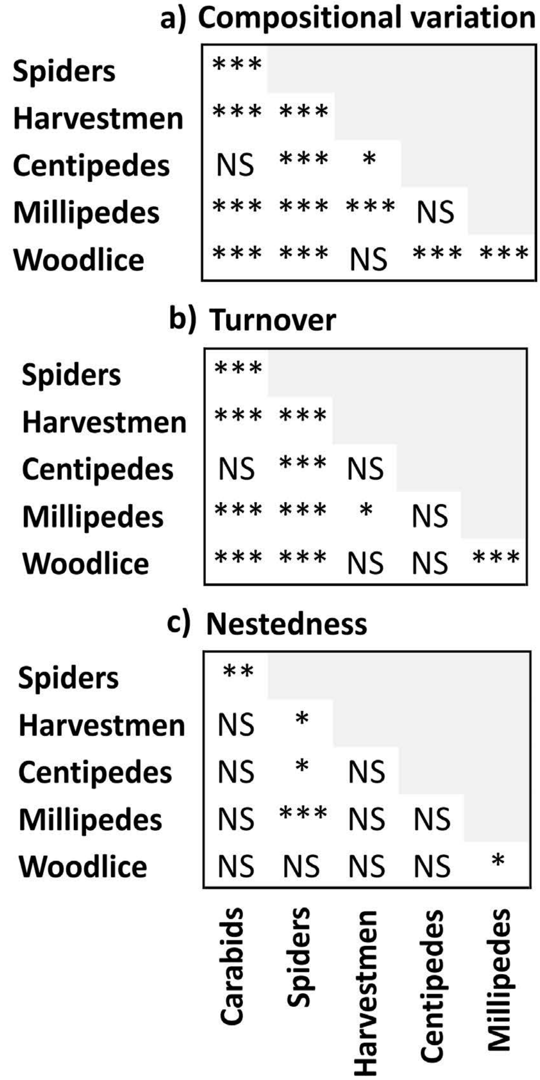


Figure A7.1.5. *Edge effect on activity-density of woodlice, calculated as a log response ratio effect size, according to distance of the forest interior from the forest edge for older and recent forests. Distance was log-transformed and centred to average to zero across all regions. Bold lines represent modelled average ± 1 SE (thin lines).*

Appendix 7.2. Significance values community composition



a) Compositional variation

	Carabids	Spiders	Harvestmen	Centipedes	Millipedes
Spiders	***				
Harvestmen	***	***			
Centipedes	NS	***	*		
Millipedes	***	***	***	NS	
Woodlice	***	***	NS	***	***

b) Turnover

	Carabids	Spiders	Harvestmen	Centipedes	Millipedes
Spiders	***				
Harvestmen	***	***			
Centipedes	NS	***	NS		
Millipedes	***	***	*	NS	
Woodlice	***	***	NS	NS	***

c) Nestedness

	Carabids	Spiders	Harvestmen	Centipedes	Millipedes
Spiders	**				
Harvestmen	NS	*			
Centipedes	NS	*	NS		
Millipedes	NS	***	NS	NS	
Woodlice	NS	NS	NS	NS	*

Figure A7.2.1. *Pairwise differences between the studied taxa for (a) compositional variation (SØrensen dissimilarity index) and its two additive components: (b) turnover (Simpson Index) and (c) nestedness. Mean values and SE are presented in Figure 7.3 of the main manuscript "*": $p<0.05$, "**": $p<0.01$, "***": $p<0.001$, "NS": Not Significant.*

Appendix 7.3. Taxon-specific Sørensen dissimilarity index analysis

Table A7.3.1. *Results of the multilevel model testing the effect of distance (log-transformed), forest age, adjacent field type and edge orientation on Sørensen dissimilarity index between forest edge and forest interior for the six taxa separately. Results (F-values and degrees of freedom) of linear multilevel models. “.”: $p<0.1$, “*”: $p<0.05$*

Taxon	Explanatory variable	F-value	
Carabid beetles	Distance (Dist)	$F_{(1,165)}$	0.00
	Forest age (Age)	$F_{(1,170)}$	0.01
	Edge contrast (Cont)	$F_{(1,165)}$	0.01
	Orientation (Or)	$F_{(1,167)}$	0.11
	Dist X Age	$F_{(1,164)}$	1.84
	Dist x Cont	$F_{(1,165)}$	**3.56.**
	Dist x Or	$F_{(1,166)}$	0.25
Spiders	**Distance (Dist)**	$\mathbf{F_{(1,169)}}$	**2.86.**
	Forest age (Age)	$F_{(1,174)}$	0.04
	Edge contrast (Cont)	$F_{(1,170)}$	**2.91.**
	Orientation (Or)	$F_{(1,171)}$	0.05
	Dist X Age	$F_{(1,168)}$	1.89
	Dist x Cont	$F_{(1,169)}$	0.92
	Dist x Or	$F_{(1,169)}$	**5.57***
Harvestmen	Distance (Dist)	$F_{(1,110)}$	0.00
	Forest age (Age)	$F_{(1,113)}$	2.16
	Edge contrast (Cont)	$F_{(1,117)}$	0.03
	Orientation (Or)	$F_{(1,111)}$	0.11
	Dist X Age	$F_{(1,109)}$	0.88
	Dist x Cont	$F_{(1,109)}$	1.51
	Dist x Or	$F_{(1,112)}$	1.90
Centipedes	Distance (Dist)	$F_{(1,11)}$	1.32
	Forest age (Age)	$F_{(1,11)}$	0.03
	Edge contrast (Cont)	$F_{(1,11)}$	1.10
	Orientation (Or)	$F_{(1,10)}$	0.01
	Dist X Age	$F_{(1,9)}$	0.04
	Dist x Cont	$F_{(1,9)}$	0.11
	Dist x Or	$F_{(1,8)}$	0.01
Millipedes	Distance (Dist)	$F_{(1,139)}$	0.04
	Forest age (Age)	$F_{(1,134)}$	0.19

	Edge contrast (Cont)	$F_{(1,82)}$	0.08
	Orientation (Or)	$F_{(1,140)}$	1.79
	Dist X Age	$F_{(1,137)}$	**4.49***
	Dist x Cont	$F_{(1,139)}$	0.13
	Dist x Or	$F_{(1,139)}$	0.99
Woodlice	Distance (Dist)	$F_{(1,168)}$	1.50
	Forest age (Age)	$F_{(1,172)}$	0.13
	Edge contrast (Cont)	$F_{(1,153)}$	0.86
	Orientation (Or)	$F_{(1,170)}$	2.18
	Dist X Age	$F_{(1,167)}$	1.99
	Dist x Cont	$F_{(1,168)}$	0.00
	Dist x Or	$F_{(1,169)}$	0.03

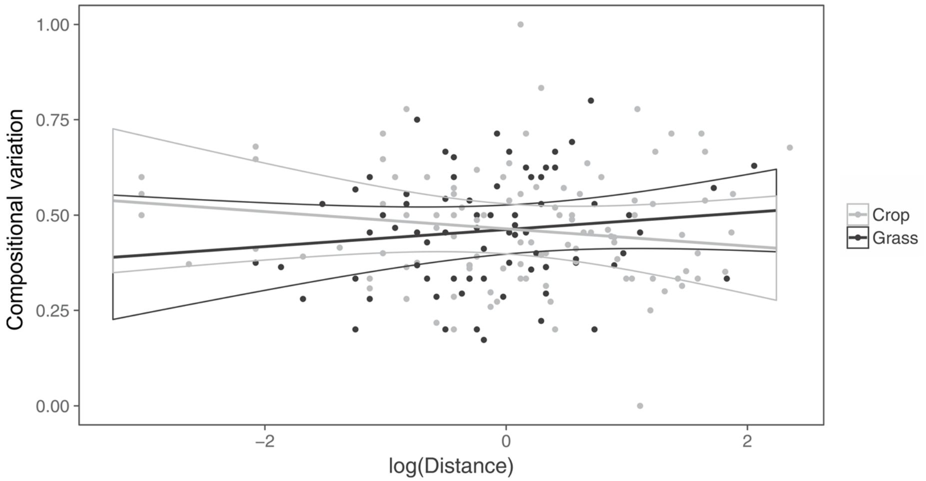


Figure A7.3.1. *Compositional variation (SØrensen dissimilarity index) of carabid beetles according to distance of the forest interior from the forest edge for different edge contrasts (grass: lower contrast, crop: higher contrast). Distance was log-transformed and centred to average to zero across all regions. Bold lines represent modelled average ± 1 SE (thin lines).*

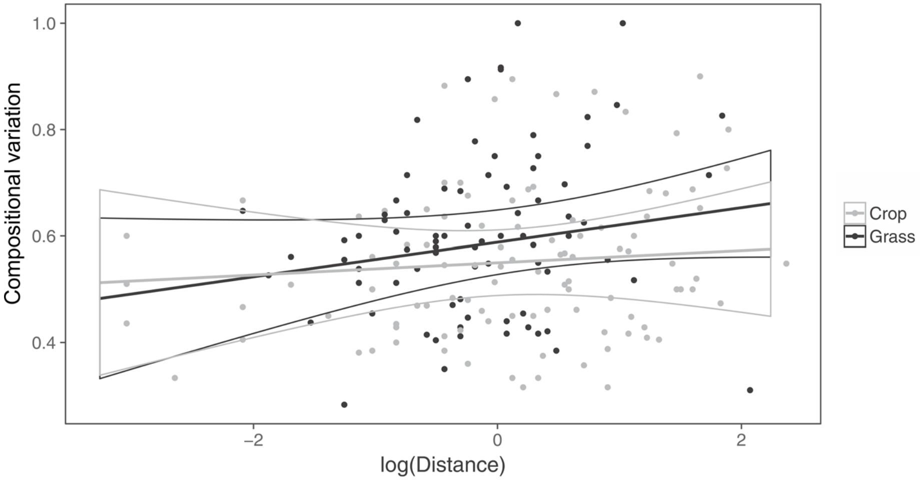


Figure A7.3.2. *Compositional variation (SØrensen dissimilarity index) of spiders according to distance of the forest interior from the forest edge for different edge contrasts (grass: lower contrast, crop: higher contrast). Distance was log-transformed and centred to average to zero across all regions. Bold lines represent modelled average ± 1 SE (thin lines).*

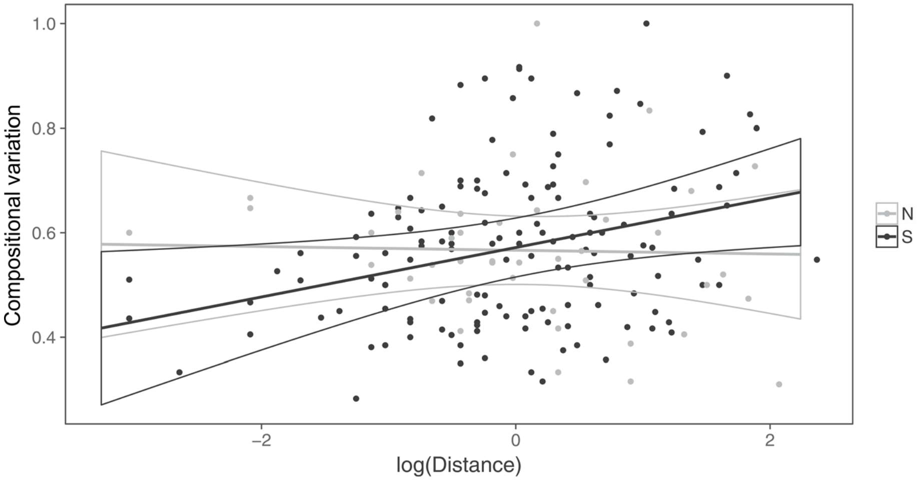


Figure A7.3.3. *Compositional variation (SØrensen dissimilarity index) of spiders according to distance of the forest interior from the forest edge for different edge orientations (N: North, S: South). Distance was log-transformed and centred to average to zero across all regions. Bold lines represent modelled average ± 1 SE (thin lines).*

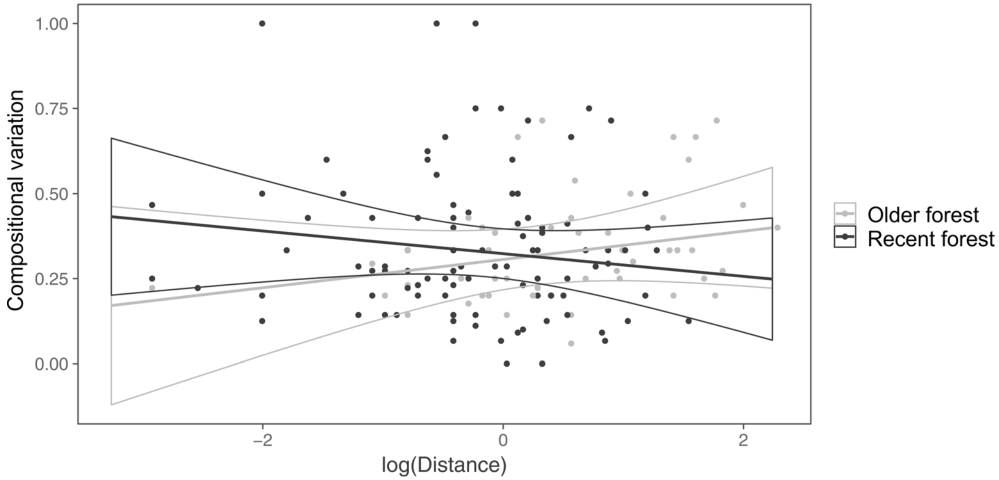


Figure A7.3.4. *Compositional variation (SØrensen dissimilarity index) of millipedes according to distance of the forest interior from the forest edge for older and recent forests. Distance was log-transformed and centred to average to zero across all regions. Bold lines represent modelled average ± 1 SE (thin lines).*

Appendix 7.4. Species lists

Table A7.4.1. *Carabid species list and species activity-density per region. FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, SS: Southern Sweden and SC: central Sweden.*

		Region						
		FS	FN	BE	GW	SS	SC	All
1	*Abax parallelus* (Duftschmid, 1812)		649	6	10			665
2	*Abax parallelepipedus* (Piller & Mitterpacher, 1783)	173	950	446	673			2242
3	*Acupalpus exiguus* (Dejean, 1829)					1		1
4	*Agonum afrum* (Duftschmid, 1812)		4	11	13			28
5	*Agonum duftschmidi* (J. Schmidt, 1994)					2		2
6	*Agonum fuliginosum* (Panzer, 1809)					35		35
7	*Agonum muelleri* (Herbst, 1784)					1		1
8	*Agonum viduum* (Panzer, 1796)			34	3	10		47
9	*Amara aenea* (DeGeer, 1774)	2	2	1			3	8
10	*Amara anthobia* (A. Villa & G.B. Villa, 1833)	13			1			14
11	*Amara apricaria* (Paykull, 1790)					14		14
12	*Amara aulica* (Panzer, 1796)					4	1	5
13	*Amara brunnea* (Gyllenhal, 1810)					121		121
14	*Amara communis* (Panzer, 1797)		2	1	3	4	1	11

15	*Amara consularis* (Duftschmid, 1812)				3		2		3			1	9
16	*Amara convexior* (Stephens, 1828)				6		17		12			1	36
17	*Amara curta* (Dejean, 1828)									1			1
18	*Amara equestris* (Duftschmid, 1812)									1			1
19	*Amara erratica* (Duftschmid, 1812)						1			4			5
20	*Amara eurynota* (Panzer, 1796)		5		23				4	1			33
21	*Amara familiaris* (Duftschmid, 1812)				1		1		8	7			17
22	*Amara glabrata* (Dejean, 1828)						3		3				6
23	*Amara lunicollis* (Schiodte, 1837)		3				54		5	48		6	116
24	*Amara montivaga* (Sturm, 1825)				3				1				4
25	*Amara plebeja* (Gyllenhal, 1810)						1			7			8
26	*Amara proxima* (Putzeys, 1866)								7				7
27	*Amara similata* (Gyllenhal, 1810)		1		3					2			6
28	*Amara spreta* (Dejean, 1831)									2			2
29	*Anchomenus dorsalis* (Pontoppidan, 1763)		81		8		20		3	29			141
30	*Anisodactylus binotatus* (Fabricius, 1787)		2		1		1		2				6
31	*Anysodactylus signatus* (Panzer, 1796)											1	1
32	*Asaphidion gr. flavipes* (Linnaeus, 1761)				14		37		1	3			55
33	*Badister bullatus* (Schrank, 1798)				12		46			39		31	128
34	*Badister lacertosus* (Sturm, 1815)						4			22			26
35	*Badister sodalis* (Duftschmid, 1812)						5			5			10
36	*Badister unipustulatus* (Bonelli, 1813)				2		3		5				10
37	*Blemus discus* (Fabricius, 1801)									1			1
38	*Brachinus crepitans* (Linnaeus, 1758)		9										9
39	*Brachinus elegans* (Chaudoir, 1842)		2										2
40	*Brachinus explodens* (Duftschmid, 1812)		2										2
41	*Brachinus immaculicornis* (Dejean, 1826)		1										1
42	*Brachinus sclopeta* (Fabricius, 1792)		6										6
43	*Calathus erratus* (C.R. Sahlberg, 1827)		1							9			10
44	*Calathus fuscipes* (Goeze, 1777)		26						115	70		33	244
45	*Calathus luctuosus* (Latreille, 1804)	2							2		2		6
46	*Calathus melanocephalus* (Linnaeus, 1758)								5	18			23
47	*Calathus micropterus* (Duftschmid, 1812)									17		10	27
48	*Calathus rotundicollis* (Dejean, 1828)			12		19		75		615		5	726
49	*Calosoma inquisitor* (Linnaeus, 1758)				1				2				3
50	*Carabus arcensis* (Herbst, 1784)									6		1	7
51	*Carabus auratus* (Linnaeus, 1761)	1134						4					1138
52	*Carabus auronitens* (Fabricius, 1792)				96								96
53	*Carabus cancellatus* (Illiger, 1798)	18						15					33
54	*Carabus convexus* (Fabricius, 1775)				28				71	20			119
55	*Carabus coriaceus* (Linnaeus, 1758)								42	93		1	136
56	*Carabus granulatus* (Linnaeus, 1758)					37			80	73		2	192

57	*Carabus hortensis* (Linnaeus, 1758)								317		488		59	864
58	*Carabus monilis* (Fabricius, 1792)			12		3					1			16
59	*Carabus nemoralis* (O.F. Müller, 1764)	135			4				345		489		19	992
60	*Carabus problematicus* (Herbst, 1786)								2					2
61	*Carabus violaceus* (Linnaeus, 1758)	1							36		12	14		63
62	*Chlaeniellus nigricornis* (Fabricius, 1787)		1											1
63	*Clivina gr. fossor* (Linnaeus, 1758)		2		1	13		2		5				23
64	*Cychrus caraboides* (Linnaeus, 1758)								10		27		70	107
65	*Dicheirotrichus placidus* (Gyllenhal, 1827)										6			6
66	*Dromius agilis* (Fabricius, 1787)												2	2
67	*Dromius quadrimaculatus* (Linnaeus, 1758)									1				1
68	*Dyschiriodes chalceus* (Erichson, 1837)										1			1
69	*Dyschiriodes globosus* (Herbst, 1784)			1										1
70	*Elaphrus cupreus* (Duftschmid, 1812)						4							4
71	*Harpalus affinis* (Schrank, 1781)			2						9				11
72	*Harpalus anxius* (Duftschmid, 1812)	1												1
73	*Harpalus atratus* (Latreille, 1804)		1		3									4
74	*Harpalus dimidiatus* (P. Rossi, 1790)		63											63
75	*Harpalus distinguendus* (Duftschmid, 1812)		3											3
76	*Harpalus laevipes* (Zetterstedt, 1828)									166		6		172
77	*Harpalus latus* (Linnaeus, 1758)	2		32		18		18			247		66	383
78	*Harpalus luteicornis* (Duftschmid, 1812)										37			37
79	*Harpalus oblitus* (Dejean, 1829)	1												1
80	*Harpalus rubripes* (Duftschmid, 1812)		3		15	2		31		48		2		101
81	*Harpalus smaragdinus* (Duftschmid, 1812)				2				1					3
82	*Harpalus tardus* (Panzer, 1796)	21									40	1		62
83	*Laemostenus terricola* (Herbst, 1784)				6									6
84	*Lamprias chlorocephalus* (J.J. Hoffmann, 1803)						1							1
85	*Leistus ferrugineus* (Linnaeus, 1758)	3		2			4		9	11		6		35
86	*Leistus fulvibarbis* (Dejean, 1826)		2		4		2		2				1	11
87	*Leistus rufomarginatus* (Duftschmid, 1812)		1		7		2		10		7			27
88	*Leistus terminatus* (Panzer, 1793)										6			6
89	*Licinus depressus* (Paykull, 1790)												4	4
90	*Limodromus assimilis* (Paykull, 1790)			140		211		63		182				596
91	*Loricera pilicornis* (Fabricius, 1775)				78		11		14		51		3	157
92	*Metallina lampros* (Herbst, 1784)				17		20		7		32		3	79
93	*Microlestes* sp.	17							1		1			19
94	*Molops piceus* (Panzer, 1793)				70									70
95	*Nebria brevicollis* (Fabricius, 1792)	107			489		195	474		168		4		1437
96	*Nebria salina* (Fairmaire & Laboulbene, 1854)		67		264		13		1		10			355

97	*Notiophilus aestuans* (Dejean, 1826)										7			7
98	*Notiophilus aquaticus* (Linnaeus, 1758)												1	1
99	*Notiophilus biguttatus* (Fabricius, 1779)	1		33		21		60		28			5	148
100	*Notiophilus germinyi* (Fauvel, 1863)										3		8	11
101	*Notiophilus marginatus* (Gene, 1839)	2												2
102	*Notiophilus palustris* (Duftschmid, 1812)				14	3		30		17		22		86
103	*Notiophilus quadripunctatus* (Dejean, 1826)	6			68		5		26					105
104	*Notiophilus rufipes* (Curtis, 1829)		7				10				75			92
105	*Notiophilus substriatus* (G.R. Waterhouse, 1833)		5											5
106	*Ocys harpaloides* (Audinet-Serville, 1821)		1											1
107	*Ocydromus saxatilis* (Gyllenhal, 1827)									3				3
108	*Ocydromus tetracolus* (Say, 1823)			3		47		2			14			66
109	*Ophonus azureus* (Fabricius, 1775)				1									1
110	*Ophonus gr. puncticeps* (Stephens, 1828)									1				1
111	*Ophonus laticollis* (Mannerheim, 1825)			17										17
112	*Ophonus rufibarbis* (Fabricius, 1792)				1		1			18		4		24
113	*Oxypselaphus obscurus* (Herbst, 1784)				2		33		2		66			103
114	*Panagaeus cruxmajor* (Linnaeus, 1758)				1		3							4
115	*Paranchus albipes* (Fabricius, 1796)						6							6
116	*Paradromius linearis* (Olivier, 1795)									1				1
117	*Parophonus mendax* (P.Rossi, 1790)	5												5
118	*Patrobus atrorufus* (Stroem, 1768)									215		1		216
119	*Pedius longicollis* (Duftschmid, 1812)					2		1						3
120	*Philochthus aeneus* (Dejean, 1825)										1			1
121	*Philochthus biguttatus* (Fabricius, 1779)					33								33
122	*Philochthus mannerhemi* (C.R. Sahlberg, 1827)						3			7				10
123	*Philorhizus melanocephalus* (Dejean, 1825)										2			2
124	*Phyla obtusa* (Audinet-Serville, 1821)	1				14								15
125	*Phyla tethys* (Netolitzky, 1926)		1											1
126	*Platynus livens* (Gyllenhal, 1810)				3	6				9				18
127	*Poecilus cupreus* (Linnaeus, 1758)	3			6		4		92		11		3	119
128	*Poecilus lepidus* (Leske, 1785)										11			11
129	*Poecilus versicolor* (Sturm, 1824)			2		6		4			161		10	183
130	*Pseudoophonus rufipes* (De Geer, 1774)	11			27		1		129		338		437	943
131	*Pterostichus anthracinus* (Illiger, 1798)				1		31		15					47
132	*Pterostichus cristatus* (L. Dufour, 1820)						4							4
133	*Pterostichus diligens* (Sturm, 1824)						5					4		9
134	*Pterostichus macer* (Marsham, 1802)			3										3
135	*Pterostichus madidus* (Fabricius, 1775)	538			3383		298			11				4230
136	*Pterostichus melanarius* (Illiger, 1798)				749		103		651		3323		1052	5878

