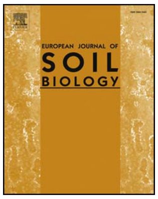
European Journal of Soil Biology 85 (2018) 1–3

Contents lists available at ScienceDirect

European Journal of Soil Biology

journal homepage: www.elsevier.com/locate/ejsobi



Desiccation resistance determines distribution of woodlice along forest edge-to-interior gradients

Pallieter De Smedt[a,*], Lander Baeten[a], Matty P. Berg[b,c], Emilie Gallet-Moron[d], Jörg Brunet[e], Sara A.O. Cousins[f], Guillaume Decocq[d], Martin Diekmann[g], Brice Giffard[h,i], Pieter De Frenne[a], Martin Hermy[j], Dries Bonte[k], Kris Verheyen[a]

[a] Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, B-9090 Melle (Gontrode), Belgium
[b] Department of Ecological Science/Animal Ecology, Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands
[c] Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands
[d] Jules Verne University of Picardie, UR Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN, FRE 3498 CNRS), 1 rue des Louvels, F-80037 Amiens Cedex 1, France
[e] Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, Box 49, SE-230 53 Alnarp, Sweden
[f] Biogeography and Geomatics, Department of Physical Geography, Stockholm University, SE-106 91 Stockholm, Sweden
[g] Institute of Ecology, FB02, University of Bremen, Leobener Str., D-28359 Bremen, Germany
[h] UMR 1201 DYNAFOR, INRA, Chemin de Borde Rouge, CS 52627, F-31326 Castanet, France
[i] Bordeaux Sciences Agro, Université Bordeaux, F-33170 Gradignan, France
[j] Division of Forest, Nature and Landscape, University of Leuven, Celestijnenlaan 200E, B-3001 Leuven, Belgium
[k] Terrestrial Ecology Unit (TEREC), Dept. Biology, Ghent University, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium

ARTICLE INFO

Handling editor: Thibaud Decaens

Keywords:
Drought tolerance
Edge effects
Isopoda
Response trait
Small forest fragments

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 species composition and their associated trait distribution remains a poorly explored research-field. We sampled woodlice in 160 forest patches across 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.

Habitat fragmentation impacts forest around the world, inducing both abiotic and biotic edge-to-interior gradients [1]. Such edge effects can alter forest community composition and ecosystem processes [2]. 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 [3–5]. Abiotic drivers, like moisture availability, show particularly strong edge-to-interior gradients [6,7], and are crucial for the distribution and activity of detritivores [8–10]. Although less well known, the distribution patterns of soil organisms are strongly influenced by the effects of forest edges [11], but the importance of underlying mechanisms, such as soil moisture availability remains poorly studied [12]. In this context, species desiccation resistance (a key soil fauna functional trait) has been proposed as an important predictor for woodlice (Isopoda) distribution [11,13], a dominant taxonomic group of leaf litter-dwelling macro-detritivores [14]. 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.

The study was carried out using data of the smallFOREST research

---

[*] Corresponding author.
E-mail addresses: pallieter.desmedt@ugent.be (P. De Smedt), lander.baeten@ugent.be (L. Baeten), m.p.berg@vu.nl (M.P. Berg), emilie.moron@u-picardie.fr (E. Gallet-Moron), jorg.brunet@slu.se (J. Brunet), sara.cousins@natgeo.su.se (S.A.O. Cousins), guillaume.decocq@u-picardie.fr (G. Decocq), mdiekman@uni-bremen.de (M. Diekmann), brice.giffard@gmail.com (B. Giffard), pieter.defrenne@ugent.be (P. De Frenne), martin.hermy@ees.kuleuven.be (M. Hermy), dries.bonte@ugent.be (D. Bonte), kris.verheyen@ugent.be (K. Verheyen).

https://doi.org/10.1016/j.ejsobi.2017.12.002
Received 27 September 2017; Received in revised form 13 November 2017; Accepted 5 December 2017

platform [15] from five regions across western Europe, along a latitudinal gradient from northern France to central Sweden. In each region, two 5 × 5 km landscapes were investigated who varied in land-use intensity. In every landscape, we selected 16 forest patches, from diverse size and age classes, resulting in 160 patches. Woodlice were sampled using pitfall traps (Ø 10 cm, depth 11 cm). Their abundance was expressed as activity-density, a composite measure of activity and abundance rather than true abundances (see e.g. Woodcock [16]). The pitfall traps contained ethylene glycol and water (200 ml, 1/1 mixture). In each forest patch, we sampled at two locations i.e. the forest centre and the south facing forest edge (between the first row of trees). At every location, we installed two sampling points spaced 5 m from each other and parallel to the sampled forest edge. This resulted in four sampling points per forest patch (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 A). 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 northern edge was used. Pitfall traps were emptied twice between April and August 2013 (based on the regional temperature sum, i.e. more northern regions were sampled later in the year to match phenology with more southern regions) after they were open for 14 consecutive days. 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. [13] complemented with own measurements using the same method.

We analysed the survey data in three steps. First, 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 patches, we added a group-level effect for forest patch and allowed the activity-density at the forest edge (intercept) and its relationship with distance (slope) to vary between forest patches. Second, 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 patches (see Appendix B). Both region and forest patch were added as group-level effects and intercepts and slopes were again allowed to vary between patches. Third, 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 [17] using the packages *lme4* [18] and *MCMCglmm* [19] for the multilevel and meta-analytic models. Both the activity-density and distance were modelled on a log-scale.

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. 1). In all regions, we found an exponential decrease in activity-density from the forest edge towards the forest interior, with effects diminishing after 25–50 m 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. 2a), while a reverse pattern was found for the drought-sensitive species *Ligidium hypnorum* (Fig. 2c). Species with an intermediate drought resistance, like *Oniscus asellus*, did not show a response (Fig. 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. 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.

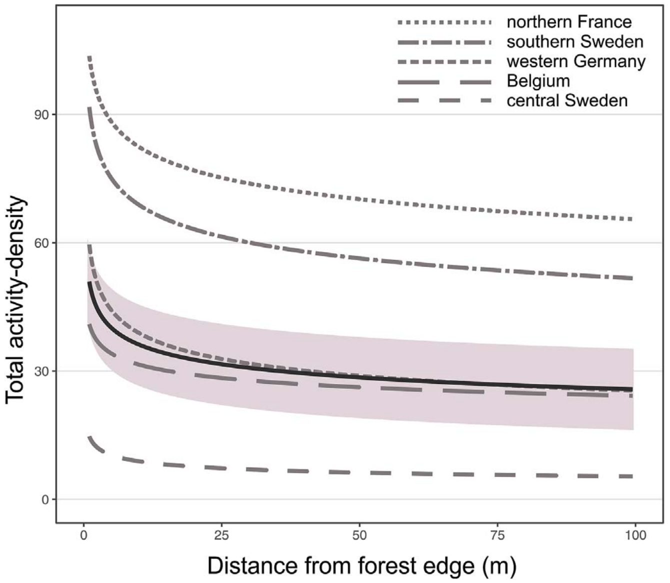


Fig. 1. Total activity-density of woodlice along forest edge-to-interior gradients per region (dotted lines). Displayed are data per sampling point summed for two trapping periods of fourteen days. The solid black line represents the average across all regions with 95% confidence interval (shaded area).

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 [12]. Traits like desiccation resistance and water loss rate have been suggested to predict macro-detritivore and, more specifically, woodlice distribution [11,13]. Desiccation resistance is related to soil moisture availability [13], and studies have pointed out that moisture might be more important than temperature for soil arthropod performance [20]. 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 patches 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. [21], 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.

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