137	*Pterostichus niger* (Schaller, 1783)		1	27	193	764	635	1620
138	*Pterostichus nigrita* (Paykull, 1790)			19	1	17		37
139	*Pterostichus oblongopunctatus* (Fabricius, 1787)		97	5	939	705	152	1898
140	*Pterostichus strenuus* (Panzer, 1796)		3	93	6	126	5	233
141	*Pterostichus vernalis* (Panzer, 1796)		5	2			2	9
142	*Semiophonus signaticornis* (Duftschmid, 1812)				1			1
143	*Stenolophus skrimshiranus* (Stephens, 1828)					1		1
144	*Stomis pumicatus* (Panzer, 1796)		1	8	1	49	24	83
145	*Syntomus foveatus* (Geoffroy, 1785)					8		8
146	*Syntomus truncatellus* (Linnaeus, 1761)					1		1
147	*Synuchus vivalis* (Illiger, 1798)		1	1		9	1	12
148	*Trechus gr. quadristriatus* (Schrank, 1781)	216	87	11	4	6	79	403
149	*Trechus secalis* (Paykull, 1790)			2		35	10	47
150	*Zabrus tenebroides* (Goeze, 1777)	2						2
	All species	2711	7478	2056	4668	9373	2814	29100

Table A7.4.2. *Spider species list and species activity-density per region. FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, SS: Southern Sweden and SC: central Sweden.*

		Region						
		FS	FN	BE	GW	SS	SC	All
1	*Abacoproeces saltuum* (L. Koch, 1872)				1		116	117
2	*Acantholycosa lignaria* (Clerck, 1757)						4	4
3	*Agelena labyrinthica* (Clerck, 1757)			1				1
4	*Agraecina lineata* (Simon, 1878)	145						145
5	*Agroeca brunnea* (Blackwall, 1833)	3	2	11	20		36	72
6	*Agroeca cuprea* (Menge, 1873)						1	1
7	*Agroeca inopina* (O.P-Cambridge, 1886)	14						14
8	*Agroeca lusatica* (L. Koch, 1875)	1						1
9	*Agroeca proxima* (O.P.-Cambridge, 1871)						6	6
10	*Agyneta affinis* (Kulczyn'ski, 1898)						1	1
11	*Agyneta conigera* (O.P.-Cambridge, 1863)						18	18
12	*Agyneta decora* (O.P-Cambridge, 1871)		1					1
13	*Agyneta ramosa* (Jackson, 1912)			57	5	2	17	81
14	*Agyneta rurestris* (C.L. Koch, 1836)	1	3				1	5
15	*Agyneta saxatilis* (Blackwall, 1844)		1	1	27	24	19	72
16	*Agyneta subtilis* (O.P.-Cambridge, 1863)				2			2
17	*Allomengea scopigera* (Grube, 1859)					1		1
18	*Alopecosa albofasciata* (Brullé, 1832)	28						28

19	*Alopecosa cuneata* (Clerck, 1757)	24	1		2			27
20	*Alopecosa pinetorum* (Thorell, 1856)						10	10
21	*Alopecosa pulverulenta* (Clerck, 1757)	63	5	15	11	16	21	131
22	*Alopecosa taeniata* (C.L. Koch, 1835)						1	1
23	*Amaurobius erberi* (Keyserling, 1863)	11						11
24	*Amaurobius fenestralis* (Ström, 1768)				5	4		9
25	*Amaurobius similis* (Blakwall, 1861)	1						1
26	*Anelosimus vittatus* (C.L. Koch, 1836)		1		1			2
27	*Anguliphantes angulipalpis* (Westring, 1851)						3	3
28	*Antistea elegans* (Blackwall, 1841)			2			2	4
29	*Anyphaena accentuata* (Walckenaer, 1802)		15	1	6	3	5	30
30	*Apostenus fuscus* (Westring, 1851)		5		5		6	16
31	*Araeoncus humilis* (Blackwall, 1841)				1			1
32	*Araneus alsine* (Walckenaer, 1802)						2	2
33	*Araneus diadematus* (Clerck, 1757)					2		2
34	*Araneus sturmi* (Hahn, 1831)				1			1
35	*Arctosa leopardus* (Sundevall, 1833)		3		1			4
36	*Arctosa lutetiana* (Simon, 1876)	15						15
37	*Argenna subnigra* (O.P.-Cambridge, 1861)	2						2
38	*Asagena phalerata* (Panzer, 1801)						1	1
39	*Atypus affinis* (Eichwald, 1830)	3		1				4
40	*Aulonia albimana* (Walckenaer, 1805)	152						152
41	*Ballus chalybeius* (Walckenaer, 1802)	2	2	2				6
42	*Bathyphantes gracilis* (Blackwall, 1841)		4	22	2	3	1	32
43	*Bathyphantes nigrinus* (Westring, 1851)		1	7	13	12	8	41
44	*Bathyphantes parvulus* (Westring, 1851)			3	39	143	78	263
45	*Bathyphantes similis* (Kulczyn'ski, 1894)					1		1
46	*Bolyphantes alticeps* (Sundevall, 1833)					2	5	7
47	*Callilepis nocturna* (Linnaeus, 1758)						2	2
48	*Centromerus albidus* (Simon, 1929)	20						20
49	*Centromerus arcanus* (O.P.-Cambridge, 1873)						1	1
50	*Centromerita bicolor* (Blackwall, 1833)				1			1
51	*Centromerus brevipalpus* (Menge, 1866)			2				2
52	*Centromerus leruthi* (Fage, 1933)		1	1				2
53	*Centromerus pabulator* (O.P.-Cambridge, 1875)				4			4
54	*Centromerus prudens* (O.P.-Cambridge, 1873)	1						1
55	*Centromerus sellarius* (Simon, 1884)	1						1
56	*Centromerus serratus* (O.P.-Cambridge, 1875)		1					1
57	*Centromerus sylvaticus* (Blackwall, 1841)	6	10	4	9	12	5	46

58	*Ceratinella brevis* (Wider, 1834)	5	1		11	60	57	134
59	*Ceratinella scabrosa* (O.P.-Cambridge, 1871)		30	33	29		9	101
60	*Cercidia prominens* (Westring, 1851)	1					4	5
61	*Chorizomma subterraneum* (Simon, 1872)	5						5
62	*Cicurina cicur* (Frabricius, 1793)		6		2			8
63	*Civizelotes civicus* (Simon, 1878)	4						4
64	*Clubiona brevipes* (Blackwall, 1841)		1		1	1		3
65	*Clubiona comta* (C.L. Koch, 1839)	1	31	5	12	3	1	53
66	*Clubiona corticalis* (Walckenaer, 1802)				6			6
67	*Clubiona lutescens* (Westring, 1851)			5	8	5	9	27
68	*Clubiona neglecta* (O.P.-Cambridge, 1862)					1		1
69	*Clubiona pallidula* (Clerck, 1757)	1	6	4	19	7	3	40
70	*Clubiona pseudoneglecta* (Wunderlich, 1994)	1						1
71	*Clubiona reclusa* (O.P.-Cambridge, 1863)			4		4	2	10
72	*Clubiona terrestris* (Westring, 1851)	2	8	15	67	95	19	206
73	*Cnephalocotes obscurus* (Blackwall, 1834)	1						1
74	*Coelotes atropos* (Walckenaer, 1830)				14			14
75	*Coelotes terrestris* (Wider, 1834)		17	14	11			42
76	*Collinsia inerrans* (O.P.-Cambridge, 1885)		2		1			3
77	*Cozyptila blackwalli* (Simon, 1875)	37						37
78	*Crustullina guttata* (Wider, 1834)	15			4		18	37
79	*Cyclosa conica* (Pallas, 1772)			1				1
80	*Diaea dorsata* (Fabricius, 1777)	1						1
81	*Dicymbium nigrum* (Blackwall, 1834)	2			1	1		4
82	*Dicymbium tibiale* (Blackwall, 1836)		3	20	18	41	18	100
83	*Diplostyla concolor* (Wider, 1834)	19	201	118	500	319	44	1201
84	*Diplocephalus cristatus* (Blackwall, 1833)					45	29	74
85	*Diplocephalus latifrons* (O.P.-Cambridge, 1863)	2	38	14	25	108	80	267
86	*Diplocephalus picinus* (Blackwall, 1841)	3	24	146	927	147	97	1344
87	*Dismodicus bifrons* (Blackwall, 1841)			2	1			3
88	*Drapetisca socialis* (Sundevall, 1833)						1	1
89	*Drassodes cupreus* (Blackwall, 1834)						8	8
90	*Drassodes lapidosus* (Walckenaer, 1802)	9						9
91	*Drassyllus lutetianus* (L. Koch, 1866)					10	2	12
92	*Drassyllus praeficus* (L. Koch, 1866)	32				1	32	65
93	*Drassodes pubescens* (Thorell, 1856)	3					78	81
94	*Drassyllus pusillus* (C.L. Koch, 1833)		1			4		5
95	*Drassyllus villicus* (Thorell, 1875)	120						120
96	*Dysdera crocata* (C.L. Koch, 1838)	1						1
97	*Dysdera erythrina* (Walckenaer, 1802)	86	72	7				165
98	*Enoplognatha ovata* (Clerck, 1757)		22	6	2	4	1	35

99	*Enoplognatha thoracica* (Hahn, 1833)	10	2	10	3	1	5	31
100	*Entelecara acuminata* (Wider, 1834)						1	1
101	*Entelecara erythropus* (Westring, 1851)						1	1
102	*Episinus angulatus* (Blackwall, 1836)			1			8	9
103	*Episinus maculipes* (Cavanna, 1876)		1					1
104	*Episinus truncatus* (Latreille, 1809)	4						4
105	*Eratigena fuesslini* (Pavesi, 1873)	4						4
106	*Eratigena picta* (Simon, 1870)	22	61	8				91
107	*Erigone atra* (Blackwall, 1833)		92	58	27	9	17	203
108	*Erigone dentipalpis* (Wider, 1834)		22	5	2		1	30
109	*Erigonella hiemalis* (Blackwall, 1841)					3	15	18
110	*Erigone longipalpis* (Sundevall, 1830)				2			2
111	*Ero furcata* (Villers, 1789)	5	4	5		1	2	17
112	*Euophrys frontalis* (Walckenaer, 1802)	2			2	4	9	17
113	*Euophrys herbigrada* (Simon, 1871)	1						1
114	*Euryopis flavomaculata* (C.L. Koch, 1836)			9	25	8	25	67
115	*Evarcha falcata* (Clerck, 1757)				1		6	7
116	*Floronia bucculenta* (Clerck, 1757)						2	2
117	*Glyphesis servulus* (Simon, 1881)			1				1
118	*Gnaphosa bicolor* (Hahn, 1833)						37	37
119	*Gonatium rubellum* (Blackwall, 1841)		2	5	8	83	1	99
120	*Gonatium rubens* (Blackwall, 1833)						4	4
121	*Gongylidiellum latebricola* (O.P.-Cambridge, 1871)						8	8
122	*Gongylidium rufipes* (Linnaeus, 1758)			48	40	63	8	159
123	*Gongylidiellum vivum* (O.P.-Cambridge, 1875)				1			1
124	*Hahnia helveola* (Simon, 1875)		16	13	1			30
125	*Hahnia montana* (Blackwall, 1841)				1			1
126	*Hahnia nava* (Blackwall, 1841)	15		1		1	1	18
127	*Hahnia ononidum* (Simon, 1875)	1		16				17
128	*Hahnia pusilla* (C.L. Koch, 1841)		1	5	1	2	75	84
129	*Haplodrassus moderatus* (Kulczyn'ski, 1897)						1	1
130	*Haplodrassus signifer* (C.L. Koch, 1839)	14			1	2	13	30
131	*Haplodrassus silvestris* (Blackwall, 1833)	39	11	37	175	40	105	407
132	*Haplodrassus soerenseni* (Strand, 1900)				4	2	29	35
133	*Haplodrassus umbratilis* (L. Koch, 1866)						7	7
134	*Harpactea hombergi* (Scopoli, 1763)	12						12
135	*Heliophanus cupreus* (Walckenaer, 1802)	2					7	9
136	*Helophora insignis* (Blackwall, 1841)					1		1
137	*Histopona torpida* (C.L. Koch, 1837)		96	68	14			178
138	*Hogna radiata* (Latreille, 1817)	3						3

139	*Hylyphantes graminicola* (Sundevall, 1830)		3					3
140	*Hypomma cornutum* (Blackwall, 1833)					1	3	4
141	*Hypomma fulvum* (Bösenberg, 1902)		1					1
142	*Inermocoelotes inermis* (L. Koch, 1855)		18	2				20
143	*Jacksonella falconeri* (Jackson, 1908)	2						2
144	*Kishidaia conspicua* (L. Koch, 1866)	2						2
145	*Lasiargus hirsutus* (Menge, 1869)	1						1
146	*Lathys humilis* (Blackwall, 1855)		1		1			2
147	*Lepthyphantes minutus* (Blackwall, 1833)			1				1
148	*Leptorhoptrum robustum* (Westring, 1851)			5	8			13
149	*Linyphia hortensis* (Sundevall, 1830)		18	7	31	91	6	153
150	*Linyphia triangularis* (Clerck, 1757)					1	1	2
151	*Liocranoeca striata* (Kulczyn'ski, 1882)	12						12
152	*Liophrurillus flavitarsis* (Lucas, 1846)	124						124
153	*Macrargus rufus* (Wider, 1834)		9	7	44	25	9	94
154	*Maso gallicus* (Simon, 1894)	1						1
155	*Maso sundevalli* (Westring, 1851)	1	20	19	10	32	4	86
156	*Mastigusa arietina* (Thorell, 1871)						3	3
157	*Mermessus trilobatus* (Emerton, 1882)	3	4	2	1			10
158	*Metellina mengei* (Blackwall, 1870)		2	7	1	4	2	16
160	*Metellina merianae* (Scopoli, 1763)			1	1			2
160	*Metopobactrus prominulus* (O.P.-Cambridge, 1872)	2					3	5
161	*Micaria aenea* (Thorell, 1871)						3	3
162	*Micaria pulicaria* (Sundevall, 1831)	4		1	3	2	7	17
163	*Micrargus apertus* (O.P.-Cambridge, 1871)	1						1
164	*Micrargus herbigradus* (Blackwall, 1854)		9	13	2	2	11	37
165	*Micrargus subaequalis* (Westring, 1851)	1	4	1	11	1	14	32
166	*Microctenonyx subitaneus* (O.P.-Cambridge, 1875)				1			1
167	*Microneta viaria* (Blackwall, 1841)	16	9	101	151	301	55	633
168	*Micrommata virescens* (Clerck, 1757)						1	1
169	*Minyriolus pusillus* (Wider, 1834)						7	7
170	*Moebelia penicillata* (Westring, 1851)						1	1
171	*Monocephalus castaneipes* (Simon, 1884)		1					1
172	*Monocephalus fuscipes* (Blackwall, 1836)		12	148				160
173	*Nemesia simoni* (O.P.-Cambridge, 1874)	3						3
174	*Neon reticulatus* (Blackwall, 1853)	2	1				4	7
175	*Neottiura bimaculata* (Linnaeus, 1767)		1				3	4
176	*Neottiura suaveolens* (Simon, 1879)	1						1
177	*Neriene clathrata* (Sundevall, 1830)		6	3	32	18	19	78
178	*Neriene emphana* (Walckenaer, 1841)		1				1	2

179	*Neriene montana* (Clerck, 1757)		2	1	2	1		6
180	*Neriene peltata* (Wider, 1834)		2	1				3
181	*Nesticus cellulanus* (Clerck, 1757)			1				1
182	*Nigma flavescens* (Walckenaer, 1830)			1				1
183	*Obscuriphantes obscurus* (Blackwall, 1841)					1		1
184	*Oedothorax agrestis* (Blackwall, 1853)			10				10
185	*Oedothorax apicatus* (Blackwall, 1850)		16	8	1	1		26
186	*Oedothorax fuscus* (Blackwall, 1834)		12	8	1			21
187	*Oedothorax gibbosus* (Blackwall, 1841)				3		2	5
188	*Oedothorax retusus* (Westring, 1851)		1	17		1		19
189	*Ostearius melanopygius* (O.P.-Cambridge, 1879)		1					1
190	*Ozyptila atomaria* (Panzer, 1801)	2					7	9
191	*Ozyptila praticola* (C.L. Koch, 1837)	100	102	68	192	128	284	874
192	*Ozyptila.simplex* (O.P.-Cambridge, 1862)	3						3
193	*Ozyptila trux* (Blackwall, 1846)		10	19	29	170	13	241
194	*Pachygnatha clercki* (Sundevall, 1823)	1		35	9	22		67
195	*Pachygnatha degeeri* (Sundevall, 1830)	1	1	34	230	20	4	290
196	*Pachygnatha listeri* (Sundevall, 1830)		1		33	433	42	509
197	*Paidiscura pallens* (Blackwall, 1834)		2		1			3
198	*Palliduphantes alutacius* (Simon, 1884)	45						45
199	*Palliduphantes insignis* (O.P.-Cambridge, 1913)					1		1
200	*Palliduphantes pallidus* (O.P.-Cambridge, 1871)		17	17	23	41	2	100
201	*Panamomops mengei* (Simon, 1926)				2			2
202	*Panamomops sulcifrons* (Wider, 1834)	57						57
203	*Pardosa agrestis* (Westring, 1861)	1			5		5	11
204	*Pardosa amentata* (Clerck, 1757)		250	332	16	10		608
205	*Pardosa fulvipes* (Collett, 1876)						53	53
206	*Pardosa hortensis* (Thorell, 1872)	20						20
207	*Pardosa lugubris* (Walckenaer, 1802)		248	40	1917	34	2226	4465
208	*Pardosa nigriceps* (Thorell, 1856)	8						8
209	*Pardosa palustris* (Linaeus, 1758)		1		5	6	2	14
210	*Pardosa prativaga* (L. Koch, 1870)	35	1	19	12	230	15	312
211	*Pardosa proxima* (C.L. Koch, 1847)		2	8	1			11
212	*Pardosa pullata* (Clerck, 1757)		6	9		1	40	56
213	*Pardosa saltans* (Töpfer-Hofmann, 2000)	2903	321	26	1558	1550		6358
214	*Pardosa vittata* (Keyserling, 1863)	4						4
215	*Pelecopsis bucephala* (O.P.-Cambridge, 1875)	3						3
216	*Pelecopsis radicicola* (L. Koch, 1872)				34			34
217	*Philodromus albidus* (Kulczyn'ski, 1911)		2					2
218	*Philodromus aureolus* (Clerck, 1757)	1	1			1	3	6

219	*Philodromus cespitum* (Wlackenaer, 1802)						1	1
220	*Philodromus collinus* (C.L. Koch, 1835)				2			2
221	*Philodromus dispar* (Walckenaer, 1826)		2	2	3			7
222	*Philodromus praedatus* (O.P.-Cambridge, 1871)						1	1
223	*Philodromus rufus* (Walckenaer, 1826)		1					1
224	*Phlegra fasciata* (Hahn, 1826)	3					1	4
225	*Pholcomma gibbum* (Westring, 1851)	2				1		3
226	*Phrurolithus festivus* (C.L. Koch, 1835)	61	9		4	14	26	114
227	*Phycosoma inornatum* (O.P.-Cambridge, 1861)	1						1
228	*Piratula hygrophila* (Thorell, 1872)		8	228	645	50	9	940
229	*Piratula latitans* (Blackwall, 1841)	1	4	2				7
230	*Pirata piraticus* (Clerck, 1757)				4			4
231	*Pirata uliginosus* (Thorell, 1856)	3	1	1			136	141
232	*Pisaura mirabilis* (Clerck, 1757)	7	1	1		16	4	29
233	*Pocadicnemis juncea* (Locket & Millidge, 1953)	10		2	2	20		34
234	*Pocadicnemis pumila* (Blackwall, 1841)				4	19	20	43
235	*Poecilochroa variana* (C.L. Koch, 1839)	1					3	4
236	*Porrhomma egeria* (Simon, 1884)		4			1		5
237	*Porrhomma errans* (Blackwall, 1841)					1		1
238	*Porrhomma microps* (Roewer, 1931)					2	2	4
239	*Porrhomma montanum* (Jackson, 1913)				1			1
240	*Pseudeuophrys erratica* (Walckenaer, 1826)	2					1	3
241	*Robertus lividus* (Blackwall, 1836)	3	5	57	14	116	31	226
242	*Robertus neglectus* (O.P.-Cambridge, 1871)			1		5	14	20
243	*Robertus scoticus* (Jackson, 1914)					3		3
244	*Saaristoa abnormis* (Blackwall, 1841)	2	2	10	7	32		53
245	*Saitis barbipes* (Simon, 1868)	12						12
246	*Saloca diceros* (O.P.-Cambridge, 1871)	3	2	66	10	3		84
247	*Salticus zebraneus* (C.L. Koch, 1837)	1						1
248	*Savignia frontata* (Blackwall, 1833)					2		2
249	*Scotina celans* (Blackwall, 1841)	62	19	1				82
250	*Segestria senoculata* (Linnaeus, 1758)		3		24	18	20	65
251	*Setaphis carmeli* (O.P.- Cambridge, 1872)	4						4
252	*Sintula corniger* (Blackwall, 1856)	3						3
253	*Stemonyphantes lineatus* (Linnaeus, 1758)	1		1	5	14	9	30
254	*Talavera aequipes* (O.P.-Cambridge, 1871)	1						1
255	*Tallusia experta* (O.P.-Cambridge, 1871)			1				1
256	*Tapinocyba insecta* (L. Koch, 1869)			22	7	3	1	33
257	*Tapinopa longidens* (Wider, 1834)	1						1
258	*Tapinocyba pallens* (O.P.-Cambridge, 1872)						4	4

259	*Tegenaria ferruginea* (Panzer, 1804)				2			2
260	*Tegenaria hasperi* (Chyzer, 1897)	1						1
261	*Tegenaria silvestris* (L. Koch, 1872)		2		1			3
262	*Tenuiphantes alacris* (Blackwall, 1853)						1	1
263	*Tenuiphantes cristatus* (Menge, 1866)					1	2	3
264	*Tenuiphantes flavipes* (Blackwall, 1854)	54	27	58	64	86	121	410
265	*Tenuiphantes mengei* (Kulczyn'ski, 1887)			4	2	1	27	34
266	*Tenuiphantes tenebricola* (Wider, 1834)	10	10	3	20	269	88	400
267	*Tenuiphantes tenuis* (Blackwall, 1852)	71	53	32	33	16	10	215
268	*Tenuiphantes zimmermanni* (Bertkau, 1890)	3	24	40	57	13		137
269	*Tetragnatha montana* (Simon, 1874)			1		1		2
270	*Tetragnatha pinicola* (L. Koch, 1870)						1	1
271	*Textrix denticulata* (Olivier, 1789)			3	4			7
272	*Thanatus formicinus* (Clerck, 1757)						2	2
273	*Thanatus striatus* (C.L. Koch, 1845)	1						1
274	*Theonina cornix* (Simon, 1881)	2						2
275	*Theridion varians* (Hahn, 1833)		1	2				3
276	*Thyreosthenius biovatus* (O.P.-Cambridge, 1875)					1	3	4
277	*Tibellus oblongus* (Walckenaer, 1802)						2	2
278	*Tiso vagans* (Blackwall, 1834)	1		4	4		1	10
279	*Titanoeca tristis* (L. Koch, 1872)	1						1
280	*Trachyzelotes fuscipes* (L. Koch, 1866)	4						4
281	*Trachyzelotes pedestris* (C.L. Koch, 1837)	111	12	7				130
282	*Trichoncus hackmani* (Millidge, 1955)	25						25
283	*Trochosa hispanica* (Simon, 1870)	107						107
284	*Trochosa robusta* (Simon, 1876)	3						3
285	*Trochosa ruricola* (De Geer, 1778)		2		11	2	32	47
286	*Trochosa spinipalpis* (F.O.P.-Cambridge, 1895)			2			11	13
287	*Trochosa terricola* (Thorell, 1856)	2	214	101	125	152	339	933
288	*Troxochrus scabriculus* (Westring, 1851)			3			1	4
289	*Typhochrestus digitatus* (O.P._Cambridge, 1872)						4	4
290	*Walckenaeria acuminata* (Blackwall, 1833)	5	1	19	25	14		64
291	*Walckenaeria antica* (Wider, 1834)	4	5		1	5	8	23
292	*Walckenaeria atrotibialis* (O.P.-Cambridge, 1878)		47	152	6	7	98	310
293	*Walckenaeria corniculans* (O.P.-Cambridge, 1875)	6	12		137			155
294	*Walckenaeria cucullata* (C.L. Koch, 1836)			1	31	15	10	57
295	*Walckenaeria cuspidata* (Blackwall, 1833)		1					1
296	*Walckenaeria dysderoides* (Wider, 1834)		8	2	10	12	1	33

297	*Walckenaeria furcillata* (Menge, 1869)	2		13			19	34
298	*Walckenaeria incisa* (O.P.-Cambridge, 1871)				1			1
299	*Walckenaeria kochi* (O.P.-Cambridge, 1872)						3	3
300	*Walckenaeria mitrata* (Menge, 1868)		1					1
301	*Walckenaeria monoceros* (Wider, 1834)		1	1				2
302	*Walckenaeria nudipalpis* (Westring, 1851)		1	6	1	12	5	25
303	*Walckenaeria obtusa* (Blackwall, 1836)				2	4		6
304	*Walckenaeria unicornis* (O.P.-Cambridge, 1861)			2		1		3
305	*Walckenaeria vigilax* (Blackwall, 1853)					1		1
306	*Xerolycosa miniata* (C.L. Koch, 1834)					1		1
307	*Xerolycosa nemoralis* (Westring, 1861)					2	7	9
308	*Xysticus cristatus* (Clerck, 1757)	2		1	2	3	1	9
309	*Xysticus erraticus* (Blackwall, 1834)						15	15
310	*Xysticus kochi* (Thorell, 1872)	1	1			3		5
311	*Xysticus lanio* (C.L. Koch, 1835)		1	2	2		1	6
312	*Xysticus lineatus* (Westring, 1851)						50	50
313	*Xysticus luctator* (L. Koch, 1870)	3						3
314	*Xystiscus luctuosus* (Blackwall, 1836)						68	68
315	*Xysticus robustus* (Hahn, 1832)						12	12
316	*Xysticus ulmi* (Hahn, 1831)					6		6
317	*Zelotes apricorum* (L. Koch, 1876)	100	1					101
318	*Zelotes atrocaeruleus* (Simon, 1878)	49						49
319	*Zelotes clivicola* (L. Koch, 1870)				16	4	11	31
320	*Zelotes exiguus* (Müller & Schenkel, 1895)	1						1
321	*Zelotes gallicus* (Simon, 1914)	3						3
322	*Zelotes latreillei* (Simon, 1878)					6	26	32
323	*Zelotes petrensis* (C.L. Koch, 1839)	10					14	24
324	*Zelotes praeficus* (L. Koch, 1866)						1	1
325	*Zelotes subterraneus* (C.L. Koch, 1833)	2	5		14	7	15	43
326	*Zelotes tenuis* (L. Koch, 1866)	6						6
327	*Zodarion italicum* (Canestrini, 1868)	447	19					466
328	*Zora nemoralis* (Blackwall, 1861)						151	151
329	*Zora parallela* (Simon, 1878)	3						3
330	*Zora pardalis* (Simon, 1878)	33						33
331	*Zora spinimana* (Sundevall, 1833)	31	11	2	35	8	93	180
	All species	5626	2467	2644	7832	5403	5712	29684

Table A7.4.3. *Harvestman species list and species activity-density per region. FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, SS: Southern Sweden and SC: central Sweden.*

		Region					
		FN	BE	GW	SS	SC	All
1	*Anelasmocephalus cambridgei* (Westwood, 1874)	7	8	1			16
2	*Dicranopalpus ramosus* (Simon, 1909)	6					6
3	*Homalenotus quadridentatus* (Cuvier, 1795)	289	23				312
4	*Lacinius ephippiatus* (C.L. Koch, 1835)	799	16	2303	3908	524	7550
5	*Lacinius horridus* (Panzer, 1794)					3	3
6	*Leiobunum blackwalli* (Meade 1861)			10			10
7	*Leiobunum rotundum* (Latreille, 1798)	7		7	20		34
8	*Lophopilio palpinalis* (Herbst, 1799)	78	4	102	13	13	210
9	*Mitopus morio* (Fabricius, 1799)	10	12	10			32
10	*Mitostoma chrysomelas* (Hermann, 1804)	2	2	232	180	256	672
11	*Nelima gothica* (Lohmander ,1945)					13	13
12	*Nelima sempronii* (Szalay, 1951)			90			90
13	*Nemastoma bimaculatum* (Fabricius, 1775)	25	30	1			56
14	*Nemastoma dentigerum* (Canestrini, 1873)			22			22
15	*Nemastoma lugubre* (Müller, 1776)	59	39	68	245	105	516
16	*Oligolophus tridens* (C.L. Koch, 1836)	886	7	1813	5029	1209	8944
17	*Opilio canestrinii* (Thorell, 1876)			67	1		68
18	*Opilio saxatilis* (C.L. Koch, 1839)	1					1
19	*Paranemastoma quadripunctatum* (Perty, 1833)		2	19			21
20	*Phalangium opilio* (Linnaeus, 1758)	4		1	12	136	153
21	*Platybunus pinetorum* (C.L. Koch, 1839)			3	16		19
22	*Rilaena triangularis* (Herbst, 1799)	717	240	1987	1160	27	4131
23	*Trogulus closanicus* (Avram, 1971)	363	30				393
24	*Trogulus nepaeformis* (Scopoli, 1763)	53	43				96
25	*Trogulus tricarinatus* (Linnaeus, 1767)	4	6				10
	All species	3310	462	6736	10584	2286	23378

Table A7.4.4. *Centipede species list and species activity-density per region. FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, SS: Southern Sweden and SC: central Sweden.*

		Region					
		FN	BE	GW	SS	SC	All
1	*Geophilus truncorum* (Bergsoë & Meinert, 1866)	1					1
2	*Cryptops hortensis* (Donovan, 1810)		2	2	1		5
3	*Cryptops parisi* (Brölemann, 1920)	5	9	1			15
4	*Geophilus carpophagus* (Leach, 1814)	4	2		1		7
5	*Geophilus electricus* (Linnaeus, 1758)	3					3
6	*Geophilus flavus* (De Geer, 1778)					1	1
7	*Geophilus insculptus* (Attems, 1895)	1					1
8	*Geophilus proximus* (Koch, 1847)				1		1
9	*Stigmatogaster subterranea* (Shaw, 1789)		2				2
10	*Henia vesuviana* (Newport, 1844)	2					2
11	*Lamyctes emarginatus* (Newport, 1844)	7	1			19	27
12	*Lithobius borealis* (Meinert, 1868)				2	1	3
13	*Lithobius calcaratus* (Koch, 1844)	1	4		4		9
14	*Lithobius crassipes* (Koch, 1862)	3	6	2	18	106	135
15	*Lithobius curtipes* (Koch, 1847)				2	2	4
16	*Lithobius dentatus* (Koch, 1844)		15	11			26
17	*Lithobius forficatus* (Linnaeus, 1758)	35	11	10	21	12	89
18	*Lithobius lusitanus* (Verhoeff, 1925)			1			1
19	*Lithobius macilentus* (Koch, 1862)	7					7
20	*Lithobius microps* (Meinert, 1868)	81	208	6	25	138	458
21	*Lithobius muticus* (Koch, 1847)	5	41	3			49
22	*Lithobius tenebrosus* (Meinert, 1872)			1	1		2
23	*Lithobius tricuspis* (Meinert, 1872)	2					2
24	*Schendyla nemorensis* (Koch, 1837)	17	27	1	4		49
25	*Strigamia acuminata* (Leach, 1814)	1	2	1			4
26	*Strigamia crassipes* (Koch, 1835)	1	1		4		6
	All species	176	331	39	84	279	909

Table A7.4.5. *Millipede species list and species activity-density per region. All individuals were identified to the species level if possible. Female millipedes of the Julidae family, which cannot be identified morphologically to species level with 100% certainty, were identified as Julidae spp. FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, SS: Southern Sweden and SC: central Sweden.*

		Region						
		FS	FN	BE	GW	SS	SC	All
1	*Allajulus nitidus* (Verhoeff, 1891)	13	103	30	7	10	27	190
2	*Blaniulus guttulatus* (Fabricius, 1798)		2	1			2	5
3	*Brachyiulus pusillus* (Leach, 1814)	7	21	186		1		215
4	*Brachydesmus superus* (Latzel, 1884)	11	15	64	25	90	117	322
5	*Choneiulus palmatus* (Nemec, 1895)						4	4
6	*Chordeuma sylvestre* (C.L. Koch, 1847)		5					5
7	*Craspedosoma rawlinsi* (Leach, 1814)		6	12	7	89	2	116
8	*Craspedosoma* spec.	5						5
9	*Cylindroiulus caeruleocinctus* (Wood, 1864)	2	440	80		344	1689	2555
10	*Cylindroiulus latestriatus* (Curtis, 1845)			1		1		2
11	*Cylindroiulus londinensis* (Leach, 1814)	35						35
12	*Cylindroiulus punctatus* (Leach, 1815)	8	24	160	33	28	5	258
13	*Glomeris intermedia* (Latzel, 1884)		104	83				187
14	*Glomeris marginata* (Villers, 1789)	273	3	217	232	142		867
15	*Hirudisoma latum* (Ribaut, 1908)	1						1
16	*Julidae* spec.	7	56	85	139	717	355	1359
17	*Julus scandinavius* (Latzel, 1884)		26	66	146	190	182	610
18	*Julus terrestris* (Linnaeus, 1758)						21	21
19	*Leptoiulus belgicus* (Latzel, 1884)			5				5
20	*Leptoiulus kervillei* (Brolemann, 1896)		133	287				420
21	*Melogona gallica* (Latzel, 1884)		47	70				117
22	*Melogona voigtii* (Verhoeff, 1899)					1		1
23	*Mycogona* sp.				4			4
24	*Nemasoma varicorne* (C.L. Koch, 1847)			3			3	6
25	*Ommatoiulus rutilans* (C.L. Koch, 1847)	32						32
26	*Ommatoiulus sabulosus* (Linnaeus, 1758)	1	4	3	185	14	273	480
27	*Ophiodesmus albonanus* (Latzel, 1895)		2					2
28	*Ophyiulus pilosus* (Nemport, 1842)				11	305	125	441
29	*Orthochordeumella pallida* (Rothenbuhler, 1899)		7					7
30	*Polydesmus angustus* (Latzel, 1884)	5	202	31	198			436
31	*Polydesmus complanatus* (Linaeus, 1761)					21	2	23
32	*Polydesmus coriaceus* (Porat, 1871)	44		409				453
33	*Polydesmus denticulatus* (C.L. Koch, 1847)	9	24	25	43	2	570	673
34	*Polyzonium germanicum* (Brandt, 1837)					335		335

35	*Polydesmus inconstans* (Latzel, 1884)	19	18	43	29	412	232	753
36	*Propolydesmus testaceus* (C.L. Koch, 1847)		53					53
37	*Proteroiulus fuscus* (Am Stein, 1857)	1		4	18	181	15	219
38	*Tachypodoiulus niger* (Leach, 1814)		900	709	33			1642
39	*Unciger foetidus* (C.L. Koch, 1838)				3	453	12	468
	All species	473	2195	2574	1113	3336	3636	13327

Table A5.6. *Woodlouse species list and species activity-density per region. FS: Southern France, FN: Northern France, BE: Belgium, GW: Western Germany, SS: Southern Sweden and SC: Central Sweden.*

		Region						
		FS	FN	BE	GW	SS	SC	All
1	Armadillidium nasatum (Budde-Lund, 1885)	71						71
2	Armadillidium opacum (C. Koch, 1841)			174		237	333	744
3	Armadillidium pictim (Brandt, 1833)				29		138	167
4	Armadillidium pulchellum (Zenker, 1798)				394		312	706
5	Armadillidium vulgare (Latreille, 1804)	3696	19986	184	1	3027		26894
6	Chaetophiloscia elongata (Dollus, 1884)	1389						1389
7	Cylisticus convexus (De Geer, 1778)		1					1
8	Haplophthalmus mengii/montivagus		1					1
9	Ligidium hypnorum (Cuvier, 1792)		207	366	324	320		1217
10	Lucasius pallidus (Budde-Lund, 1885)	5						5
11	Oniscus asellus (Linnaeus, 1758)	3	1007	973	773	518	8	3282
12	Oniscus simonii (Budde-Lund, 1885)	3						3
13	Orthometopon planum (Budde-Lund, 1885)	76						76
14	Philoscia affinis (Verhoeff, 1908)	1623			60			1683
15	Philoscia muscorum (Scopoli, 1763)	2223	7281	3948	4938	7616		26006
16	Porcellio dilatatus (Brandt, 1833)	4	4					8
17	Porcellio gallicus (Dollfus, 1904)	454	1024					1478
18	Porcellio monticola (Lereboullet, 1853)	397	70					467
19	Porcellio scaber (Latreille, 1804)	18	10280	1838	3893	2710		18739
20	Porcellionides pruinosus (Brandt, 1833)	1	2		3			6
21	Porcellium conspersum (C. Koch, 1841)				3			3
22	Sphaerobathytropa ribauti (Verhoeff, 1908)	215						215
23	Trachelipus rathkii (Brandt, 1833)		2	73		201	1772	2048
24	Trichoniscoides albidus (Budde-Lund, 1880)			15				15
25	Trichoniscoides helveticus (Carl, 1908)		1					1
26	Trichoniscus provisorius (Racovitza, 1908)			5				5
27	Trichoniscus pusillus (Brandt, 1833)	103	68	142	9	105	112	539
	All species	10281	39934	7718	10427	14734	2675	85769

Haplophthalmus danicus | Gert Arijs

Chapter 8

SYNTHESIS

Forest fragmentation has resulted in European landscapes consisting of small forest fragments in an agricultural matrix. Small forest fragments have a large edge-to-interior ratio, and forest edges therefore cover a significant part of the forest habitat in these small forests. Forest edges cause edge-to-interior gradients in abiotic conditions as well as in abundance and community composition of biota. These gradients are relatively well studied for plants (Honnay et al. 2002; Harper et al. 2005; Chabrerie et al. 2013, Normann et al. 2016), birds (Brand & George 2001, Bank-Leite et al. 2010), or above-ground invertebrates (Jokimäki et al. 1998, Ewers & Didham 2006), but have remained poorly explored for the soil fauna community. This thesis contributed to filling the knowledge gap for litter-dwelling macro-arthropods. We saw that the distribution of litter-dwelling macro-detritivores can be (1) related to abiotic conditions along the forest edge-to-interior gradient and (2) explained by species-specific desiccation resistances. Experimental evidence pointed towards soil moisture content as probably the most important determinant of the distribution of litter-dwelling macro-detritivores in forest edges. We stress that a good knowledge of taxonomy is necessary for gaining insights in litter-dwelling macro-arthropod distribution patterns. The observed patterns at the small spatial scale of a forest fragment were consistent across forest fragments at the larger spatial scales of landscapes throughout Western Europe. Besides macro-detritivores, we observed strong edge effects for multiple macro-arthropod taxa.

In this synthesis chapter, we further explore the importance of different environmental drivers for the distribution of litter-dwelling arthropods. In addition, we discuss the possible consequences for ecosystem functioning of the distribution of litter-dwelling arthropods along edge-to-interior gradients. The chapter ends with management suggestions for small forests and an outlook for future research.

Litter-dwelling macro-fauna in forest edges

Different trophic levels of the soil fauna food web showed strong responses to forest edges (Fig. 8.1, next page). We subsequently discuss detritivores, omnivores and carnivores.

Detritivores

Detritivore taxa, such as woodlice and millipedes, were more abundant in forest edges compared to forest interiors. Woodlice strongly decreased in abundance (**Chapter 3**) and activity-density (**Chapter 4**) along forest edge-to-interior gradients; millipedes showed a more unimodal response (**Chapter 3**). Although both taxa strongly depend on soil moisture content (Warburg 1964; Hopkin & Read 1992; Hornung 2011), millipedes have, on average, a higher desiccation resistance (Wolters & Ekschmitt 1997; pers. comm. Matty P. Berg). Desiccation resistance has been shown to be a good estimator for species-specific habitat choice (Dunger & Steinmetzger 1981, Dias et al. 2013); we also found a tight link between species-specific desiccation resistance and the observed abundance patterns of woodlice in forest edges (**Chapter 4**). Drought-tolerant species (often r-strategists) built up large populations in forest edges, which shaped the overall taxa-level patterns. Woodlice and millipedes are more susceptible to water loss compared to insects or arachnids (Mantel 1979) because, for instance, their cuticle generally lacks a waxy waterproof layer and their gas-exchange system cannot be closed (Wolters & Ekschmitt 1997).

Two dominant macro-detritivore taxa not analysed in this thesis are earthworms and molluscs (slugs and snails). The few available earthworm data suggest that earthworms are more abundant in forest interiors than in forest edges (Nachtergale et al. 2002), but that the trends can be species-specific (Eisenhauer et al. 2007). For slugs and snails, literature is also limited. Data from the smallFOREST-consortium suggest that slugs are far more abundant in forest interiors compared to forest edges (Box 1). Slugs and snails have a permeable skin and quickly lose water due to evapotranspiration and the production of mucus; lost water has to be replaced quickly via water uptake from moist environments (Wolters & Ekschmitt 1997). We found no clear edge-to-interior trend in snail abundance, probably because their shell enables them to withstand drier conditions compared to slugs (Mantel 1979, Wolters & Ekschmitt 1997). Many of the detritivore taxa we mentioned (e.g. millipedes, slugs and earthworms) show strong behavioural responses to drought; they burrow deeper into the soil or stay inactive until conditions are better again (Mantel 1979, Hopkin & Read 1992). Not encountering these animals in a certain biotope during a sampling campaign therefore not necessarily means that they are absent; they may be active at other times of the year. Hence, we recommend to study edge-to-interior gradients of litter-dwelling detritivores in forests across seasons.

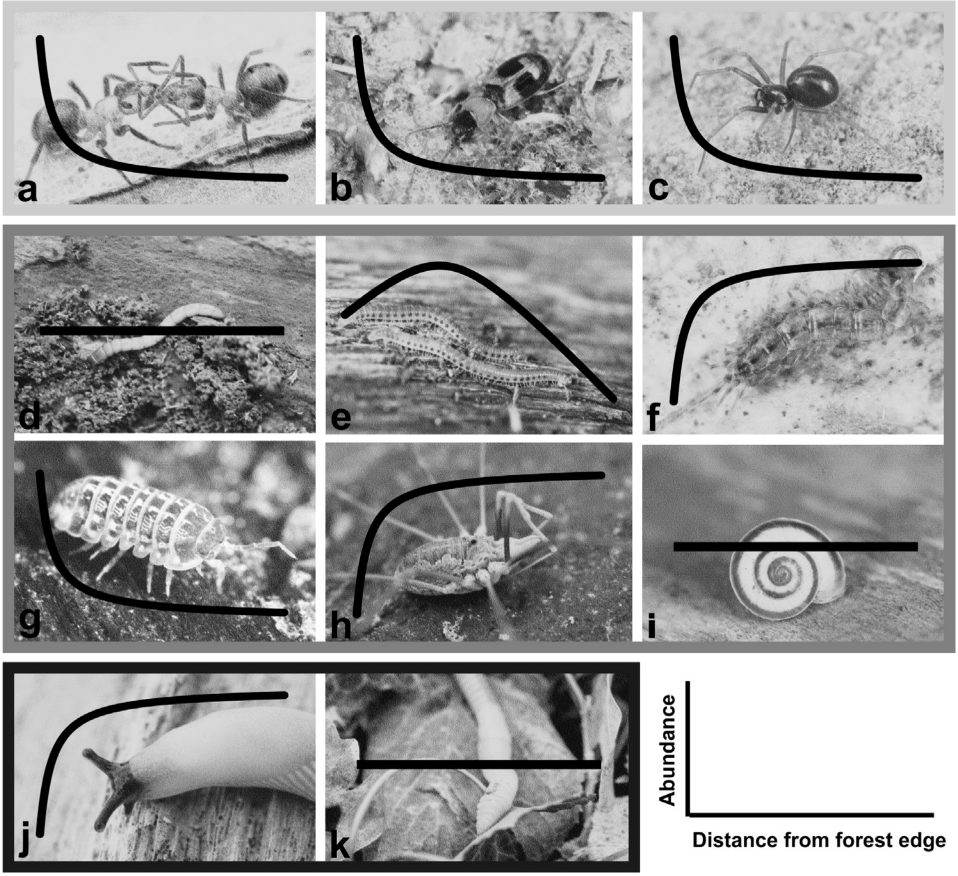


Figure 8.1. *Summary of responses along forest edge-to-interior gradients for dominant macro-fauna taxa in temperate forest fragments based on the outcomes in the different chapters and literature data. (a) Ants, (b) carabid beetles and (c) spiders are considered the most drought-tolerant taxa. (d) Beetle/diptera larvae, (e) millipedes, (f) centipedes, (g) woodlice, (h) harvestmen and (i) snails are considered intermediately drought-tolerant while (j) slugs and (k) earthworms are considered drought sensitive. Classification based on Hadley (1994). Taxa that are more tolerant to drought (light grey rectangle) showed higher abundances at forest edges; intermediate taxa (dark grey rectangle) showed highly variable patterns; and drought-sensitive taxa (black rectangle) decreased in abundance towards the forest edge or showed a neutral response. Pictures: Theodoor Heijerman (a), Anne Krediet (b,c,d,e,f,g,h,i,j), Stephanie Schelfhout (k).*

Omnivores

Omnivorous[1] harvestmen are the only group of the six taxa covered in this thesis that tended to be more abundant in forest interiors (**Chapter 7**, Van de Poel 2016). Harvestmen are drought-sensitive and are most abundant in forests, (Curtis & Machado 2007; Bragagnolo et al. 2007). Little is known, however, if harvestmen are more or less drought tolerant relative to other arthropod taxa (Santos 2007). Two other important groups of omnivorous soil biota are beetle and diptera larvae living in the soil. These larvae are the soft-bodied and drought-sensitive life stage of arthropods with a complete metamorphosis (i.e. holometabolism; Topp 1994). Beetle and diptera larvae are often neglected in soil arthropod studies since their identification is challenging. Yet, they can reach high densities in forest soils (Jabin et al. 2004, Jefferey et al. 2010, Frouz et al. 2015) and are functionally important for e.g. decomposing animal remains and litter fragmentation (Jefferey et al. 2010). Abundance data for these larvae is scarce, especially for dipterans (but see Frouz et al. 2015). Jabin et al. (2004) showed no difference in beetle larvae abundance between forest edges and forest interiors. As these beetle larvae are dominantly soil-dwelling, they might be less affected by the lower soil moisture content levels in forest edges.

Carnivores

Predators such as spiders and carabid beetles were more abundant in forest edges compared to forest interiors, but centipedes were not affected (**Chapter 7**). Carabid beetles and spiders are more tolerant to drought than other arthropod subphyla because they have a waxy epicuticular layer and can close their respiratory system to reduce respiratory water loss (i.e. spiracular control; Mantle 1979). Centipedes are more sensitive to drought than e.g. their closest relatives, the millipedes, because of the higher permeability of their cuticle (Dunger 1983, Lewis 2006), which may explain their neutral (**Chapter 7**) or negative response to forest edges (Fig. 8.1, Jabin et al. 2004, Lacasella et al. 2015). Ants form another important taxon of predators and omnivores, for which forest edge effects are well studied in the tropics (see e.g. Carvalho & Vasconcelos 1999, Guimarães & Cogni 2002, Meyer et al. 2009) where ants are important ecosystem engineers (Folgarait 1998). In temperate regions, data are scarce, but research on wood ants (*Formica rufa* group) showed higher numbers of nests in forest edges compared to forest interiors (Eichhorn 1964, Punttila 1996). Ant distribution in temperate forests has been related to the social status of the species; monogynous species with one queen and one nest show a stronger response to forest edges compared to polygynous species with more than one queen, which are relatively more abundant in forest interiors. Monogynous species are more mobile than polygynous species and can therefore react faster to changes in environmental conditions in dynamic systems such as forest edges. Ants prefer the warmer forest edges to build their nests, which potentially has a strong impact on the other forest edge invertebrates (Reznikova & Dorosheva 2004).

---

[1] Harvestmen are regarded as omnivorous or carnivorous, depending on the species (Acosta & Machado 2007). Generally, we can assume that harvestmen are omnivores with a strong preference for tissue of living animals.

Box 1. Slug and snail abundance in forest edges and interiors

Litter-dwelling fauna were collected using pitfall traps in the smallFOREST-consortium (Valdés et al. 2015). Slugs and snails are commonly attracted to these traps because of the sweet smell of ethylene glycol, or they just pass by and fall into the traps. Trapped slugs and snails were counted in three of the seven studied regions, namely Belgium, Western Germany and central Sweden.

We compared the activity-density of slugs and snails in forest edges and interiors. We fitted a multilevel model with the activity-density per sampling point as the response variable, and the sampling location (edge or interior), the sampled region (Belgium, western Germany or central Sweden) and their interaction as predictor variables, using the *glmer*-function from the lme4-package (Bates et al. 2015) in R (R Core Team 2017). To account for the paired nature of the sampling points within fragments, we added a group-level effect for forest fragment. Since this is all count data, we used a Poisson distribution.

In total, we collected 4467 slugs (BE: 2505, GW: 1585, SC: 377) and 1103 snails (BE: 740, GW: 205, SC: 158). Slug activity-density was significantly influenced by location in the forest (F(1)=235.73, p<0.001) and region (F(2)=32.05, p<0.001). The slug activity-density was highest in Belgium followed by Western Germany and central Sweden and higher in forest interiors than in forest edges across all regions (Fig. B1.1a). Snail activity-density did not differ by location in the forest (F(1)=3.95, p>0.05), but was higher in Belgium compared to Western Germany and central Sweden (F(2)=33.60, p<0.001) (Fig. B1.1b).

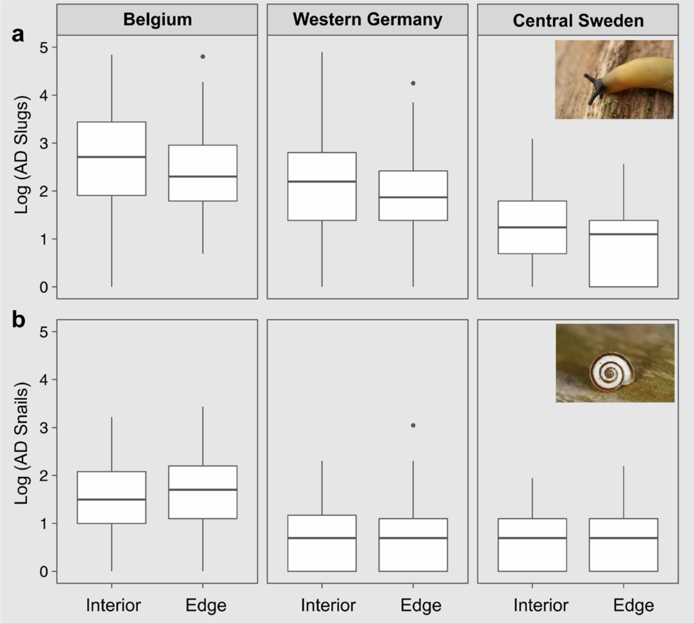


Figure B1.1. *Log-transformed activity-density (AD) of (a) slugs and (b) snails in forest edges versus interiors in Belgium, Western Germany and central Sweden. Pictures: Anne Krediet.*

Predicting species distribution

Context dependency

Macro-arthropod responses along forest edge-to-interior gradients depend strongly on the context e.g. forest age, edge orientation, edge contrast (Chapter 7), landscape-use intensity (Chapter 6), the sampling season (Ohwaki et al. 2015, Ng et al. 2018) and sampling method (De Smedt & Van de Poel, 2017) influence the strength of edge effects. Therefore, it is important to describe the edge context if one wants to assess the potential impact of the edge on species distribution. We saw that forest edge effects were stronger in south-oriented forest edges, older forests and high land-use intensity landscapes (high agricultural intensity). The 'edge contrast', which is low when the land-use at either side of the edge is similar and high when the land-use strongly differs (Ries et al. 2004, López-Barrera et al. 2006), may also play a role. Weaker edge effects are expected at low-contrast edges, but the edge contrast effect is still poorly understood (Ries et al. 2017). We saw weaker edge responses in forest edges bordered by cropland compared to forest edges bordered by grasslands (**Chapter 7**) although cropland is generally more intensely managed (recurrent disturbance, periodic spray of insecticides). Yet, our studied edge contrasts are probably all relatively high, which makes it hard to draw general conclusions about the effect of edge contrasts. However, one of the surprising findings of this thesis is the strong effect of landscape-use intensity. Higher land-use intensity landscapes result in higher activity-densities of both woodlice and millipedes. This is consistent along forest edge-to-interior gradients in these landscapes i.e. both edges and interiors have higher activity-densities. Higher input of nutrients seems the most important driver, but this remains a hypothesis.

Functional traits as predictors for distribution patterns

Next to differences in abundance and activity-density, also the community composition of edge and interior communities differed. The environmental conditions in forest edges acted as a filter for species through species' response traits. We found that edge-to-interior distribution patterns of specific species were linked to a key functional trait of the species, i.e. their desiccation resistance (**Chapter 3, 4, 6**). The desiccation resistance is the ability of an animal to withstand dry conditions. The desiccation resistance of a species relates to the water loss rate of the animals (Appendix 6.3 of **Chapter 6,** Dias et al. 2013). As the water loss rate is a function of the animal's surface-to-volume ratio, easy-to-measure metrics such as body length or body mass can probably also be used to explain distribution patterns of drought-sensitive organisms (i.e. many soil arthropod taxa). Body length ($F_{(1,187)}=23.90$, $p<0.001$) and body mass ($F_{(1,187)}=17.56$, $p<0.001$) indeed showed similar, although less strong, community-level patterns as desiccation resistance ($F_{(1,187)}=65.55$, $p<0.001$, Fig. 8.2).

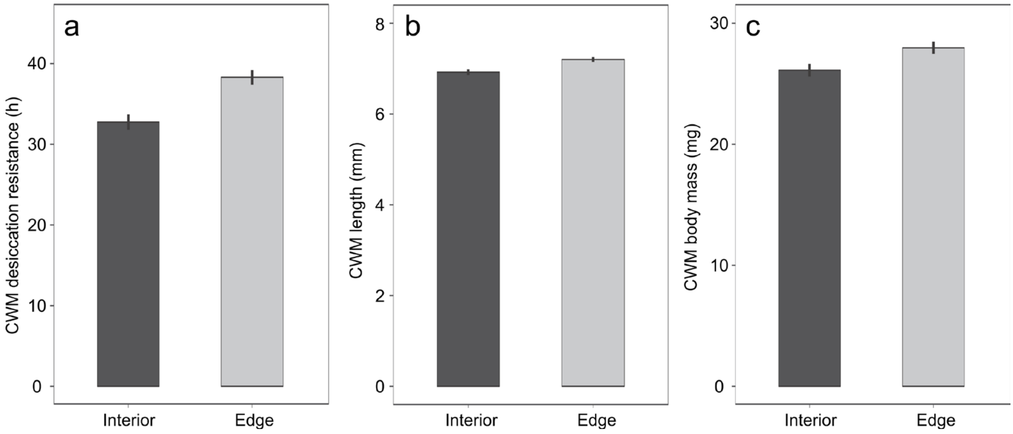


Figure 8.2. *The community-weighted mean (a) desiccation resistance, expressed as the survival time in hours under 85% relative humidity (see Chapter 6), (b) body length and (c) body mass of woodlice in forest edges vs interiors. Mean with standard error; data and data analysis cf. Fig. 6.6.*

Similar to using desiccation resistance to explain differences in forest edge and interior communities, (1) running speed or leg length (as a proxy for mobility) might be used to assess the effects of habitat fragmentation and isolation on soil community composition (see e.g. Martins da Silva et al. (2012) or (2) inundation resistance may be used to predict how communities will change after extreme floods (see Box 2). Using species response traits may hence be a tool for predicting changes in community composition under environmental change.

From responses to effects

The difference in community composition between forest edge and interior communities, driven by the response traits of species (such as desiccation or inundation resistance) and the ambient environmental conditions, will also affect the functioning of the ecosystem through the effect traits (such as feeding rate or burrowing activity) of the species present in the community. The framework of response and effect traits (Lavoral & Garnier 2002; Moretti et al. 2013) links community responses to environmental conditions and ecosystem functioning. Linking response and effect traits is a powerful tool to predict how community changes (through response traits) affect ecosystem processes (via effect traits) (Lavorel et al. 2013). Astor et al. (2015) for example linked response traits (shell volume or shape) and effect traits (feeding rate and faeces production) of snails to estimate potential total consumption rates of snail communities along environmental gradients based on the distribution in shell sizes.

Our litter decomposition experiment (**Chapter 5**) showed a net decrease in litter decomposition by macro-detritivores with soil moisture content. Taking into account the response traits (desiccation resistance) and effect traits (consumption rate) of the species in the studied arthropod community can enable us to understand the net effect of soil moisture content on an ecosystem process (litter decomposition, see Fig. 8.3). Such a response-effect framework may thus be helpful in predicting the effect of changes in community composition on ecosystem functioning. However, we could not prove this yet using the experiment in **Chapter 5**; therefore, the hypothesis remains to be tested. Yet, standardised measurements of species response traits (see Moretti et al. 2017) and particularly for species effect traits still need to be carried out for many taxa.

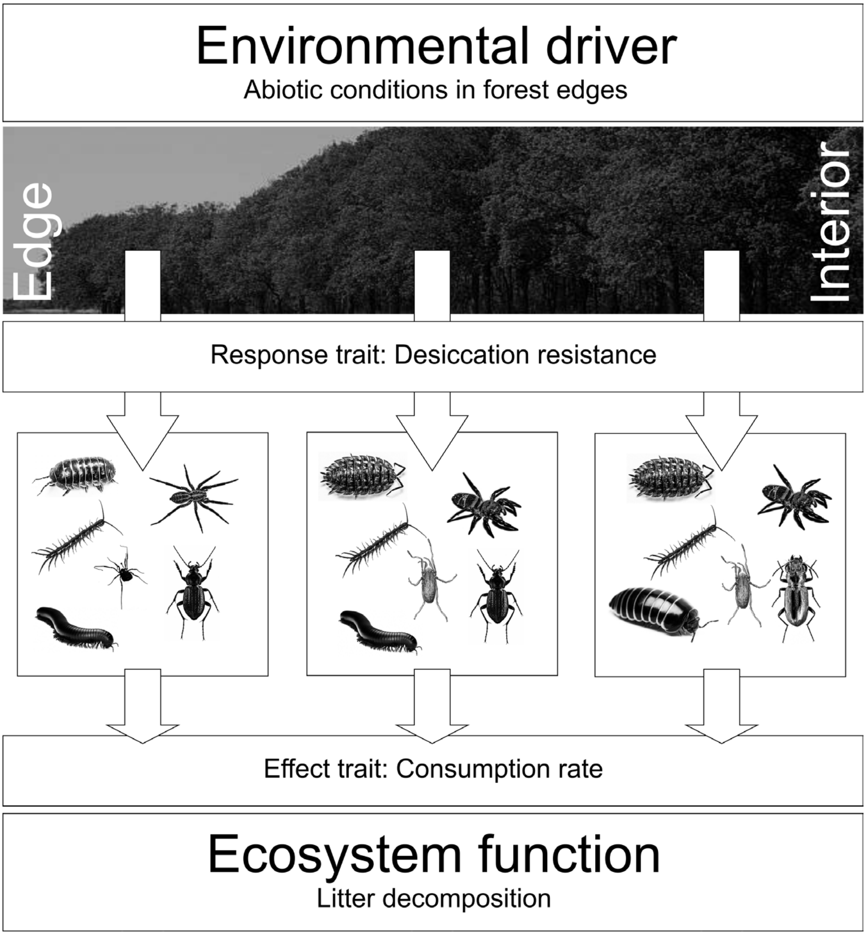


Figure 8.3. *The response-effect trait framework implemented in this thesis, based on Lavorel et al. (2013). The gradient in abiotic conditions in forest edges results in different macro-detritivore communities at different distances from the forest edge. Differences in community composition may lead to differences in ecosystem functions and processes (such as litter decomposition) through the effect traits (such as consumption rate) of the species present in the community. Species presence in a certain community is determined by the response traits (such as desiccation resistance) of the species. Other trophic levels, such as plants, can be added to this schematic representation of the framework (see Lavorel et al. 2013) by adding a trophic effect trait and a trophic response trait between two trophic levels.*

Box 2. Inundation resistance after an exceptional flood

Exceptional flooding has been shown to decrease woodlice abundance and alter woodlice community composition (Tajovský 1999). Tuf et al. (2008) investigated the epigeic and endogeic isopod fauna in a hardwood floodplain forest (Querco-Ulmetum) in a protected landscape area in the Czech Republic every month for seven years after an exceptional summer flooding in 1998. As a pre-flooding reference they used a dataset collected in a nearby forest in 1997, i.e. a year before the flood. We used their data on endogeic woodlice only, since an introduced species dominated in the epigeic dataset (Tuf et al. 2008). Tuf et al. (2008) gathered the data on endogeic woodlice using intact soil cores (five per month) and Tullgren extraction of soil fauna with a heat source. The full endogeic dataset comprised 1789 individuals of eight species (Table B8.1).

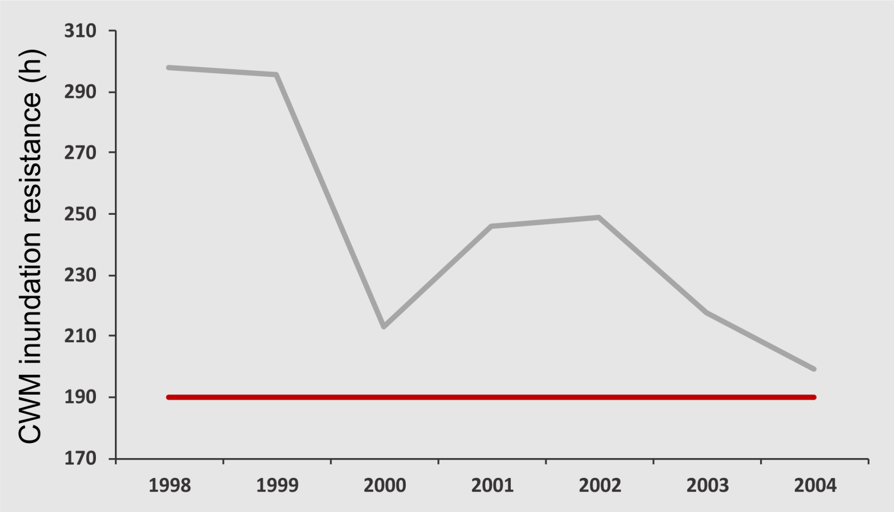
We linked the observed difference in the dominance of individual species in the woodlice community (Table B8.1) to the community-weighted mean inundation resistance. Inundation resistance is the capacity of a terrestrial organism to survive submergence without direct access to atmospheric oxygen for a set period (Moretti et al. 2017), and can be highly variable within a taxonomic group. For instance, the woodlouse Hyloniscus riparius can be submerged for up to a month, while the common Philoscia muscorum cannot survive longer than one day. We used data about the inundation resistance of woodlice species collected under standardised conditions (Moretti et al. 2016) at the Vrije Universiteit Amsterdam (unpublished data Matty P. Berg). We excluded Protracheoniscus politus and Androniscus roseus from our analysis since inundation resistance data were not available for these species and they are rare in the dataset.

Table B8.1. *Dominance of individual species (%) in the endogeic woodlice community before an exceptional summer flooding (1997) and during 7 years after the flooding (1998-2004). Adapted from Tuf et al. (2008).*

Species	1997	1998	1999	2000	2001	2002	2003	2004
Ligidium hypnorum	-	11.4	8.3	30.9	12.0	11.8	6.5	7.7
Trachelipus rathkii	1.0	2.2	1.1	2.4	2.9	7.2	4.4	3.3
Protracheoniscus politus	-	-	0.2	-	0.5	2.6	2.4	3.3
Porcellium conspersum	0.7	-	0.7	0.4	0.5	-	1.0	2.2
Trichoniscus pusillus	80.6	26.8	34.5	28.5	51.2	45.8	66.3	66.1
Hyloniscus riparius	0.3	53.1	51.5	32.5	32.1	32.7	17.3	14.2
Androniscus roseus	-	-	0.7	3.6	1.0	-	-	2.7
Haplophthalmus mengii	17.4	6.6	3.0	1.6	-	-	2.0	0.5

The community-weighted mean inundation resistance was 190 hours before the flooding and 298 hours the year after the flooding, because of an increased dominance of the inundation-resistant H. riparius (Fig. B2.8.1). After seven years, the community-weighted mean inundation resistance again approached the community-weighted mean inundation resistance of the reference period. The composition of the woodlice community was strongly altered by the exceptional inundation event, resulting in a dominance of species able to cope with long-time inundation. The disturbance filtered out species based on their inundation resistance. This short study illustrates that community restoration after a disturbance may take several years.

Figure B2.8.1: *Community-weighted mean inundation resistance (in hours) after an exceptional summer flood. The red line represents the community-weighted mean inundation resistance from the reference period (before the flood).*



Impact on forest ecosystem functions

Litter decomposition

The decomposition of organic matter performed by the complex detrital food web is the engine behind nutrient and carbon cycles worldwide. Changes in the abundance of the different components of this food web have therefore the potential to alter litter decomposition. Many lab and field experiments have indicated that decomposition slows down in the absence of soil fauna (Lavelle 1997, Wall et al. 2008, Frouz et al. 2018, **Chapter 5**). Litter decomposition experiments along forest edge-to-interior gradients are scarce though. Remy et al. (2017) found increased litter decomposition in southwest-oriented edges compared to interiors of oak forests; while Riutta et al. (2012) found decreased litter decomposition in north-oriented edges of deciduous forests. We showed effects of edge orientation on litter-dwelling macro-fauna distribution (**Chapter 7**): a strong positive edge effect on macro-fauna community composition in south-oriented edges compared to interiors while there was a weak negative edge effect in north-oriented edges. The presence/absence of a difference in community composition of litter-dwelling arthropods between forest edge in interiors in the south-/north-oriented edge in our study coincides with the higher/lower litter decomposition in the studies of Remy et al. (2017) and Riutta et al. (2012). Different species dominating opposite oriented forest edges might explain the differences. Remy et al. (2017) found no edge effects for litter decomposition in pine forests. We studied the same forest edges as Remy et al. (2017) and found highly variable and inconsistent macro-detritivore distribution patterns (in particular for millipedes, **Chapter 3**). As earthworms are scarce in the studied pine forests (Muys & Lust 1992), we sampled the main detritivore community (woodlice and millipedes) in these forests, and the lack of clear detritivore distribution patterns might explain the lack of forest edge effect in litter decomposition in Remy et al. (2017). Seeing these potential links between macro-detritivore distribution and litter decomposition, macro-detritivores might play a major role in litter decomposition in small forest fragments. Macro-arthropod predators can influence this relationship by preying on detritivores (Lawrence & Wise 2000), but the importance of this potential indirect effect on litter decomposition requires further investigation.

Nutrient cycling and carbon sequestration

Forest edges store more carbon and nutrients than forest interiors per m² (Remy et al. 2016; Reinmann & Hutyra 2017). Temperate forest edges can store around 43% more carbon in above- and below-ground biomass and the topsoil compared to forest interiors (Remy et al. 2016). Not accounting for forest edge effects would underestimate carbon sequestration by about 13% in temperate forests in Southern New England (Reinmann & Hutyra 2017), jeopardizing the accuracy of carbon sequestration and stock predictions, which is essential for global climate models. In addition, shifts in nutrient cycling have been observed, with higher soil nitrogen stocks, lower inorganic nitrogen leaching and lower nitrogen oxide emissions in forest edges (Wuyts et al. 2011; Remy et al. 2016, 2017a). How abiotic edge-to-interior gradients result in higher carbon and nutrient stocks in forest edges is still poorly understood (de Vries et al. 2013). The higher atmospheric nitrogen deposition in forest edges might be an important factor (De Schrijver et al. 2007), besides an effect of the soil community, which could additionally be an important factor in synthesizing nutrient cycling along forest edge-to-interior gradients. Soil fauna contributes significantly to carbon and nitrogen mineralisation and immobilisation (Osler & Sommerkorn 2007), and litter has been shown to lose nutrients such as nitrogen and phosphorus faster in forest edges (Remy et al. 2017), where decomposer activity is high. Different chains of the detrital food web may be responsible for the links between edge conditions and carbon and nutrient cycling and need further investigation.

Primary production

Forest growth and biomass increase are 89% and 64% higher in forest edges compared to forest interiors (Reinmann & Hutyra 2017). Of course, abiotic conditions in forest edges are more favourable compared to forest interiors. Light availability (Honnay et al. 2002, Delgado et al. 2007) and temperature (Honnay et al. 2002; Heithecker & Halpern 2007, Delgado et al. 2007) are higher in forest edges, which enhances plant growth (Rustad et al. 2001, Hart 2012). The role of soil fauna in enhancing plant growth in forests is a poorly studied field. Probably, the positive effects of soil fauna on plant growth are achieved via enhanced nutrient mineralisation, soil formation and mediating vegetation succession (Makeschin 1997, Bardgett & Chan 1999, De Deyn et al. 2003, Schue 2003). We can therefore assume that increased abundance of soil fauna in forest edges has the potential to increase primary production. Increased root herbivory by certain soil fauna such as beetle larvae or nematodes can counteract this positive effect, but assessment of root herbivory along forest edge-to-interior gradients still needs to be done.

Natural pest control

Natural pest control by generalist predators is an important ecosystem service with great economic value (Losey & Vaughan 2006). Although natural pest control is largely performed on agricultural fields, and predators like spiders and carabid beetles need perennial vegetation to complete their life cycle. In intensively used agricultural landscapes, small forest fragments that harbour large numbers of predators that migrate to agricultural fields to prey on pest species (Nyffeler & Sunderland 2003) may result in reduced needs for pesticide application (Symondson et al. 2002, Meehan et al. 2011). We found two important pest predators, i.e. spiders and carabid beetles, to be more abundant in forest edges compared to interiors. Woody elements enhance natural pest predator activity (Bianchi et al. 2006). We can therefore expect small forest fragments to significantly contribute to natural pest control on agricultural fields. High predator abundances in forest edges have the potential to enhance natural pest control not only outside but also within forest fragments. Martinson & Fagan (2014) showed that resource consumption by generalist predators was higher at forest edges compared to forest interiors, with significant effects on herbivory.

Other ecosystem functions

Because of their high abundances, different components of the detrital food web are important as bulk food for higher taxa such as birds and mammals (Vickery et al. 2001, Mooney et al. 2010). The higher abundances of macro-detritivores in forest edges can therefore also result in higher abundances of e.g. insectivorous birds or insectivorous mammals in forest edges (van Wilgenburg et al. 2001). There is, however, little support for this hypothesis for birds (Brand & George 2001) and mammals in general (Heske 1995, Bayne & Hobson 1998). As an example, we found no difference in the abundance of insectivorous shrews between edge and interior in 32 forest fragments in Belgium (these were the same forests as studied for litter-dwelling arthropods within the smallFOREST-consortium). Vertebrates have large home ranges compared to their prey, and other factors may therefore be more important in shaping their distribution patterns. A recent study by Pfeifer et al. (2017) revealed strong declines in vertebrate populations across the globe due to forest fragmentation and edge creation. Negative effects of edge habitat properties for vertebrates probably overrule a potential positive effect of high macro-arthropod abundances.

A last important function provided by soil macro-arthropods is their role as flagship species for the soil ecosystem. Soils do not have giant pandas, dolphins, orang utans or, at European scale, lynxes or moose. The key species are much smaller and generally less attractive for the public. Macro-arthropods are often used as billboards for the soil ecosystem since they are the largest and most well-known representatives of the soil community. They are used to stress the importance of a healthy soil with all its functions to ecosystems and society. Involving people in monitoring soil organisms, through citizen science, can raise awareness of the importance of soil quality to maintain soil functions and it can contribute to knowledge about soil fauna distribution (Fig. 8.4).

Implications for forest management and policy

In densely populated regions such as Flanders, 58% of the forest area lies within 50 m from a forest edge (De Schrijver et al. 2007). We can thus expect modified soil fauna mediated ecosystem functioning in almost 60% of the forest area in Flanders. A thorough management of forest edges could therefore be crucial to sustain effective and high levels of forest functioning such as primary production, carbon sequestration and nutrient cycling. For litter-dwelling fauna, sustaining high levels of soil moisture content is crucial. Therefore, **forest edges should have the possibility to mature,** which will induce conditions with higher soil moisture contents. **Harvesting of edges should be done partially or in phases**, so that older edges are still present as refuge for litter dwellers. Partial or phased harvesting also increases edge length, which could result in increased primary production, tree growth and carbon sequestration. However, the positive effects of these measures are theoretical and need to be investigated.

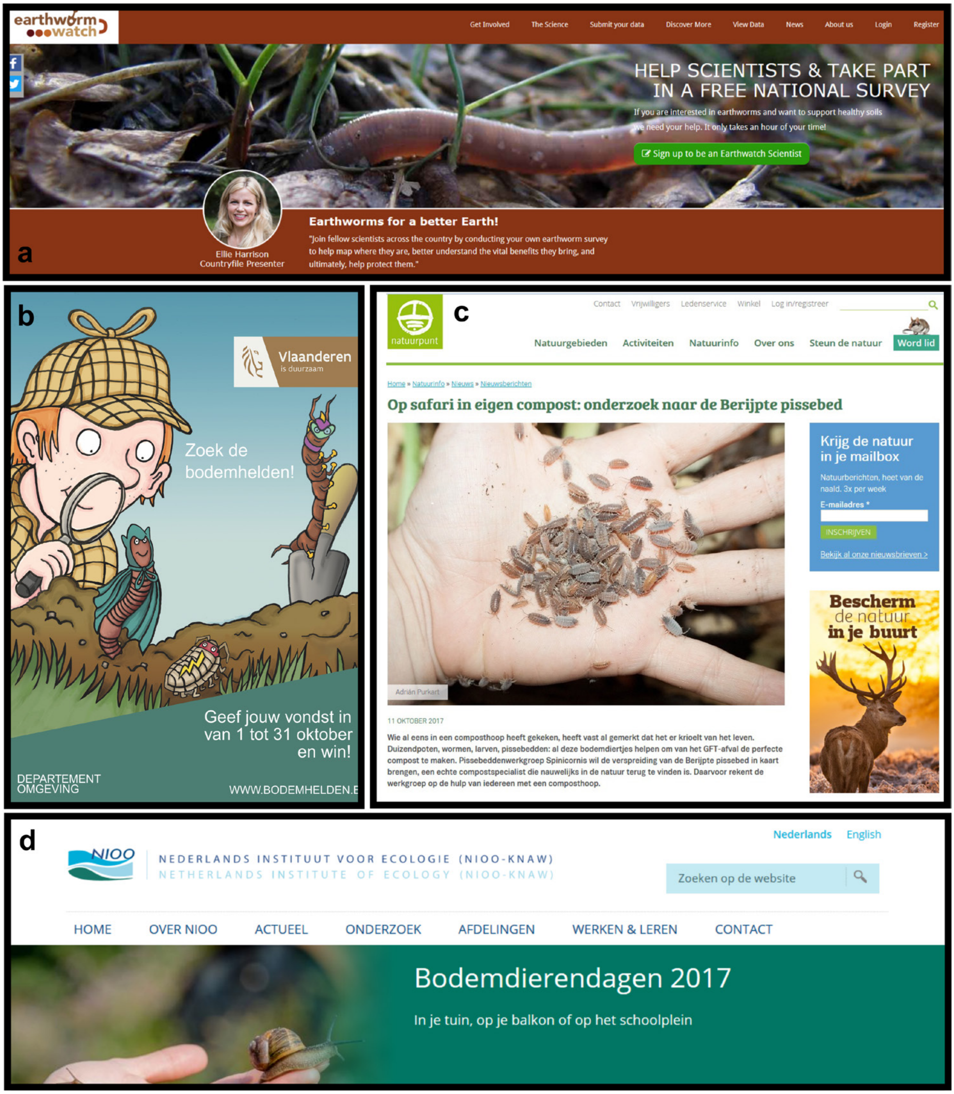
Older forests (both stand age and temporally continued) showed stronger edge gradients in activity-density and community composition of arthropods. Stressing the unique environment of older forest interiors with specialised (soil) fauna. Despite the positive effects of forest edges on different forest ecosystem services, protecting and creating large and robust forest ecosystems remains important. The negative effect of forest fragmentation is strongest for specialist forest species with large home ranges (Pfeifer et al. 2017). **To maximise species conservation, the protection of older large forest complexes should be prioritised to prevent further species loss in Western Europe.**

In intensely used landscapes, small forest fragments are hotspots for litter-dwelling arthropods; numbers of litter-dwelling arthropods are much lower in the agricultural matrix (Lacasella et al. 2015). Moreover, forest edges of small forest fragments have the ability to sustain high populations of natural pest control agents (Bianchi et al. 2006). **Small forest fragments are therefore of key importance to support different ecosystem functions in intensely managed landscapes, and the conservation of these small habitat islands should be prioritised.**

Future research

This thesis significantly contributed to the knowledge of forest edge effects on the distribution of litter-dwelling arthropods. Different taxonomic groups showed contrasting responses to forest edges, and even within taxonomic groups, patterns were species-specific. We assessed dominant macro-arthropod groups from different trophic levels, but several macro-fauna taxa remain understudied, e.g. earthworms, slugs, ants and insect larvae. The strong responses of macro-arthropods to abiotic edge-to-interior gradients should also trigger the investigation of abundance gradients for meso-fauna and micro-organisms, which would allow to finally map a larger part of the detrital food web. The literature we reviewed often-showed contrasting litter-dwelling arthropod distribution patterns compared to our work, but the results of this thesis were consistent within the context of deciduous forest fragments across Western Europe. Special attention should go to context dependency, still a major gap in forest edge research (Ries et al. 2017). Landscape-use intensity is a key factor in understanding context dependency of edge-to-interior gradients but it is challenging to study landscapes only differing in landscape-use intensity. The studied landscapes in this thesis differ in landscape-use intensity but therefore also in topography, soil fertility,… Higher land-use intensity landscapes have in general a flatter topography and higher soil fertility. A future challenge will be to disentangle landscape-use intensity (management) effects and effects resulting from the physiochemical environment of the landscapes on arthropod distribution.

If we aim to understand these distribution patterns, species-specific data is key. However, taxonomy is a major problem to study soil taxa and should receive more attention (Eisenhauer et al. 2017). A second step is to investigate species response and effect traits, as measured under standardised conditions (Moretti et al. 2017) to predict community changes under changing environmental conditions. In this way, we can understand how environments filter species, and consequently also affect ecosystem functioning. The response and effect trait framework will allow us to understand, predict and assess the impact of forest edges for ecosystem functioning.



HELP SCIENTISTS & TAKE PART IN A FREE NATIONAL SURVEY

If you are interested in earthworms and want to support healthy soils we need your help. It only takes an hour of your time!

Earthworms for a better Earth!

"Join fellow scientists across the country by conducting your own earthworm survey to help map where they are, better understand the vital benefits they bring, and ultimately, help protect them."

Op safari in eigen compost: onderzoek naar de Berijpte pissebed

11 OKTOBER 2017

Wie al eens in een composthoop heeft gekeken, heeft vast al gemerkt dat het er krioelt van het leven. Duizendpoten, wormen, larven, pissebedden: al deze bodemdiertjes helpen om van het GFT-afval de perfecte compost te maken. Pissebeddenwerkgroep Spinicornis wil de verspreiding van de Berijpte pissebed in kaart brengen, een echte compostspecialist die nauwelijks in de natuur terug te vinden is. Daarvoor rekent de werkgroep op de hulp van iedereen met een composthoop.

Natuurberichten, heet van de naald. 3x per week

Bodemdierendagen 2017

In je tuin, op je balkon of op het schoolplein

Figure 8.4. *Examples of how soil fauna is used to stress the importance of a healthy soil environment and motivate people to gather distribution data. (a) Earthworm watch from the UK. Citizens can participate in a scientific study by looking for earthworms in their garden according to a standard protocol. They contribute knowledge about earthworm distribution and learn about the functional role of earthworms for a healthy soil environment (www.earthwormwatch.org). (b) Campaign of the Flemish government (department of environment) to get people in touch with soil biodiversity and the functions by looking for soil heroes (i.e. soil macro-fauna) in their garden/school (www.lne.be/bodemhelden). (c) A call from the Belgian woodlice interest group "Spinicornis" (www.spinicornis.be) on the nature news website natuurbericht.be. Citizens are asked to*

look out for Porcellinoides pruinosus, a woodlouse typical for compost heaps, and to report their sightings. The distribution of this species is poorly known, because of its specific habitat preference, but it is an indicator of a healthy compost heap. (d) Campaign from the Netherlands Institute of Ecology to search for soil fauna in your garden or school during so-called "soil animal days", to stress the importance of soil animals (www.nioo.knaw.nl/nl/bodemdierendag).

Despite the importance of the detrital food web for soil functions and overall ecosystem functioning, the direct links between soil fauna and ecosystem functioning are poorly explored and hence we cannot quantify the contribution of the soil food web to ecosystem functioning. Research on understanding how soil fauna communities in forest edges mediate ecosystem functioning, as compared to forest interiors, will be a great step forward. Besides empirical studies on poorly studied ecosystem functions and neglected groups, there is a clear need for experimental studies on ecosystem functioning (Noriega et al. 2018). The complex nature of forest edges stresses the need for field experiments to grasp the effects of the different abiotic gradients from forest edge to forest interior. A few examples:

- Translocation experiments of intact soil cores between forest edges and interiors can transplant whole soil communities from the forest edge to the forest interior to study their functioning in the forest interior conditions, and vice versa for forest interior soil cores transplanted to the forest edge. Following, for instance, leaf litter breakdown and soil community composition over time will generate new insights in the effects of edge-interior differences on ecosystem functioning. Adding litter labelled with stable isotopes (^{15}N and ^{13}C, see e.g. Cliquet et al. 1990) enables tracking nutrients through the soil food web, which will allow us to understand the functional role of the different components of the soil food web for **nutrient cycling and carbon sequestration** in forest edges and forest interiors.
- Experiments with fenced and unfenced potted plants across "forest interior – forest edge – adjacent arable land"-gradients can quantify **natural pest control** by litter-dwelling predators (such as carabid beetles, spiders and harvestmen). Directional pitfall traps (see e.g. Royauté & Buddle 2012) can be used to assess arthropod fluxes between forest edges and adjacent agricultural land.
- Hydrological soil properties could be assessed using standardised soil buried in the upper soil layer along forest edge-to-interior gradients that could be colonised by site-specific soil fauna. At the end of the experiment, **soil structure and water infiltration** could be measured in the lab (see e.g. Brown et al. 2010).
- At last, food web modelling can be used to model the flow of resources and energy through the soil food web incorporating species' interactions in the trophic structure of the soil food web (see e.g. Berg et al. 2001). Underpinned with a litter bag experiment as model inputs, this approach can be carried out in both forest edges and interiors and give us critical insights in how forest edges influence ecosystem function from **nutrient cycling to predator-prey relations**.

A bunch of *Armadillidium vulgare* | Edwin Brosens

REFERENCES

Acosta LE, Machado G (2007) Diet and Foraging. In: Pinto-da-Rocha R et al. (Eds) Harvestmen: the biology of Opiliones. Harvard University Press, Cambridge.

Adam W, Leloup E (1940) La distribution en Belgique de Leucochloridium paradoxum, Rhynchodemus terrestris, Arion intermedius, Platvarthrus hoffmannseggi et Atyaephyra desmaresti. Bulletin du Musée royal d'histoire naturelle de Belgique 16: 1-8.

Allan E et al. (2013) Interannual variation in land-use intensity enhances grassland multidiversity. Proceedings of the National Academy of Sciences 111: 308-313.

Anderson JM (1988) Invertebrate-mediated transport processes in soils. Agriculture, Ecosystems & Environment 24: 5–19.

Anderson MJ (2001) A new method for non-parametric multi-variate analysis of variance. Austral Ecology 26: 32–46.

Anderson MJ et al. (2006) Multivariate dispersion as a measure of beta diversity. Ecology Letters 9: 683-693.

Andersson G et al. (2005) Nationalnyckeln till Sveriges flora och fauna. Mångfotingar. Myriapoda. ArtDatabanken, SLU, Uppsala.

Arcangeli A (1935) Eoniscus Simplicissimus, Un Pigmeo Degli Isopodi Terrestri, Appartenente a Nuova Specie, Nuovo Genere, Nuova Famiglia. Bolletino di zoologia 6: 203-212.

Arx G von et al. (2013) Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. Journal of Ecology 101: 1201-1213.

Astor T et al. (2015) Measuring feeding traits of a range of litter-consuming terrestrial snails: leaf litter consumption, faeces production and scaling with body size. Oecologia 178: 833-845.

Baeté H et al. (2002) Monitoring-programma Vlaamse Bosreservaten–Bosreservaat Kersselaerspleyn (Zoniënwoud)–Monitoringrapport. Rapport IBW Bb 02.005. Instituut voor Bosbouw en Wildbeheer, Geraardsbergen.

Baeté H et al. (2003a) Monitoringprogramma Vlaamse bosreservaten – Monitoring van een transect in het Vlaams natuurreservaat Hannecartbos – Basisrapport. IBW Bb 03.012. Instituut voor Bosbouw en Wildbeheer, Geraardsbergen.

Baeté H et al. (2003b) Monitoringprogramma Vlaamse bosreservaten – Monitoring van kernvlakte en transecten in het Vlaams Natuurreservaat Walenbos – Basisrapport. IBW Bb 03.014. Instituut voor Bosbouw en Wildbeheer, Geraardsbergen.

Baeté H et al. (2004) Monitoringprogramma Vlaamse bosreservaten - Bosreservaat Wijnendalebos - Basisrapport. IBW Bb 04.009. Instituut voor Bosbouw en Wildbeheer, Geraardsbergen.

Baeté H et al. (2006a) Bosreservaat Bos Ter Rijst (Heikruis) - Basisrapport. INBO.R.2006.15. Instituut voor Natuur- en Bosonderzoek, Brussel.

Baeté H et al. (2006b) Bosreservaat Jansheideberg (Hallerbos) - Basisrapport. INBO.R.2006.13. Instituut voor Natuur- en Bosonderzoek, Brussel.

Bagnall RS (1907) On some terrestrial lsopod Crustacea new to the Fauna of Belgium. Annales de la Société royale zoologique et malacologique de Belgique 42: 263-266.

Bagnall RS (1908) On the occurrence in Belgium of a recently described terrestrial Isopod, Trichoniscus Stebbingi, Patience. Annales de la Société royale zoologique et malacologique de Belgique 43: 127-129.

Baker TP et al. (2014) Microclimate through space and time: microclimatic variation at the edge of regeneration forests over daily, yearly and decadal time scales. Forest ecology and management 334: 174-184.

Báldi A (2008) Habitat heterogeneity overrides the species-area relationship. Journal of Biogeography 35: 675-681.

Baldissera R et al. (2004) Web spider community response along an edge between pasture and Araucaria forest. Biological Conservation 118: 403-409.

Banks-Leite C et al. (2010) Edge effects as the principal cause of area effects on birds in fragmented secondary forest. Oikos 119: 918-926.

Bardgett RD, Chan KF (1999) Experimental evidence that soil fauna enhance nutrient mineralization and plant nutrient uptake in montane grassland ecosystems. Soil Biology and Biochemistry 31: 1007-1014.

Bardgett RD, van der Putten WH (2014) Belowground biodiversity and ecosystem functioning. Nature 515: 505-511.

Bartoń K (2015) MuMIn: Multi-Model Inference. R-package version 1.15.6.

Baselga A et al. (2017) Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.4-1.

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19: 134-143.

Bates D et al. (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67: 1-48.

Bates D et al. (2016) lme4: Linear mixed-effects models using 'Eigen' and S4. R package version 1.1-12.

Bayne EM, Hobson KA (1998) The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. Canadian Journal of Zoology 76: 62-69.

Beier C, Gundersen P (1989) Atmospheric deposition to the edge of a spruce forest in Denmark. Environmental pollution 60: 257-271.

Bellynck A (1865) Résumé du cours de zoologie professé au collège Notre Dame de la Paix à Namur. 1864-1865: 1-375.

Belovsky GE, Slade JB (2000) Insect herbivory accelerates nutrient cycling and increases plant production. Proceedings of the National Academy of Sciences 97: 14412-14417.

Berg M et al. (2001) Community food web, decomposition and nitrogen mineralisation in a stratified Scots pine forest soil. Oikos 94: 130-142.

Berg MP et al. (2008) Verspreidingsatlas Nederlandse landpissebedden, duizendpoten en miljoenpoten (Isopoda, Chilopoda, Diplopoda). EIS-Nederland, Leiden & Vrije Universiteit-Afdeling Dierecologie, Amsterdam.

Berg MP, Krediet A (2017) De kalkribbel Haplophthalmus montivagus, een nieuwe pissebed in Zuid-Limburg. Nederlandse Faunistische Mededelingen 48: 63-68.

Berg MP, Wijnhoven H (1997) Landpissebedden – Wetenschappelijke Mededelingen KNNV 221. KNNV Uitgeverij, Utrecht.

Bianchi FJ et al. (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society of London B: Biological Sciences 273: 1715-1727.

Bindlish R et al. (2008) Aircraft based soil moisture retrievals under mixed vegetation and topographic conditions. Remote Sensing of Environment 112: 375-390.

Birkhofer K et al. (2015) Land-use effects on the functional distinctness of arthropod communities. Ecography 38: 889-900.

Blossey B, Hunt-Joshi TR (2003) Belowground herbivory by insects: influence on plants and aboveground herbivores. Annual Review of Entomology 48: 521-547.

Boeraeve P et al. (2017) Philoscia affinis Verhoeff, 1908 new to Belgium (Isopoda: Philosciidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 153: 183-188.

Boetzl FA et al. (2016) Asymmetric carabid beetle spillover between calcareous grasslands and coniferous forests. Journal of Insect Conservation 20: 49-57.

Bogyó D et al. (2015) Distribution of millipedes (Myriapoda, Diplopoda) along a forest interior – forest edge – grassland habitat complex. ZooKeys 510: 181-195.

Boon B, Wijns K (2000) ICP onderzoek op zware metalen in pissebedden van Vlaamse bossen. Eindwerk tot het behalen van de graad van gegradueerde in de Chemie, optie Milieuzorg. Erasmus Hogeschool Brussel.

Boon N et al. (1993) Landpissebedden. Verspreiding en Ecologisch Onderzoek. 22 UTM-hokken rond Tienen. Koninklijk Atheneum Tienen.

Bowman WD et al. (2008) Negative impact of nitrogen deposition on soil buffering capacity. Nature Geoscience 1: 767-770.

Bradford MA et al. 2002. Microbiota, fauna, and mesh size interactions in litter decomposition. Oikos 99: 317-323.

Bragagnolo C et al. (2007) Harvestmen in an Atlantic forest fragmented landscape: evaluating assemblage response to habitat quality and quantity. Biological Conservation 139: 389-400.

Brand LA, George TL (2001) Response of passerine birds to forest edge in coast redwood forest fragments.

The Auk 118: 678-686.

Branquart E et al. (1995) Macroarthropod-habitat relationships in oak forests in South Belgium. 1. Environments and communities. Pedobiologia 39: 243-263.

Broly P et al. (2015) Body shape in terrestrial isopods: a morphological mechanism to resist desiccation? Journal of Morphology 276: 1283-1289.

Broly P et al. C (2014) Effects of group size on aggregation against desiccation in woodlice (Isopoda: Oniscidea). Physiological Entomology 39: 165-171.

Broly, P et al. (2013) Benefits of aggregation in woodlice: a factor in the terrestrialization process? Insectes Sociaux 60: 419-435.

Brown, J et al. (2010) Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties. Applied Soil Ecology 46: 9-16.

Brunke AJ (2012) Guilty by association: an evaluation of millipedes as pests of carrot and sweet potato. Journal of Applied Entomology 136: 772–780.

Cappart A (1942) Note sur les isopodes terrestres de la faune Belge. I. Liste des espèces connues actuellement en Belgique. Bulletin du Musée royal d'histoire naturelle de Belgique 18: 1-5.

Carlier A (1831) Dictionnaire géographique de la province de Liége. Vander Maelen, Bruxelles.

Carpenter B et al. (2015) Stan: a probabilistic programming language. Journal of Statistical Software.

Carpenter D et al. (2012) Mapping of earthworm distribution for the British Isles and Eire highlights the under-recording of an ecologically important group. Biodiversity and Conservation 21: 475–485.

Carvalho KS, Vasconcelos HL (1999) Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. Biological Conservation 91: 151-157.

Chabrerie O et al. (2013) Maturation of forest edges is constrained by neighbouring agricultural land management. Journal of Vegetation Science 24: 58-69.

Chen J et al. (1993) Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. Agricultural and Forest Meteorology 63: 219-237.

Chen J et al. (1995) Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. Ecological Applications 5: 74-86.

Chen J et al. (1999) Microclimate in forest ecosystems and landscape ecology. Variations in local climate can be used to monitor and compare the effects of different management regimes. Bioscience 49: 288-297.

Cliquet JB et al. (1990) Estimation of carbon and nitrogen allocation during stalk elongation by 13C and 15N tracing in Zea mays L. Plant Physiology 92: 79-87.

Collart A (1936) Assemblée mensuelle du 6 juin 1936. Bulletin et Annales de la Société royale d'Entomologie de Belgique 76: 227-228.

Collison EJ et al. (2013) Macrofauna assemblage composition and soil moisture interact to affect soil ecosystem functions. Acta Oecologia 47: 30-36.

Costanza R et al. (2017) Twenty years of ecosystem services: How far have we come and how far do we still need to go? Ecosystem Services 28: 1-16.

Curtis DJ, Machado G (2007) Ecology. In: Pinto-da-Rocha R. et al. (Eds), Harvestmen: the biology of Opiliones: 208–308. Harvard University Press, Cambridge.

Dailey TM et al. 2009. The effects of temperature, desiccation, and body mass on the locomotion of the terrestrial isopod, *Porcellio laevis*. Comparative Biochemistry and Physiology A-Physiology 153: 162-166.

Daro MH (1969) Etude écologique d'un brise-lames de la côte belge: 1. Description et zonation des organismes. Annales de la Société Royale Zoologique de Belgique 99: 111-152.

Dauber J et al. (2005) Local vs. landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of differing mobility. Global Ecology and Biogeography 14: 213-221.

David JF (1998) How to calculate leaf litter consumption by saprophagous macrofauna? European Journal of Soil Biology 34: 111-115.

David JF (2009) Ecology of millipedes (Diplopoda) in the context of global change. Soil Organisms 81: 719-733.

David JF (2014) The role of litter-feeding macroarthropods in decomposition processes: a reappraisal of common views. Soil Biology and Biochemistry 76: 109-118.

David JF et al. (1999) Belowground biodiversity in a Mediterranean landscape: relationships between saprophagous macroarthropod communities and vegetation structure. Biodiversity and Conservation 8: 753-767.

David JF, Handa IT (2010) The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. Biological Reviews 85: 881-895.

De Bakker D et al. (2000) Determinatie en bioindicatie van bosgebonden ongewervelden. 1. Bioindicatie van standplaatsvariabelen. Onderzoeksopdracht B&G/29/98, AMINAL. Rapport ENT200001. KBIN, Brussel.

De Deyn et al. (2003) Soil invertebrate fauna enhances grassland succession and diversity. Nature 422: 711-713.

De Frenne P et al. (2010) The use of open-top chambers in forests for evaluating warming effects on herbaceous understory plants. Ecological Research 25: 163-171.

De Frenne P et al. (2015) Light accelerates plant responses to warming. Nature Plants 1: 15110.

De Oliveira T et al. (2010) Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. Functional Ecology 24: 937-946.

De Schrijver A (2007) Acidification and eutrophication of forests on sandy soil: effects of forest type and deposition load. Ph.D. thesis, Ghent University, Belgium.

De Schrijver A et al. (2007) On the importance of incorporating forest edge deposition for evaluating exceedance of critical pollutant loads. Applied Vegetation Science 10: 293-298.

De Smedt P et al. (2015) Porcellio monticola Lereboullet, 1853 a new species for Belgium (Isopoda: Porcellionidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 151: 118-121.

De Smedt P et al. (2016a) Confirmation of Metatrichoniscoides leydigii (Weber, 1880) in Belgium, 60 years after discovery (Isopoda: Trichoniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 152: 18-21.

De Smedt P et al. (2016b) Trichoniscus alemannicus Verhoeff, 1917 a new species of woodlouse for Belgium (Isopoda: Trichoniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 152: 104-108.

De Smedt P et al. (2016c) Complementary distribution patterns of arthropod detritivores (woodlice and millipedes) along forest edge-to-interior gradients. Insect Conservation and Diversity 9: 456-469.

De Smedt P et al. (2017a) Woodlice of the green houses at Ghent Botanical Garden and Botanic Garden Meise with two new exotic species for Belgium (Isopoda: Oniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 153: 109-112.

De Smedt P et al. (2017b) A long-expected finding: the first record of the isopod Eluma caelatum (Miers, 1877) from Belgium (Crustacea: Isopoda: Armadillidiidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 153: 89-93.

De Smedt P et al. (2018a) Desiccation resistance determines distribution of woodlice along forest edge-to-interior gradients. European Journal of Soil Biology 85: 1-3.

De Smedt P et al. (2018b) Linking macrodetritivore distribution to desiccation resistance in small forest fragments embedded in agricultural landscapes in Europe. Landscape Ecology 33: 407-421.

De Smedt P, Van de Poel S (2017) Succession in harvestman (Opiliones) communities within an abandoned sand quarry in Belgium. Belgian Journal of Zoology 147: 155-169.

de Vries FT et al (2013) Soil food web properties explain ecosystem services across European land use systems. Proceedings of the National Academy of Sciences 110: 14296-14301.

Decaëns T (2010) Macroecological patterns in soil communities. Global Ecology and Biogeography 19: 287-302.

Decocq G et al. (2016) Ecosystem services from small forest patches in agricultural landscapes. Current Forestry Reports 2: 30-44.

Dekoninck W et al. (2005) Comparative study of the terrestrial isopod faunas of ancient and afforested former agricultural fields. Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 75: 271-279.

Dekoninck W et al. (2007) Acceptance of two native myrmecophilous species, Platyarthrus hoffmannseggii (Isopoda: Oniscidea) and Cyphoderus albinus (Collembola: Cyphoderidae) by the introduced invasive garden ant Lasius neglectus (Hymenoptera: Formicidae) in Belgium. European Journal of Entomology 104:

159-161.

Delasalle JF, Séchet E (2014) Contribution à la connaissance des Isopodes terrestres de Picardie (Crustacea, Isopoda, Oniscidea). L'Entomologiste Picard 24: 1-29.

Delgado JD et al. (2007) Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). Landscape and Urban Planning 81: 328-340.

Delhez F et al. (1973) Étude préliminaire de la faune de la grotte de Ramioul. Bulletin de la société royale belge d'études géologiques et archéologiques "Les chercheurs de la Wallonie" 22: 329-349.

Delhez F et al. (1999) Contribution à la connaissance de la faune des grottes de Wallonie. Bulletin de la société royale belge d'études géologiques et archéologiques "Les chercheurs de la Wallonie" 39: 27-54.

Delhez F, Houssa M (1969) L'araine de Richeronfontaine à Liège. Etude écologique de la faune cavernicole d'un réseau souterrain artificiel. Les Naturalistes belges 50: 194-212.

Delhez F, Kersmaekers M (1973) Aspect Biologique de la Grotte de Pré-au-Tonneau à Rochefort. Speleologia Belgica 1: 3-9.

Dethier M, Hubart JM (2010) Évolution de la fauna invertébrée des grottes de Ramioul (commune de Flémalle, province de Liège, Belgique). Bulletin des Chercheurs de la Wallonie hors-série 3: 15-44.

Dethier M, Willems L (2005) Les invertébrés des carrières souterraines de craie de la Montagne Saint-Pierre (Province de Liège, Belgique). Note préliminaire. Notes fauniques de Gembloux 57: 17-27.

Devaere N (1999) Het voorkomen en de ecologie van pissebedden (Oniscidea, Crustacea) in Vlaamse bossen. Universiteit Gent.

Dias ATC et al. (2013) Traits underpinning desiccation resistance explain distribution patterns of terrestrial isopods. Oecologia 172: 667-677

Dias N et al. (2012) The influence of microclimate on foraging and sheltering behaviours of terrestrial isopods: implications for soil carbon dynamics under climate change. Pedobiologia 55: 137-144.

Didham RK et al. (2015) Agricultural intensification exacerbates spillover effects on soil biochemistry in adjacent forest remnants. PLoS ONE 10: e0116474.

Diekötter T et al. (2010) Landscape and management effects on structure and function of soil arthropod communities in winter wheat. Agriculture, Ecosystmes & Environment 137: 108-112.

Dixie B et al. (2015) Effects of microclimate on behavioural and life history traits of terrestrial isopods: implications for responses to climate change. ZooKeys 515: 145-157.

Donker MH (1992) Energy reserves and distribution of metals in populations of the isopod Porcellio scaber from metal-contaminated sites. Functional ecology 6: 445-454.

Donker MH et al. (1993) Early reproduction and increased reproductive allocation in metal-adapted populations of the terrestrial isopod *Porcellio scaber*. Oecologia 96: 316-323.

Donker MH, Bogert CG (1991) Adaptation to cadmium in three populations of the isopod Porcellio scaber. Comparative Biochemistry and Physiology Part C: Comparative Pharmacology 100: 143-146.

Dumont H, Gijsels H (1971) Etude faunistique et écologique sur les criques de la Flandre orientale et le long de L'Escaut. Considérations sur leur chimisme, leur faune planktonique, entomologique et malacologique et discussion de leur état biologique actuel. Annales de la Société Royale Zoologique de Belgique 101: 157-182.

Dunger W (1983) Tiere im boden. Wittenberg, Ziemsen.

Dunger W, Steinmetzger K (1981) Okologische Untersuchungen an Diplopoden einer Rasen-Wald-Catena im Thuringer Kalkgebiet. Zoologische Jahrbucher. Abteilung fur Systematik, Okologie und Geographie der Tiere.

Echeverria C et al. (2008) Spatially explicit models to analyse forest loss and fragmentation between 1976 and 2020 in southern Chile. Ecological Modelling 212: 439-449.

Edney EB (1977) Water balance in land arthropods. Springer-Verlag, Berlin Heidelberg, New York.

Eichhorn O (1964) Zur Verbreitung und Ökologie der hügelbauenden Waldameisen in den Ostalpen. Journal of Applied Entomology 54: 253-289.

Eisenhauer N et al. (2007) Invasion of a deciduous forest by earthworms: changes in soil chemistry, microflora, microarthropods and vegetation. Soil Biology and Biochemistry 39: 1099-1110.

Eisenhauer N et al. (2017) Priorities for research in soil ecology. Pedobiologia 63: 1-7.

Eneman E (1984) Uit het Natuurhistorisch archief. De Strandvlo 4: 14.

Engledow H et al. (2001) Onderzoek naar (1) de fysische karakterisatie en (2) de biodiversiteit van strandhoofden en andere harde constructies langs de Belgische kust: eindrapport van de onderhandse overeenkomst dd. 17.02.2000 i.o.v. de Afdeling Waterwegen Kust van het Ministerie van de Vlaamse Gemeenschap, Departement Leefmilieu en infrastructuur, Administratie Waterwegen en Zeewezen. Instituut voor Natuurbehoud, Brussel.

Entling W et al. (2007) Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. Global ecology and biogeography 16: 440-448.

Estreguil C et al. (2013) Forest landscape in Europe: pattern, fragmentation and connectivity. Executive report. Joint Research Centre of the European Commission, Institute for Environment and Sustainability, Forest Resources and Climate Unit, T.P. 261, Via E. Fermi 1, 21020 Ispra (VA), Italy.

Ewers RM, Didham RK (2006) Continuous response functions for quantifying the strength of edge effects. Journal of applied ecology 43: 527-536.

Ewers RM, Didham RK (2008) Pervasive impact of large-scale edge effects on a beetle community. Proceedings of the National Academy of Sciences 105: 5426-5429.

Fletcher RJ (2007) The role of habitat and edge in fragmented landscapes: definitively distinct or inevitably interwined? Canadian Journal of Zoology 85: 1017-1030.

Flinn KM, Vellend M (2005) Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3: 243-250.

Foley JA et al. 2005. Global consequences of land use. Science 309: 570–574.

Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity & Conservation 7: 1221-1244.

Forman RT, Godron M (1981) Patches and structural components for a landscape ecology. BioScience 31: 733-740.

Fraver S (1994) Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River Basin, North Carolina. Conservation Biology 8: 822-832.

Frouz J (2018) Effects of soil macro-and mesofauna on litter decomposition and soil organic matter stabilization. Geoderma: in press.

Frouz J et al. (2015) The life cycle, population dynamics, and contribution to litter decomposition of Penthetria holosericea (Diptera: Bibionidae) in an alder forest. European Journal of Soil Biology 71: 21-27.

Fussey GD (1984) The distribution of the two forms of the woodlouse Trichoniscus pusillus Brandt (Isopoda: Oniscoidea) in the British Isles: a reassessment of geographic parthenogenesis. Biological Journal of the Linnean Society 22: 309-321.

Gascon C et al. (2000) Receding forest edges and vanishing reserves. Science 288: 1356-1358.

Gaston KJ (2000) Global patterns in biodiversity. Nature 405: 220-227.

Gehlhausen S et al. (2000) Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecology 147: 21-35.

Gelman A, Hill J (2007) Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press, Cambridge.

Gerlach A et al. (2014) Feeding preferences of native terrestrial isopod species (Oniscidea, Isopoda) for native and introduced litter. Applied Soil Ecology 83: 95-100.

Gillingham PK et al. (2012) The relative importance of climate and habitat in determining the distributions of species at different spatial scales: a case study with ground beetles in Great Britain. Ecography 35: 831-838.

Gillooly JF et al. (2001) Effects of size and temperature on metabolic rate. Science 293: 2248-2251.

Gils A (1947) Les Crustacés du Littoral belge. Les Naturalistes belges 7-8: 1-15.

Gilson G (1900) Exploration de la mer sur les côtes de la Belgique en 1899. Mémoires du Musée royal d'histoire naturelle de Belgique. Polleunis & Ceuterick, Bruxelles.

Gilson R, Hubart JM (1973) Protection du biotope de la grotte Lyell. Bulletin de la société royale belge d'études géologiques et archéologiques "Les chercheurs de la Wallonie" 12: 367-681.

Gregory S (2009) Woodlice and Waterlice:(Isopoda: Oniscidea & Asellota) in Britain and Ireland. FSC Publications, Shrewsbury.

Grelle C et al. (2000) Myriapod and isopod communities in soils contaminated by heavy metals in northern France. European Journal of Soil Science 51: 425–433.

Grüner HE (1965) Krebstiere oder Crustacea. V. Isopoda. Die Tierwelt Deutschlands 51: 1-380.

Guimarães Jr PR, Cogni, R. (2002) Seed cleaning of Cupania vernalis (Sapindaceae) by ants: edge effect in a highland forest in south-east Brazil. Journal of Tropical Ecology 18: 303-307.

Gysels H e tal. (1976) Tien jaar zoölogische stages in en om de Ardennen. Natuurwetenschappelijk tijdschrift 58: 3-68.

Haacker U (1968) Descriptive, Experimental and Comparative Investigations on the Ecology of Diplopoda of the Rhein-Main-Region. Oecologia 1: 87-129.

Haddad NM et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1: e1500052.

Hadfield J. (2016) MCMCglmm: MCMC Generalised linear mixed models, R package version 2.24.

Hadley NF (1994) Water relations of terrestrial arthropods. Academic Press, San Diego, California.

Handa IT et al. 2014. Consequences of biodiversity loss for litter decomposition across biomes. Nature 509: 218-221.

Hansen MC et al. (2013) High-resolution global maps of 21st-century forest cover change. Science 342: 850–853.

Hantsch L et al. (2014) No plant functional diversity effects on foliar fungal pathogens in experimental tree communities. Fungal Diversity 66: 139-151.

Harding PT (2016) Is Porcellio laevis (Latreille) declining in Britain and Ireland? Bulletin of the British Myriapod and Isopod Group 29: 23-27.

Harper KA et al. (2005) Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19: 768-782.

Harris LD (1988) Edge effects and conservation of biotic diversity. Conservation Biology 2: 330-332.

Harrison S, Bruna E (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22: 225-232.

Hart JW (2012) Light and plant growth (Vol. 1). Springer Science & Business Media.

Hassall et al. (2002) Effects of spatial heterogeneity on feeding behaviour of *Porcellio scaber* (Isopoda: Oniscidea). European Journal of Soil Biology 38: 53-57.

Hatley CL, Macmahon JA (1980) Spider community organization: seasonal variation and the role of vegetation architecture. Environmental entomology 9: 632-639.

Hättenschwiler S et al. (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology, Evolution and Systematics 36: 191-218.

Hättenschwiler S, Gasser P (2005) Soil animals alter plant litter diversity effects on decomposition. Proceedings of the National Academy of Sciences USA 102: 1519-1524.

Haygarth PM, Ritz K (2009) The future of soils and land use in the UK: soil systems for the provision of land-based ecosystem services. Land Use Policy 26: S187-S197.

Hedges LV et al. (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80: 1150-1156.

Heithecker TD, Halpern CB (2007) Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. Forest Ecology and Management 248: 163-173.

Hendrickx F et al. (2003) Storage mediums affect metal concentration in woodlice (Isopoda). Environmental Pollution 121: 87-93.

Heske EJ (1995) Mammalian abundances on forest-farm edges versus forest interiors in southern Illinois: is there an edge effect? Journal of Mammalogy 76: 562-568.

Hoffmann M (2006) Beheerplan VNR De Ijzermonding.

Holland JM, Luff ML (2000) The effects of agricultural practices on Carabidae in temperate agroecosystems. Integrative Pest Management Reviews 5: 109-129.

Holthuis LB (1950) Isopodes et Tanaidacés marins de la Belgique; remarques sur quelques espèces de la zone méridionale de la Mer du Nord. Bulletin de I'Institut royal des Sciences naturelles de Belgique 36: 1-19.

Holthuis LB (1983) De Pissebedden (Crustacea, lsopoda, Oniscidea) van de ondergrondse kalksteengroeven in Zuid-Limburg. Zoölogische bijdragen (Bijdragen tot de faunistiek van Nederland X) 29: 77-98.

Honnay O et al. (2002) Permeability of ancient forest edges for weedy plant species invasion. Forest Ecology and Management 161: 109-122.

Honnay O et al. (2005) Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytologist 166: 723–736.

Hopkin SP, Read HJ (1992) *The biology of millipedes*. Oxford University Press., Oxford.

Hornung E (2011) Evolutionary adaptation of oniscidean isopods to terrestrial life: Structure, physiology and behaviour. Terrestrial Arthropod Reviews 4: 95-130.

Horvathova T et al. (2016) Biofilm feeding: microbial colonization of food promotes the growth of a detritivorous arthropod. ZooKeys 577: 25-41.

Hothorn T et al. (2016) multcomp: Simultaneous inference in general parametric models. R package version 1.4-6.

Huhta V et al. (1998) Functional implications of soil fauna diversity in boreal forests. Applied Soil Ecology 10: 277-288.

Huwae P, Rappé G (2003) Waterpissebedden: een determineertabel voor de zoet-, brak- en zoutwaterpissebedden van Nederland en België. Wetenschappelijke Mededelingen van de Koninklijke Nederlandse Natuurhistorische Vereniging, 226. KNNV Uitgeverij, Utrecht.

Ibisch PL et al. (2016) A global map of roadless areas and their conservation status. Science 354: 1423-1427.

Ihnen K, Zimmer M (2008) Selective consumption and digestion of litter microbes by *Porcellio scaber* (Isopoda: Oniscidea). Pedobiologia 51: 335-342.

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva.

Jabin M et al. (2004) Influence of deadwood on density of soil macro-arthropods in a managed oak–beech forest. Forest Ecology and Management 194: 61-69.

Janzen DH (1986) The eternal external threat. In: Soulé ME (Ed) Conservation Biology: The Science of Scarcity and Diversity. Sinauer Assoc., Sunderland.

Jeanneret P et al. (2003) Arthropod reaction to landscape and habitat features in agricultural landscapes. Landscape ecology 18: 253-263.

Jeffery S et al. (Eds) (2010) European Atlas of Soil Biodiversity. European Commission, Publications Office of the European Union, Luxembourg.

Jocqué R, Van Damme D (1971) Inleidende oecologische studie van klei-en turfbanken in de getijdenzone te Raversijde (België). Biologisch Jaarboek Dodonaea 40: 157-190.

Jokimäki, J et al. (1998) Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. Canadian Journal of Forest Research 28: 1068-1072.

Joly FX et al. (2015) Litter-type specific microbial responses to the transformation of leaf litter into millipede feces. Soil Biology & Biochemistry 86: 17-23.

Jonckheere I et al. (2004) Review of methods for in situ leaf area index determination Part I. Theories, sensors and hemispherical photography. Agricultural and Forest Meteorology 121: 19-35.

Jonckheere I, Van Rillaer L (2001) Strandexcursie op 12 maart 2001 in de Baai van Heist. De Strandvlo 21: 84-86.

Jones CG et al. (1994) Organisms as ecosystem engineers. Oikos 69: 373-386.

Kautz G et al. (2000) Responses of the parthenogenetic isopod, *Trichoniscus pusillus* (Isopoda: Oniscidae), to changes in food quality. Pedobiologia 44: 75-85.

Kersmaekers M (1972a) Note sur deux nouvelles stations pour la Belgique d'un Oniscoïde du genre Armadillidium, Armadillidium nasatum (Budde-Lund). Bulletin d'lnformation de l'Equipe Spéléologique de Bruxelles 51: 14-17.

Kersmaekers M (1972b) Un cas de tératologie chez un Oniscoïde (lsopode). Bulletin et Annales de la Société royale d'Entomologie de Belgique 109: 94-96.

Kersmaekers M (1973a) Communications a l'Assemblée mensuelle du 7 novembre 1973. Bulletin et Annales de la Société royale d'Entomologie de Belgique 109: 221-223.

Kersmaekers M (1973b) Note sur plusieurs captures d'un Oniscoïde du genre Trichorhina dans les serres du Jardin Botanique à Gand. Biologisch Jaarboek Dodonaea 41: 194-197.

Kersmaekers M (1973c) Nouvelle sous-espèce d'Oniscoïde pour la faune belge: Trichoniscus pusillus provisorius Racovitza, 1908. Bulletin et Annales de la Société royale d'Entomologie de Belgique 109: 305-307.

Kersmaekers M (1974) Communications a l' Assemblée mensuelle du 6 mars 1974. Bulletin et Annales de la Société royale d'Entomologie de Belgique 110: 34-35.

Kersmaekers M (1988) Communications a l'Assemblée mensuelle du 2 décembre 1987. Armadillidium (Duplocarinatum) album (Dollfus, 1889), nouvel Oniscoïde pour la faune belge (Crustacea, Isopoda). Bulletin et Annales de la Société royale d'Entomologie de Belgique 124: 67-69.

Kersmaekers M, Deroeck R (1973) Comparaison de la faune des Isopodes de deux massifs karstiques: Massif de Boine et Massif de Dieupart. Speleologia Belgica 2: 6-11.

Kesteloot E (1956) Zeebrugge: une curiosité biologique de notre littoral. Association Nationale des Professeurs de Biologie de Belgique 2: 9.

Kime RD (1992) On abundance of West-European millipedes (Diplopoda). Proceedings of the 8th International Congress of Myriapodology. Berichte des Naturwissenschaftlich-medizinischen Vereins in Innsbruck 10: 393-399.

Koivula M et al. (1999) Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. Ecography 22: 424-435.

Kolb A, Diekmann M (2004) Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. Journal of Vegetation Science 15: 199-208.

Kowal VA, Cartar RV (2012) Edge effects of three anthropogenic disturbances on spider communities in Alberta's boreal forest. Journal of Insect Conservation 16: 613-627.

Krauss J et al. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology Letters 13: 597-605.

Lacasella F et al. (2015) Asymmetrical responses of forest and "beyond edge" arthropod communities across a forest–grassland ecotone. Biodiversity and conservation 24: 447-465.

Laliberté E et al. (2015) FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Lambrechts J (1997) Spinnen en pissebedden van autosnelwegbermen rond Gent en het voorkomen van zware metalen in deze organismen. Universiteit Gent.

Lameere A (1895) Manuel de la Faune de Belgique. H. Lamertin, Bruxelles.

Lameere A (1897) Documents pour la faune de Belgique. Annales de la Société Royale de Microscopie 22:

41-46.

Lameere A (1909) Assemblée mensuelle du 4 septembre 1909. Annales de la Société d'Entomologie de Belgique 53: 405-406.

Lameere A (1913) La faune du môle de Zeebrugge. Annales de la Société royale zoologique et malacologique de Belgique 44: 259-260.

Lameere A (1931) Excursion à Blankenberge. 25-26 mai 1931. Annales de la Société royale zoologique et malacologique de Belgique 62: 10-11.

Lameere A (1938) Les animaux de Belgique. Tome II. Vers Mollusques, Arachnomorphes, Crustacés, Myriapodes. Les Naturalistes belges 1938: 88-89.

Lavelle P (1997) Faunal activities and soil processes: adaptive strategies that determine ecosystem function. Advances in Ecological Research 27: 93-132.

Lavelle P et al. (2006) Soil invertebrates and ecosystem services. European Journal of Soil Biology 42: S3-S15.

Lavorel S et al. (2013) A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. Journal of Vegetation Science 24: 942-948.

Lavorel S, Garnier É (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional ecology 16: 545-556.

Lawrence KL, Wise DH (2000) Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44: 33-39.

Leclercq J (1957) Etude Biospéléologique. Fons de Forêts. Commission de Topographie et de Toponymie de la FSB 13: 2-6.

Lefevere S (1965) Le recouvrement biogène le long de la côte belge. Bulletin de I'Institut royal des Sciences naturelles de Belgique 26: 1-10.

Lefevere S et al. (1956) Observations biologiques dans le port d'Ostende. Mémoires de l'lnstitut royal des Sciences naturelles de Belgique 133: 1-110.

Leleup N (1948) Contribution à l'étude des arthropodes nidicoles et cavernicoles de Belgique. Mémoires de la Société royale d'Entomologie de Belgique 25: 1-56.

Leloup E (1957) Contributions à l'étude de la faune belge: XXV. Observations écologiques sur le fossé d'eau saumâtre entourant la "Demi-Lune" d'Ostende. Bulletin de I'Institut royal des Sciences naturelles de Belgique 33: 1-9.

Leloup E et al. (1954) Recherches hydrobiologiques sur trois mares d'eau douce des environs de Liège. Mémoires de l'lnstitut royal des Sciences naturelles de Belgique 131: 1-145.

Leloup E et al. (1963) Recherches sur l'ostréiculture dans le bassin de chasse d'Ostende en 1962. Ministère de l'Agriculture. Commission TWOZ. Groupe de Travail Ostréiculture: Ostende.

Leloup E, Konietzko B (1956) Recherches biologiques sur les eaux saumâtres du Bas-Escaut. Mémoires de l'lnstitut royal des Sciences naturelles de Belgique 132: 1-100.

Leloup E, Miller G (1940) La flore et la faune du bassin de chasse d'Ostende (1937-1938). Mémoires de l'lnstitut royal des Sciences naturelles de Belgique 94: 1-122.

Leloup E, Polk Ph (1967) La flore et la faune du bassin de chasse d'Ostende (1960-1961): III. étude zoologique. Mémoires de l'lnstitut royal des Sciences naturelles de Belgique 157: 1-114.

Leloup E, Van Meel L (1958) Quelques considerations hydrobiologiques sur un étang à Lombise. Bulletin de l'Institut royal des Sciences naturelles de Belgique 34: 1-16.

Leruth R (1936a) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 25: 29-32.

Leruth R (1936b) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 25: 52-56.

Leruth R (1936c) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 25: 66-68.

Leruth R (1936d) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 25: 95-98.

Leruth R (1936e) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 25: 130.

Leruth R (1937a) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 26: 9-11.

Leruth R (1937b) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 26: 22-23.

Leruth R (1937c) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 26: 99-103.

Leruth R (1937d) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 26: 129-132.

Leruth R (1937e) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. XXI. Contribution (Deuxième liste des grottes visitées). Natuurhistorisch Maandblad 26: 141-146.

Leruth R (1937f) Etudes biospéologiques. I. lsopoda (Crustacea). Bulletin du Musée royal d'histoire naturelle de Belgique 13: 1-25.

Leruth R (1939) La biologie du domaine souterrain et la faune cavernicole de la Belgique. Mémoires du Musée royal d'Histoire naturelle, Série 1 87: 1-506.

Lewis JGE (2006) The biology of centipedes. Cambridge university press., Cambridge.

Li YF et al. (2014) Effects of substratum type on bacterial community structure in biofilms in relation to settlement of plantigrades of the mussel *Mytilus coruscus*. International Biodeterioration Biodegradation 96: 41-49.

Lindsey AA, Newman JE (1956) Use of official weather data in spring time: temperature analysis of an Indiana phenological record. Ecology 37: 812-823.

Lock K (2001) Trichoniscoides sarsi (Patience, 1908): a newspecies for the fauna of Belgium (Isopoda Trichoniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 137: 29-31.

Lock K (2007) Haplophthalmus montivagus Verhoeff, 1940: a new species for Belgium (Isopoda Trichoniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 143: 22-25.

Lock K, Durwael L (2000) Miktoniscus patiencei (Vandel, 1946): reported for the first time in Belgium (Isopoda Trichoniscidae). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 136: 21-23.

Lock K, Vanacker S (1999) Isopods on the gravelbanks of the Meuse (Isopoda). Bulletin van de Koninklijke Belgische Vereniging voor Entomologie 135: 193-196.

Loescher H et al. (2014) Spatial variation in soil properties among North American ecosystems and guidelines for sampling designs. Plos One 9, e83216.

Loones J et al. (2008) De rode bosmier in Vlaanderen: voorkomen, bedreigingen en herstelmaatregelen aan de hand van een detailstudie in de Sixtusbossen (Poperinge-Vleteren). Rapporten van het Instituut voor Natuur-en Bosonderzoek 2008 (INBOR200801). Instituut voor Natuur en Bosonderzoek, Brussel.

López-Barrera F et al. (2006) Effects of the type of montane forest edge on oak seedling establishment along forest–edge–exterior gradients. Forest Ecology and Management 225: 234-244.

Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. Bioscience 56: 311-323.

Loureiro S et al. (2006) Feeding behaviour of the terrestrial isopod *Porcellionides pruinosus* Brandt, 1833 (Crustacea, Isopoda) in response to changes in food quality and contamination. Science of the Total Environment 369: 119-128.

Mac Leod J (1880) Deux crustacés nouveaux pour la faune belge. Annales de la Société d'Entomologie de Belgique 23: 74-75.

Madeira F et al. (2016) Spillover of arthropods from cropland to protected calcareous grassland – the neighbouring habitat matters. Agriculture, Ecosystems and Environment 235: 127-133.

Maelfait J-P et al. (2004) Annex 4: Terrestrische arthropoden. In: Speybroeck J et al. (Eds) Studie over de impact van zandsuppleties op het ecosysteem Eindrapport Dossiernr 202165. Ministerie van de Vlaamse Gemeenschap, Brussel.

Magura T (2002) Carabids and forest edge: spatial pattern and edge effect. Forest Ecology and management 157: 23-37.

Maitland RT (1897) Prodrome de la Faune des Pays-Bas et de la Belgique Flamande. Uitgave Boekhandel en Drukkerij voorheen Brill, Leiden.

Makeschin F (1997) Earthworms (Lumbricidae: Oligochaete): Important promotors of soil development and soil fertility. In: Benckiser G (Ed) Fauna in soil ecosystems Marcel Dekker Inc., New York.

Mantel L H (1979) Terrestrial invertebrates other than insects. Comparative physiology of osmoregulation in animals 1: 175-218.

Marc P, Canard A (1997) Maintaining spider biodiversity in agroecosystems as a tool in pest control. Agriculture, Ecosystems & Environment 62: 229-235.

Mares J (1994) Strandexcursie te Oostende (Opex) op 30 april 1994. De Strandvlo 14: 103-106.

Martins da Silva P et al (2012) Environmental factors at different spatial scales governing soil fauna community patterns in fragmented forests. Landscape Ecology 27: 1337-1349.

Martins da Silva P et al. (2015) Soil fauna through the landscape window: factors shaping surface-and soil-dwelling communities across spatial scales in cork-oak mosaics. Landscape Ecology 30: 1511-1526.

Martinson HM, Fagan WF (2014) Trophic disruption: a meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. Ecology letters 17: 1178-1189.

Massart J (1912) Pour Ia protection de la nature en Belgique. H. Lamertin, Bruxelles.

Matlack GR (1993) Microenvironment variation within and among forest edge sites in the eastern United States. Biological conservation 66: 185-194.

McGill BJ et al. (2006) Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21: 178-185.

Meehan TD et al. (2011) Agricultural landscape simplification and insecticide use in the Midwestern United States. Proceedings of the National Academy of Sciences 108: 11500-11505.

Meyer E, Eisenbeis G (1985) Water relations in millipedes from some alpine habitat types (Central Alps, Tyrol) (Diplopoda). Bijdragen tot de Dierkunde 55: 131-142.

Meyer ST et al. (2009) Persisting hyper-abundance of leaf-cutting ants (*Atta* spp.) at the edge of an old Atlantic forest fragment. Biotropica 41: 711-716.

Moe SJ et al. (2005) Recent advances in ecological stoichiometry: insights for population and community ecology. Oikos 109: 29-39.

Moghadam FS, Zimmer M (2014) Effects of Warming and Nutrient Enrichment on How Grazing Pressure Affects Leaf Litter–Colonizing Bacteria. Journal of Environmental Quality 43: 851-858.

Moniez R (1886) Comptes-rendus des séances. Assemblée mensuelle du 6 novembre 1886. Annales de la Société d'Entomologie de Belgique 30: 185.

Mooney KA et al. (2010) Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. Proceedings of the National Academy of Sciences 107: 7335-7340.

Moretti M et al. (2016) Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Functional Ecology 31: 558-567.

Moretti M et al. 2013. Linking traits between plants and invertebrate herbivores to track functional effects of environmental changes. Journal of Vegetation Science 24: 949–962.

Mosse B (1973) Plant Growth Responses to Vesicular-Arbuscular Mycorrhiza. New Phytologist 72: 127-136.

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends in ecology & evolution 10: 58-62.

Muys B, Lust N (1992) Inventory of the earthworm communities and the state of litter decomposition in the forests of Flanders, Belgium, and its implications for forest management. Soil Biology and Biochemistry 24: 1677–1681.

Nachtergale L et al. (2002) Earthworm biomass and species diversity in windthrow sites of a temperate lowland forest. Pedobiologia 46: 440-451.

Newbold T et al (2015) Global land-use impacts on local terrestrial biodiversity. Nature 520: 45-50.

Ng K et al. (2018) Beetle's responses to edges in fragmented landscapes are driven by adjacent farmland use, season and cross-habitat movement. Landscape Ecology 33: 109-125.

Niemelä J et al. (1993) Effects of Clear-Cut Harvesting on Boreal Ground-Beetle Assemblages (Coleoptera: Carabidae) in Western Canada. Conservation biology 7: 551-561.

Nijs G et al. (2016) De Grauwe klauwier in Vlaams-Brabant: inventarisatie, habitatpreferentie en voedselbeschikbaarheid. Rapport Natuurpunt Studie 2016/5, Mechelen.

Normann C et al. (2016) How forest edge-center transitions in the herb layer interact with beech dominance vs. tree diversity. Journal of Plant Ecology 9: 498-507.

Nyffeler M, Sunderland KD (2003) Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. Agriculture, Ecosystems & Environment 95: 579-612.

Ohwaki A et al. (2015) Seasonal variability in the response of ground beetles (Coleoptera: Carabidae) to a forest edge in a heterogeneous agricultural landscape in Japan. European Journal of Entomology 112: 135-144.

Oksanen J et al. (2015) vegan: Community Ecology Package. R package version 2.2-1.

Orgiazzi A et al. (2016) Global Soil Biodiversity Atlas. European Commission. Publications Office of the European Union, Luxembourg.

Osler GH, Sommerkorn M (2007) Toward a complete soil C and N cycle: incorporating the soil fauna. Ecology 88: 1611-1621.

Paoletti MG, Hassall M (1999) Woodlice (Isopoda: Oniscidea): their potential for assessing sustainability and use as bioindicators. Agriculture, Ecosystems & Environment 74: 157-165.

Parmentier T et al. (2017) Body size in the ant-associated isopod Platyarthrus hoffmannseggii is host-dependent. Biological Journal of the Linnean Society 121: 305-311.

Pearce JL, Venier LA (2006) The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. Ecological indicators 6: 780-793.

Pelseneer P (1886) Note sur la présence de Caridina Desmaresti dans les eaux de la Meuse. Bulletin du Musée royal d'histoire naturelle de Belgique 4: 211-222.

Peña, E. de la et al. (2016) Beyond plant–soil feedbacks: mechanisms driving plant community shifts due to land-use legacies in post-agricultural forests. Functional Ecology 30: 1073-1085.

Pereira HM et al. (2010) Scenarios for global biodiversity in the 21st century. Science 330: 1496-1501.

Peyras M et al. (2013) Quantifying edge effects: the role of habitat contrast and species specialization. Journal of Insect Conservation 17: 807-820.

Pfeifer M et al. (2017) Creation of forest edges has a global impact on forest vertebrates. Nature 551: 187-191.

Pinheiro J et al. (2017) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131.1

Pirson S et al. (2008) An overview of the geology of Belgium. In: Damblon F, Pirson S, Gerrienne P (Eds) Charcoal and Microcharcoal : Continental and Marine Records. Royal Belgian Institute of Natural Sciences, Brussels.

Plateau F (1870) Matériaux pour la faune belge Crustacés lsopodes terrestres. Bulletin de I'Academie Belge, série 2 29: 112-121.

Plateau F (1886) Comptes-rendus des séances. Assemblée mensuelle du 4 décembre 1886. Annales de la Société d'Entomologie de Belgique 30: 190.

Plateau MF (1873) On the occurrence of Ligidium agile in Belgium. Annals and Magazine of Natural History 12: 75.

Polk Ph (1957) Studie der landisopoden van België. Biologisch Jaarboek Dodonaea 24: 157-181.

Polk Ph (1959a) De landpissebedden (lsopoda Oniscoidea) van Belgie en Nederland. Koninklijke Nederlandse Natuurhistorische Vereniging Tabel 31: 1-12.

Polk Ph (1959b) Notes sur la distribution et la bibliographie des Oniscoïdea de la Belgique. Biologisch Jaarboek Dodonaea 27: 452-460.

Polk Ph (1963) Bijdrage tot de kennis van de mariene fauna van de Belgische Kust. V. Some observations on the Crustacean fauna of the Sluice-dock (Bassin de Chasse) of Ostend. Bulletin de I'Institut royal des Sciences naturelles de Belgique 29: 1-8.

Polk Ph (1965) Oecologie van de Spuikom te Oostende in verband met de oestercultuur. PhD Thesis, Gent: Rijksuniversiteit Gent.

Polk Ph (1976) Inventarisatie plankton, fauna en flora. In: Nihoul JCJ, De Coninck L (Eds) Projekt Zee eindverslag: 7 Inventaris van de fauna en flora Projekt Zee eindverslag 7.

Polk Ph, Oye P (1956) Studie der Landisopoden in België: systematisch-oecologisch. Licenciaatsverhandeling, Gent: Universiteit Gent.

Prescott CE (2010) Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry 101: 133-149.

Preudhomme de Borre A (1886a) Comptes-rendus des séances. Assemblée mensuelle du 5 juin 1886. Annales de la Société d'Entomologie de Belgique 30: 125.

Preudhomme de Borre A (1886b) Note sur les Crustacés Isopodes de Belgique. Annales de la Société d'Entomologie de Belgique 30: 74-86.

Punttila P (1996) Succession, forest fragmentation, and the distribution of wood ants. Oikos 75: 291-298.

Purse BV et al. (2012) Habitat use governs distribution patterns of saprophagous (litter-transforming) macroarthropods – a case study of British woodlice (Isopoda: Oniscidae). European Journal of Entomology 109: 543-552.

Qian SS, Shen Z (2007) Ecological applications of multilevel analysis of variance. Ecology 88: 2489-2495.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rainio J, Niemelä J (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodiversity & Conservation 12: 487-506.

Rand TA et al. (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecology letters 9: 603-614.

Rappé G (1977) Verslag van het weekendje in Blankenberge op 25 en 26 september 1976. Tuimelaar 4: 7.

Rappé G (1989a) Annotated checklist of the marine and brackish water lsopoda (Crustacea, Malacostraca) of Belgium. In: Wouters K, Baert L (Eds) lnvertebraten van België - lnvertébrés de Belgique, Proceedings of the Symposium "Invertebrates of Belgium". Brussels.

Rappé G (1989b) Haliclona xena De Weerdt, 1986 (Porifera, Desmospongiae), Petrobius maritimus (Leach) (Insecta, Thysanura) en enkele andere bijzondere waarnemingen van de oostelijke strekdam van Zeebrugge. De Strandvlo 9: 113-116.

Reed RA et al. (1996) Fragmentation of a forested rocky mountain landscape, 1950-1993. Biological conservation 75: 267-277.

Reich PB et al. (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecology Letters 8: 811-818.

Reichle D (1968) Relation of body size to food intake, oxygen consumption, and trace element metabolism in forest floor arthropods. Ecology 49: 538-542.

Reinmann AB, Hutyra LR (2017) Edge effects enhance carbon uptake and its vulnerability to climate change in temperate broadleaf forests. Proceedings of the National Academy of Sciences 114:107-12.

Reino L et al. (2009) Distance to edges, edge contrast and landscape fragmentation: interactions affecting farmland birds around forest plantations. Biological Conservation 142: 824-838.

Remy E et al. (2016) Strong gradients in nitrogen and carbon stocks at temperate forest edges. Forest Ecology and Management 376: 45-58.

Remy E et al. (2017) Driving factors behind litter decomposition and nutrient release at temperate forest edges. Ecosystems (in press).

Remy E et al. (2018) Altered microbial communities and nitrogen availability in temperate forest edges. Soil Biology and Biochemistry 116: 179-188.

Reznikova Z, Dorosheva H (2004) Impacts of red wood ants Formica polyctena on the spatial distribution and behavioural patterns of ground beetles (Carabidae). Pedobiologia 48: 15-21.

Richardson BA et al. (2005) Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico. Journal of Animal Ecology 74: 926-936.

Ries L et al. (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annual Review of Ecology Evolution & Systematics 35: 491-522.

Ries L et al. (2017) Closing Persistent Gaps in Knowledge About Edge Ecology. Current Landscape Ecology Reports 2: 30-41.

Riutta T et al. (2012) Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. Soil Biology and Biochemistry 49: 124-131.

Rouifed S et al. (2010) The importance of biotic factors in predicting global change effects on decomposition of temperate forest leaf litter. Oecologia 163: 247-256.

Royauté R, Buddle CM (2012) Colonization dynamics of agroecosystem spider assemblages after snow-melt in Quebec (Canada). Journal of Arachnology 40: 48-58.

Rustad LEJL et al. (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126: 543-562.

Rutgers M et al. (2016) Mapping earthworm communities in Europe. Applied Soil Ecology 97: 98-111.

Samu F, Szinetár C (2002) On the nature of agrobiont spiders. Journal of Arachnology 30: 389-402.

Santos FA (2007) Ecophysiology. In: Pinto-da-Rocha R et al. (Eds), Harvestmen: the biology of Opiliones:

473–488. Harvard University Press, Cambridge.

Sariyildiz T (2008) Effects of gap-size classes on long-term litter decomposition rates of beech, oak and chestnut species at high elevations in Northeast Turkey. Ecosystems 11: 841-853.

Schelfhout S et al. (2017) Tree species identity shapes earthworm communities. Forests 8: 85.

Scheu S (2003) Effects of earthworms on plant growth: patterns and perspectives: the 7th international symposium on earthworm ecology Cardiff Wales 2002. Pedobiologia 47 : 846-856.

Scheu S, Poser G (1996) The soil macrofauna (Diplopoda, Isopoda, Lumbricidae and Chilopoda) near tree trunks in a beechwood on limestone: indications for stemflow induced changes in community structure. Applied Soil Ecology 3: 115-125.

Schmalfuss H (2003) World catalog of terrestrial isopods (Isopoda: Oniscidea). Stuttgarter Beitrage zur Naturkunde, Serie A 654.

Schollen K (1999) Evaluatie van de mogelijkheden van het bebossen van baggergronden aan de hand van enkele invertebratengroepen. Scriptie voorgelegd tot het behalen van de graad van Licentiaat in de Biologie (richting dierkunde). Academiejaar 2000, Gent: Universiteit Gent.

Schouteden H (1901) Résultat de ses chasses faites le 14 avril lors de l'excursion de la Société à Samson. Annales de la Société d'Entomologie de Belgique 45: 163-164.

Séchet E, Noël F (2015) Catalogue commenté des Crustacés Isopodes terrestres de France métropolitaine (Crustacea, Isopoda, Oniscidea). Mémoires de la Société Linnéenne de Bordeaux 16: 156.

Segers S (2015) Eenvoudig landpissebedden determineren [Zoekkaart]. Spinicornis, i.s.m. JNM vzw, Gent.

Segers S et al. (2017) Philoscia affinis Verhoeff, 1908 new to the UK (Isopoda: Philosciidae). Bulletin of the British Myriapod and Isopod Group 30: 21-25.

Senden L (1936) Bewoners van krotten en achterbuurten. Uitgeverij De Standaard.

Slade EM, Riutta T (2012) Interacting effects of leaf litter species and macrofauna on decomposition in different litter environments. Basic and Applied Ecology 13: 423-431.

Snyder BA, Hendrix F (2008) Current and potential roles of soil macroinvertebrates (earthworms, millipedes and isopods) in ecological restoration. Restoration Ecology 16: 629-636.

Soejono Sastrodihardjo FX, Van Straalen NM (1993) Behaviour of five isopod species in standardized tests for pH preference. European Journal of Soil Biology 29: 127-131.

Soga M et al. (2013) Patch size determines the strength of edge effects on carabid beetle assemblages in urban remnant forests. Journal of insect conservation 17: 421-428.

Sterzynska M et al. (2015) Contrasting responses of millipedes and terrestrial isopods to hydrologic regime changes in forested montane wetlands. European Journal of Soil Biology 68: 33-41.

Stribling JB et al. (2003) Determining the quality of taxonomic data. Journal of the North American Benthological Society 22: 621-631.

Suding KN et al. (2006) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14: 1125-1140.

Sutton SL (1972) Woodlice. Ginn & company limited, London.

Swiecicka I, Mahillon J (2006) Diversity of commensal Bacillus cereus sensu lato isolated from the common sow bug (*Porcellio scaber*, Isopoda). FEMS microbiology ecology 56: 132-140.

Symondson WOC et al. (2002) Can generalist predators be effective biocontrol agents? Annual Reviews of Entomology 47: 561–594.

Tajovský K (1999) Impact of inundations on terrestrial arthropod assemblages in Southern Moravian floodplain forests, the Czech Republic. Ekologia(Bratislava)/Ecology(Bratislava) 18 : 177-184.

Tajovský K et al. (2012) Assemblages of terrestrial isopods (Isopoda, Oniscidea) in a fragmented forest landscape in Central Europe. Zookeys 176: 189-198.

Tavernier JM (1981) Isopoda. In: Guillemijn B, van den Bremt P (Eds) Het Honegemgebied te Erpe-Mere, Lede en Aalst Documentatiemap Landschapsonderzoek Rijksdienst voor Monumenten- en Landschapsonderzoek 3.

Tavernier JM, Kerwyn Ch (1982) Een woordje over de fauna die omgewaaide populieren in elzenbroeken kunnen herbergen. ‘t Koninkje 11: 43-46.

Tavernier JM, Wouters K (1986) De havenpissebed Ligia oceanica (Linnaeus, 1758), in België. De Wielewaal 52: 100-102.

Tavernier JM, Wouters K (1989) Check-list of the terrestrial lsopoda (Crustacea) of Belgium. In: Wouters K, Baert L (Eds) lnvertebraten van België - lnvertébrés de Belgique, Proceedings of the Symposium “Invertebrates of Belgium”. Brussels.

Tavernier JM, Wouters K (1991) Check-list and distribution of terrestrial lsopoda (Crustacea) of Belgium. Biology of Terrestrial lsopods. Third International Symposium. Poitiers.

Thiele HU (1977) Carabid beetles in their environments: a study on habitat selection by adaptations in physiology and behaviour (Vol. 10). Springer Science & Business Media, New York

Topp W (1994) Seasonal time partitioning and polymorphism in the developmental cycles of sympatric Staphylinoidea (Col.) living in an unstable environment. In: Danks HV (Ed), Insect Life Cycle Polymorphisms. Kluwer Academic Publishers, Amsterdam.

Topp W et al. (2006) Distribution pattern of Woodlice (Isopoda) and millipedes (Diplopoda) in four primeval forests of the Western Carpathians (Central Slovakia). Soil Biology and Biochemistry 38: 43-50

Topping CJ, Sunderland KD (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. Journal of Aplied Ecology 29: 485-491.

Tóthmérész B et al. (2014) Edge effects on ground-dwelling beetles (Carabidae and Staphylinidae) in oak forest-forest edge-grassland habitats in Hungary. European Journal of Entomology 111: 686-691.

Troubleyn L et al. (2009) Consumption patterns and living conditions inside Het Steen, the late medieval prison of Malines (Mechelen, Belgium). Journal of Archaeology in the Low Countries 1-2: 5-47.

Tscharntke T et al. (2005) The landscape context of trophic interactions: insect spillover across the crop—noncrop interface. Annales Zoologici Fennici 42: 421-432.

Tscharntke T et al. (2012) Landscape moderation of biodiversity patterns and processes – eight hypotheses. Biological Reviews 87: 661-685.

Tuf I et al. (2008) Length of recovery of soil macrofauna communities (Coleoptera: Carabidae, Isopoda: Oniscidea) after an irregular summer flood. Peckiana 5 : 65-75.

Tuff KT et al. (2016) A framework for integrating thermal biology into fragmentation research. Ecology Letters 19: 361-374.

Uetz GW (1991) Habitat structure and spider foraging. In Habitat structure. In: Bell SS et al. (Eds) Habitat Structure. Population and Community Biology Series, vol 8. Springer, Dordrecht.

Valdés A et al. (2015) The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across Europe. Global Ecology and Biogeography 24: 1094–1105.

Van Beneden PJ (1861) Recherches sur les crustacés du littoral de Belgique. Mémoires de l' Academie royale des Sciences, des Lettres et des Beaux-Arts 33: 1-174.

Van de Poel S (2016) Harvestman communities in small forest patches in European agricultural landscapes. MSc-thesis, University of Antwerp, Belgium.

Van De Vyver E (2009) Populatie- en ecosysteemeffecten van metaalverontreiniging in baggergronden en enkele Kempische bossen. Gent: Universiteit Gent.

Van Gompel J, Rabaut K (1976) Golfbrekeronderzoek te Blankenberge. Tuimelaar 3(3): 7-8.

Van Straalen NM, Verhoef HA (1997) The development of a bioindicator system for soil acidity based on arthropod pH preferences. Journal of Applied Ecology 34: 217–232.

Van Wilgenburg SL et al. (2001) Patterns of arthropod abundance, vegetation, and microclimate at boreal forest edge and interior in two landscapes: implications for forest birds. Ecoscience 8: 454-461.

Vandekerckhove T et al. (2003) Evolutionary trends in feminization and intersexuality in woodlice (Crustacea, Isopoda) infected with Wolbachia pipientis (alpha-Proteobacteria). Belgian journal of zoology 133: 61-69.

Vandel A (1933) Liste des espèces de Trichoniscidae signalées jusqu'ici en France. Archives de zoologie expérimentale et générale 75: 35-54.

Vandel A (1952) Isopodes terrestres (Troisième série). Archives de zoologie expérimentale et générale 88: 232-262.

Vandel A (1960) Isopodes terrestres (Première partie). Office central de faunistique, Fédération française des Sociétés de Sciences naturelles, Paris.

Vandel A (1962) Isopodes terrestres (Deuxième partie). Office central de faunistique, Fédération française des Sociétés de Sciences naturelles, Paris.

Vandepitte L et al. (2010) Belgian Register of Marine Species, compiled and validated by the VLIZ Belgian Marine Species Consortium. Vlaams Instituut voor de Zee (VLIZ), Oostende.

Vanhellemont M et al. (2014) Relating changes in understory diversity to environmental drivers in an ancient forest in northern Belgium. Plant Ecology Evolution 147: 22-32.

Vasconcelos HL, Luizão FJ (2004) Litter production and litter concentrations in a fragmented Amazonian landscape. Ecological Applications 14: 884-892.

Verheyen K et al. (2003) Herbaceous plant community structure of ancient and recent forests in two contrasting forest types. Basic and Applied Ecolog 4: 537-546.

Verhoeff KW (1937) Ueber eine angeblich neue Isopoden-Familie. Zoologischer Anzeiger 118: 173-176.

Vickery JA et al. (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology 38: 647-664.

Vos VCA et al. (2011) Macro-detritivore identity drives leaf litter diversity effects. Oikos 120: 1092-1098.

Wade TG et al. (2003) Distribution and causes of global forest fragmentation. Conservation Ecology 7: 7.

Wagg C et al. (2014) Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences 111: 5266-5270.

Wall DH et al. (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Global Change Biology 14: 2661-2677.

Wall DH et aL. (2012) Soil ecology and ecosystem services. USA: Oxford University Press.

Wang Y et al. (2016) mvabund: Statistical methods for analysing multivariate abundance data. R package version 3.11.9.

Warburg MR (1964) The response of isopods towards temperature, humidity and light. Animal Behavior 12: 175-186.

Warburg MR et al. (1984) The effects of climate on the distribution and abundance of isopods. Zoological Journal of the Linnean Society 53: 339-367.

Wardle DA (2006) The influence of biotic interactions on soil biodiversity. Ecology Letters 9: 870–86.

Warton DI et al. (2012) Distance-based multivariate analyses confound location and dispersion effects. Methods in Ecology and Evolution 3: 89-101.

Weathers KC et al. (2001) Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. Conservation Biology 15: 1506-1514.

Weber D (2013) Asseln (Crustacea, Isopoda) aus Höhlen des Grißherzogtums Luxemburg. Ferrantia 69: 171-185

Wenk ES et al. (2016) Soil macroinvertebrate communities across a productivity gradient in deciduous forests of eastern North America. Northeastern Naturalist 23: 25-44.

Wolters V (2000) Invertebrate control of soil organic matter stability. Biology and Fertility of Soils 31: 1-19.

Wolters V (2001) Biodiversity of soil fauna and his function. European Journal of Soil Biology 37: 221-227.

Wolters V, Ekschmitt K (1997) Gastropods, isopods, diplopods, and chilopods: neglected groups of the decomposer food web. In: Benckiser G (Ed) Fauna in soil ecosystems Marcel Dekker Inc., New York.

Wood SN (2006) *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC.

Woodcock BA (2004) Pitfall trapping in ecological studies. In: Leather SR (Ed) Insect sampling in forest ecosystems. Methods in Ecology Series. Blackwell Science Ltd, Oxford.

Wouters K et al. (2000) Distribution and bibliography of the terrestrial Isopoda (Crustacea) of Belgium. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 70: 193-205.

Wuyts K (2009) Patterns of throughfall deposition, nitrate seepage, and soil acidification in contrasting forest edges. Ph.D. thesis, Ghent University, Belgium.

Wuyts K et al. (2008a) The impact of forest edge structure on longitudinal patterns of deposition, wind speed, and turbulence. Atmosperic Environment 42: 8651-8660.

Wuyts K et al. (2008b) Patterns of throughfall deposition along a transect in forest edges of silver birch and Corsican pine. Canadian Journal of Forest Research 38: 449-461.

Wuyts K et al. (2008c) Comparison of forest edge effects on throughfall deposition in different forest types. Environmental Pollution 156: 854-861.

Wuyts K et al. (2011) Soil inorganic N leaching in edges of different forest types subject to high N deposition loads. Ecosystems 14: 818–834.

Wuyts K et al. (2013) Edge effects on soil acidification in forests on sandy soils under high deposition load. Water, Air, and Soil Pollution 224: 1–14.

Yekwayo I et al. (2016) Surrounding vegetation matters for arthropods of small, natural patches of indigenous forest. Insect Conservation and Diversity 9: 224-235.

Zhang D et al. (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. Journal of Plant Ecology 1: 85-93.

Ziesche TM, Roth M (2008) Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: what makes the difference, tree species or microhabitat? Forest Ecology and Management 255: 738-752.

Zimmer M (2002) Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach. Biological Reviews 77: 455-493.

Zimmer M et al. (2005) Do woodlice and earthworms interact synergistically in leaf litter decomposition? Functional Ecology 19: 7-16.

Zimmer M, Topp W (2000) Species-specific utilization of food sources by sympatric woodlice (Isopoda: Oniscidea). Journal of Animal Ecology 69: 1071-1082.

The author | Edwin Brosens

CURRICULUM VITAE

Personal data

Name	Pallieter De Smedt
Address	Mispeldonk 2 2820 Bonheiden Belgium
Place of birth	Mechelen
Date of birth	16/05/1988
Nationality	Belgian
Phone	(+32) 471 50 14 02
Email	Pallieter.desmedt@ugent.be

Education

2013 - 2018	PhD in Bioscience Engineering funded by FWO – Ghent University, Belgium
2012 – 2013	PhD in Bioscience Engineering – Ghent University, Belgium
2010 – 2012	Master of Science in Forest & Nature Conservation (Specialisation: Ecology) – Wageningen University, The Netherlands
2011-2012	MSc-Thesis: “Effect of habitat heterogeneity on intraspecific trait variability of shrub species in Australian granite inselbergs.” – Curtin University, Australia
2007 - 2010	Bachelor of Science in Forest & Nature Conservation - Wageningen University, The Netherlands
Autumn 2009	Minor in Tropical Esosystems - Norwegian University of Life Sciences (UMB), Norway
2000 - 2006	Secondary school (Science-Mathematics), Sint-Theresiacollege, Kapelle-op-den-Bos

Scientific publications

Peer reviewed scientific articles included in Web of Science

De Smedt P., Boeraeve P., Arijs G., Stijn Segers S. Woodlice of Belgium: an annotated checklist and bibliography (Isopoda: Oniscidae). *ZooKeys* (IF 1.031) (in press)

De Smedt P., Ottaviani G., Wardell-Johnson G., Sýkora K.V., Mucina L. (2018) Habitat heterogeneity promotes intraspecific trait variability of shrub species in Australian granite inselbergs. *Folia Geobotanica* 1-13 (IF 1.017)

De Smedt P., Baeten L., Proesmans W., Berg M.P., Brunet J., Cousins S.A.O., Decocq G., Deconchat M., Diekmann M., Gallet-Moron E., Giffard B., Liira J., Martin L., Ooms A., Valdés A., Wulf M., Hermy M., Bonte D., Verheyen K. (2018) Linking macrodetritivore distribution to desiccation resistance in small forest fragments embedded in agricultural landscapes in Europe. *Landscape Ecology* 33: 407-421 (IF 3.62)

De Smedt P., Baeten L., Berg M.P., Gallet-Moron E., Brunet J., Cousins S.A.O., Decocq G., Diekmann M., Giffard B., De Frenne P., Hermy M., Bonte D., Verheyen K. (2018) Desiccation resistance determines distribution of woodlice along forest edge-to-interior gradients. *European Journal of Soil Biology* 85: 1-3 (IF 2.45)
Varela E., Verheyen K., Valdés A., Soliño M., Jacobsen J.B., **De Smedt P.**, Ehrmann S., Gärtner S., Górriz E., Decocq G. (2018) Promoting biodiversity values of small forest patches in agricultural landscapes: ecological drivers and social demand. *Science of the Total Environment* 619-620: 1319-1329 (IF 4.900)

Plas van der F., Ratcliffe S., Ruiz-Benito P., Scherer-Lorenzen M., Verheyen K., Wirth C., Zavala M.A., Ampoorter E., Baeten L., Barbaro L., Bastias C.C., Bauhus J., Benavides R., Benneter A., Bonal D., Bouriaud O., Bruelheide H., Bussotti F., Carnol M., Castagneyrol B., Charbonnier Y., Cornelissen J.H.C., Dahlgren J., Checko E., Coppi A., Dawud S.M., Deconchat M., **De Smedt P.**, De Wandeler H., Domisch T., Finér L., Fotelli M., Gessler A., Granier A., Grossiord C., Guyot V., Haase J., Hättenschwiler S., Jactel H., Jaroszewicz B., Joly F.-X., Jucker T., Kambach S., Kaendler G., Kattge J., Koricheva J., Kunstler G., Lehtonen A., Liebergesell M., Manning P., Milligan H., Müller S., Muys B., Nguyen D., Nock C., Ohse B., Paquette A., Peñuelas J., Pollastrini M., Radoglou K., Raulund-Rasmussen K., Roger F., Seidl R., Selvi F., Stenlid J., Valladares F., Van Keer J., Vesterdal L., Fischer M., Gamfeldt L., Allan E. (2018) Continental mapping of forest ecosystem functions reveals a high but unrealized potential for forest multifunctionality. *Ecology Letters* 21: 31–42 (IF 9.449)

Ehrmann S., Ruyts S.C., Scherer-Lorenzen M., Bauhus J., Brunet J., Cousins S.A.O, Deconchat M., Decocq G., De Frenne P., **De Smedt P.**, Diekmann M., Gallet-Moron E., Gärtner S., Hansen K., Kolb A., Lenoir J., Lindgren J., Naaf T., Paal T., Panning M., Prinz M., Valdès A., Verheyen K., Wulf M., Liira J. (2018) Habitat properties are key drivers of Borrelia burgdorferi s.l. prevalence in Ixodes ricinus populations of deciduous forest fragments. *Parasites & Vectors* 11: 23 (IF 3.035)

De Smedt P., Van de Poel S. (2017) Succession in harvestman (Opiliones) communities from an abandoned sand quarry in Belgium. *Belgian Journal of Zoology* 147: 155–169 (IF 0.870)
Remy E., Wuyts K., Van Nevel L., **De Smedt P.**, Boeckx P., Verheyen K. (2017) Driving factors behind litter decomposition and nutrient release at temperate forest edges. *Ecosystems* https://doi.org/10.1007/s10021-017-0182-4 (IF 4.198)

Ehrmann S., Liira J., Gärtner S., Hansen K., Bauhus J., Brunet J., Cousins S.A.O., Deconchat M., Decocq G., De Frenne P., **De Smedt P.**, Diekmann M., Gallet-Moron E., Kolb A., Lenoir J., Lindgren J., Naaf T., Paal T., Valdés A., Verheyen K., Wulf M., Scherer-Lorenzen M. (2017). Environmental drivers of Ixodes ricinus abundance in forest fragments of rural European landscapes. *BMC ecology* 17: 31. (IF 2.896)

Setiawan N.N., Vanhellemont M., Baeten L., Gobin R., **De Smedt P.**, Proesmans W., Ampoorter E., Verheyen K. (2016) Does neighbourhood tree diversity affect the crown arthropod community in saplings? *Biodiversity and Conservation* 25: 169-185 (IF 2.258)

De Smedt P., Wuyts K., Baeten L., De Schrijver A., Proesmans W., De Frenne P., Ampoorter E., Remy E., Gijbels M., Hermy M., Bonte D., Verheyen K. (2016) Complementary distribution patterns of arthropod detritivores (woodlice and millipedes) along forest edge-to-interior gradients. *Insect Conservation and Diversity* 9: 456-469. (IF 2.367)

Valdés A., Lenoir J., Gallet-Moron E., Andrieu E., Brunet J., Chabrerie O., Closset-Kopp D., Cousins S.A.O., Deconchat M., De Frenne P., **De Smedt P.**, Diekmann M., Hansen K., Hermy M., Kolb A., Liira J., Lindgren J., Naaf T., Paal T., Prokofieva I., Scherer-Lorenzen M., Wulf M., Verheyen K., Decocq G. (2015) The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across Europe: drivers of herbaceous species diversity in fragmented forests. *Global Ecology and Biogeography* 24: 1094–1105 (IF 5.84)

Under review

De Smedt P., Wasof S., Van de Weghe T., Hermy M., Bonte D., Verheyen K. Macro-detritivore identity and biomass along with moisture availability control forest leaf litter breakdown in a field experiment. Accepted pending revisions in Applied Soil Ecology

Ampoorter E., Barbaro L., Jactel H., Baeten L., Boberg J., Carnol M., Castagneyrol B., Charbonnier Y., Dawud S.M., Deconchat M., **De Smedt P.**, De Wandeler H., Guyot V., Hättenschwiler S., Joly F.-X., Koricheva J., Milligan H., Muys B., Nguyen D., Ratcliffe S., Scherer-Lorenzen M., van der Plas F., Van Keer J., Verheyen K., Allan, E. Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in Europe. Under review in Diversity & Distributions

Barbaro L., Allan E., Ampoorter E., Castagneyrol B., Charbonnier Y., De Wandeler H., Kerbiriou C., Milligan H.T., Vialatte A., Carnol M., Deconchat M., **De Smedt P.**, Jactel H., Koricheva J., Le Viol I., Muys B., Scherer-Lorenzen M., Verheyen K., Plas F. van der Accounting for trophic interactions improves forest bat and bird response models to climate and tree diversity. Under review in Proceedings of the Royal Society B.

De Smedt P., Vangansbeke P., Bracke R., Schauwvliege W., Willems L., Mertens J., Verheyen K. Vertical stratification of moth communities in a deciduous forest in Belgium. Pending revisions for Insect Conservation and Diversity

Pardon P., Reheul D., Mertens J., Reubens B., De Frenne P., **De Smedt P.**, Proesmans W., Van Vooren L., Verheyen K. Gradients in abundance and diversity of ground-dwelling arthropods in temperate arable agroforestry fields. Under review in Agriculture, Ecosystems and Environment

Valdés A., Lenoir J., De Frenne P., Andrieu E., Brunet J., Chabrerie O., Cousins S.A.O., Deconchat M., **De Smedt P.**, Diekmann M., Ehrmann S., Gallet-Moron E., Gärtner S., Giffard B., Hansen K., Hermy M., Kolb A., Le Roux V., Liira J., Lindgren J., Martin L., Naaf T., Paal T., Proesmans W., Scherer-Lorenzen M., Wulf M., Verheyen K., Decocq G. Small but strong: ancient forest patches deliver high levels of ecosystem services in agricultural landscapes. Under review in PNAS

Valdés A., Lenoir J., Gallet-Moron E., Andrieu E., Brunet J., Chabrerie O., Cousins S.A.O., Deconchat M., De Frenne P., **De Smedt P.**, Diekmann M., Ehrmann S., Gärtner S., Hermy M., Kolb A., Liira J., Lindgren J., Naaf T., Paal T., Wulf M., Verheyen K., Decocq G. Habitat fragmentation hampers the distribution of forest plants in small forest patches across Europe. Pending revisions for New Phytologist

Vanneste T., Valdés A., Verheyen K., Perring M.P., Bernhardt-Römermann M., Brunet J., Cousins S.A.O., Deconchat M., **De Smedt P.**, Diekmann M., Heinken T., Hermy M., Kolb A., Lenoir J., Liira J., Naaf T., Wulf M., Decocq G., De Frenne P. Plant functional trait variation in fragmented forests across Europe. Under review in Global Ecology and Biogeography

Peer reviewed articles in other journals

Segers S., Boeraeve P., **De Smedt P.** (2018) *Philoscia affinis* Verhoeff, 1908 new to the UK (Isopoda: Philosciidae). *Bulletin of the British Myriapod & Isopod Group* 30: 21-25

Boeraeve P., **De Smedt P.**, Arijs G., Segers S. (2017) *Philoscia affinis* Verhoeff, 1908 new to Belgium (Isopoda: Philosciidae). *Bulletin de la Société royale belge d'Entomologie/Bulletin van de Koninklijke Belgische Vereniging voor Entomologie* 153: 183 - 188

De Smedt P., Arijs G., Segers S., Boeraeve P. (2017) Woodlice of the green houses at Ghent Botanical Garden and Botanic Garden Meise with two new exotic species for Belgium (Isopoda: Oniscidae). *Bulletin de la Société royale belge d'Entomologie/Bulletin van de Koninklijke Belgische Vereniging voor Entomologie* 153: 109-112

De Smedt P., Boeraeve P., Arijs G., Franken O., Mechtold O., Segers S., Berg M.P. (2017) A long-expected finding: the first record of the isopod Eluma caelatum (Miers, 1877) from Belgium (Crustacea: Isopoda: Armadillidiidae). *Bulletin de la Société royale belge d'Entomologie/Bulletin van de Koninklijke Belgische Vereniging voor Entomologie* 153: 89-93

De Smedt P., Van Keer J., Van de Poel S. (2017) The ground active spider fauna of Armenbos (Kapelle-op-den-Bos, Vlaams-Brabant, Belgium): a small stepping-stone in an agricultural matrix. *Nieuwsbrief van de*

Belgische Arachnologische Vereniging 32: 79-87

Van de Poel S., **De Smedt P.**, Lewylle I., De Smedt E. (2017) Op de salamandertafel. *Natuur.focus* 16: 45-46

De Smedt P., Boeraeve P., Arijs, G. (2016) Confirmation of *Metatrichoniscoides leydigii* (Weber, 1880) in Belgium, 60 years after discovery (Isopoda: Trichoniscidae). *Bulletin de la Société royale belge d'Entomologie/ Bulletin van de Koninklijke Belgische Vereniging voor Entomologie* 152: 18-21

De Smedt P., Boeraeve P., Arijs G., Proesmans W. (2016) *Trichoniscus alemannicus* Verhoeff, 1917 a new species of woodlouse for Belgium (Isopoda: Trichoniscidae). *Bulletin de la Société royale belge d'Entomologie/ Bulletin van de Koninklijke Belgische Vereniging voor Entomologie* 152, 104-108

De Smedt P., Schauwvliege W., Vangansbeke P., Van Camp B. (2016) Nachtvlinderinventarisatie in bos: nadenken over inventarisatiemethodes. *Natuur.focus* 15: 37-38

Decocq G., Andrieu E., Brunet J., Chabrerie O., De Frenne P., **De Smedt P.**, Deconchat M., Diekmann M., Ehrmann S., Giffard B., Mifsud E.G., Hansen K., Hermy M., Kolb A., Lenoir J., Liira J., Moldan F., Prokofieva I., Rosenqvist L., Varela E., Valdés A., Verheyen K., Wulf M. (2016) Ecosystem services from small forest patches in agricultural landscapes. *Current Forestry Reports* 2:30-44

Jocqué R., Baert L., **De Smedt P.**, Bosselaers J., Souffreau J., Henrard A., Janssen M., Alderweireldt M., Oger P., Bosmans R., Fannes W., Jansen L., Decae A., Sleeuwaert T. (2016) An introductory study of house spiders (Araneae) in Belgium. *Arachnology* 17: 129-136

Van de Poel S., **De Smedt P.** (2016) Harvestmen (Opiliones) from deciduous forest fragments in two agricultural landscapes in Flanders, Belgium. *Nieuwsbrief van de Belgische Arachnologische Vereniging* 31: 119-125

Fritzén N.R., Rinne V., Sunhede M., Uddström A., Van de Poel S., **De Smedt P.** (2015) Platybunus pinetorum (Arachnida, Opiliones) new to Sweden. *Memoranda Societatis Fauna et Flora Fennica* 91: 37-40

De Smedt P., Boeraeve P., Arijs G., Segers S., Lock K. (2015) Porcellio monticola Lereboullet, 1853 a new species for Belgium (Isopoda : Porcellionidae). *Bulletin de la Société royale belge d'Entomologie/Bulletin van de Koninklijke Belgische Vereniging voor Entomologie* 151: 118-121

Proesmans W., **De Smedt P.** (2015) The millipede *Cylindroiulus britannicus* (Verhoeff, 1891) new for the Belgian fauna (Diplopoda: Julidae). *Bulletin de la Société royale belge d'Entomologie/Bulletin van de Koninklijke Belgische Vereniging voor Entomologie* 151: 239-242

Schelfhout S., De Schrijver A., Mertens J., De Block M., Herr C., **De Smedt P.**, Verheyen, K. (2014) Natuurontwikkeling op landbouwgrond: herstelmaatregelen. *Natuur.focus* 13: 31-39

De Schrijver A., Demey A., De Frenne P., Schelfhout S., Vergeynst J., **De Smedt P.**, Verheyen K. (2013) Stikstof en biodiversiteit: een onverzoenbaar duo. *Natuur.focus* 12: 92-102

De Smedt P., Van Keer J., Van Keer K., Lambeets K. (2013) The arachnofauna of Bos van Aa (Zemst, Vlaams-Brabant, Belgium): Comparison between two faunistic studies, 25 years apart. *Nieuwsbrief van de Belgische Arachnologische Vereniging* 28: 109-124

De Smedt P., Lambeets K. (2013) Verspreiding en ecologie van doornsprinkhanen (*Orthoptera: Tetrigidae*) in het voormalig zandwinningsgebied Bos van Aa (Zemst). Jaarboek Brakona 2012 pp. 49-62

Book chapters

De Schrijver A., Ampoorter E., van der Burg R., Demey A., Schelfhout S., Olsthoorn A., **De Smedt P.,** Vangansbeke P., Van Nevel L., Hommel P., De Frenne P., Mertens J., Verheyen K. (2018) Groeiplaatsverbetering. In: Jansen P., Boosten M., Cornelis J., Thomassen E., Winnock M. Praktijkboek Bosbeheer. Stichting Probos, Wageningen

Scientific activities

Participation in symposia with oral presentation

De Smedt P. *Workshop pissebedden determineren.* BRAKONA contactdag 2018. 2018/02/03, Leuven, Belgium

De Smedt P., Van de Poel S. *Populatieschattingen van kamsalamander in Vlaams-Brabant.* 11de Herpetologische studiedag. 2017/12/16, Antwerp, Belgium

De Smedt P., Baeten L., Berg M.P., Gallet-Moron E., Brunet J., Cousins S.A.O., Decocq G., Diekmann M., Giffard B., De Frenne P., Hermy M., Bonte D., Verheyen K. *Cope or retreat: Desiccation resistance determines distribution patterns of woodlice along forest edge-to-interior gradients.* BES, GFÖ, NECOV and EEF joint annual meeting: Ecology Across Borders. 2017/12/11-14, Ghent, Belgium

De Smedt P., Vangansbeke P. *Hoofvliegers onder de nachtvlinders. Verticale distributie van nachtvlinders in een oud loofbos.* Nachtvlinderstudiedag Vlaamse Vereniging voor Entomologie. 2017/11/18, Oelegem, Belgium

De Smedt P., Baeten L., Berg M.P., Gallet-Moron E., Brunet J., Cousins S.A.O., Decocq G., Diekmann M., Giffard B., De Frenne P., Hermy M., Bonte D., Verheyen K. *Desiccation resistance determines distribution patterns of woodlice along forest edge-to-interior gradients.* 10th International Symposium on the Biology of Terrestrial Isopods. 2017/08/27-30, Budapest, Hungary

De Smedt P., Van de Poel S. *Populatieschattingen van kamsalamander in Vlaams-Brabant.* BRAKONA contactdag 2017. 2017/02/04, Leuven, Belgium

De Smedt P., Vangansbeke P. *Vertical distribution of macro-moths in a deciduous forest in Belgium.* Entomology in Belgium. 2016/12/02, Brussels, Belgium

De Smedt P., Vangansbeke P. *Hoofvliegers onder de nachtvlinders. Verticale distributie van nachtvlinders in een oud loofbos.* Vlinderstudiedag 2016. 2016/11/26, Mechelen, Belgium

De Smedt P. *Bodemfauna doorgrond.* Het belang van pissebedden en co. Warme winteravonden 2016-2017. 2016/11/15, Heverlee, Belgium

De Smedt P., Baeten L., Proesmans W., Berg M.P., Brunet J., Cousins S.A.O., Decocq G., Deconchat M., Diekmann M., Gallet-Moron E., Giffard B., Liira J., Martin L., Ooms A., Valdés A., Wulf M., Hermy M., Bonte D., Verheyen K. *Landscape disturbance and forest edges drive diversity of macro-detritivores in European small forest fragments.* 46th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland. 2016/09/05-09, Marburg, Germany

De Smedt P., Arijs G., Pepijn B., Segers S. *De verspreiding van landpissebedden in België.* Belgische entomologische studiedag. 2016/02/27, Brussels, Belgium

De Smedt P., Pepijn B., Arijs G., Segers S. *Op zoek naar juweeltjes… De verspreiding van landpissebedden in Vlaams-Brabant.* BRAKONA contactdag 2016. 2016/02/06, Leuven, Belgium

De Smedt P., Proesmans W. *Onderzoeksmethoden en ecologie van pissebedden en miljoenpoten in Vlaanderen.* Workshop bodembiodiversiteit in Vlaanderen. 2015/11/17, Brussels, Belgium

De Smedt P. *Woodlice and millipedes in small forest fragments in Europe. Possible implications for litter decomposition.* IUFRO Landscape Ecology Conference. 2015/08/23-30, Tartu, Estonia

De Smedt P. *Geleedpotigenonderzoek Bos van Aa: Geleedpotigengemeenschappen in een oud zandwinningsgebied.* BRAKONA contactdag 2014. 2014/02/01, Leuven, Belgium

Participation in symposia with poster presentation

Segers S., Arijs G., Boeraeve P., **De Smedt P.** *"Spinicornis" A Belgian working group on terrestrial isopods.* 10th International Symposium on the Biology of Terrestrial Isopods. 2017/08/27-30, Budapest, Hungary

De Smedt P., Baeten L., Proesmans W., Bonte D., Verheyen K. et al. *Patterns and processes driving macrodetritivore distribution in small forest fragments embedded in agricultural landscapes.* BEES Christmas market 2016. 2016/12/13, Ghent, Belgium

De Smedt P., Martin L., Giffard B., Verheyen K. et al. *Ecosystem services provided by soil dwelling arthropod communities of small forest fragments in European agricultural landscapes.* Biosymposium 2015 – The functions and values of biodiversity. 2015/01/6-7, Oxford, UK

Participation in specialist courses

31/08 – 02/09/2017	Post-Symposium course on Oniscidea taxonomy and systematics, Budapest, Hungary
01/04 – 06/06/2014	Field techniques for surveying invertebrates (online course), Oxford, UK
10-14/02 2014	Essential tools for R, Leuven, Belgium
22-29/09/2013	International Summerschool on Functional significance of forest biodiversity, Białowieża, Poland

Tutor of master dissertations

Willem Proesmans (2013-2014). Millipede communities in small forest patches in contrasting agricultural landscapes. Ghent University.

Rieneke Vanhulle (2013-2014). Lycosid communities in small deciduous forest fragments in Europe: Species composition and potential for natural pest control. Ghent University.

Tom Van de Weghe (2015-2016). Interactions between woodlice and millipedes for leaf litter breakdown under changing environmental conditions. Ghent University.

Co-promotor of master dissertations

Rani Bracke (2014-2015) Ups and downs van nachtvlinders. Ghent University

Sam Van de Poel (2015-2016). Harvestmen communities in small forest patches in European agricultural landscapes. University of Antwerp.

Warre Schauwvliege (2015-2016). Verticale verspreiding van nachtvlinders in een gematigd loofbos. Ghent University.

VERKENSBEESTEN

(Oniscidae)

Hier hebben we nu werkelijk wel te doen met het uitschot van de maatschappij! De geleerde, die anders zoo gauw niet vies gevallen is, heeft ze amper van ver bekeken, ze vast met een voorzichtig tangetje opgenomen om vluchtig na te meten hoe lang en hoe breed ze zijn. De man van de straat geeft zich ternauwernood de moeite om ze dood te trappen, walgend van zoo'n vuil ongediert.

Hun namen – want ze hebben er verscheidene naar gelang de streek – mogen ook niet op aristokratische aanspraak bogen: VERKENSBEESTEN, ZWIJNTJES, ZWIENTJES, WILDE VERKENS of – in het Noorden nog erger – PISSEBEDDEN: het klinkt allemaal meer dan gewoon demokratisch; KELDERWORM, dàt is ten minste nog een zondagsche titel!

Leo Senden, 1936

(Uit: Bewoners van krotten en achterbuurten)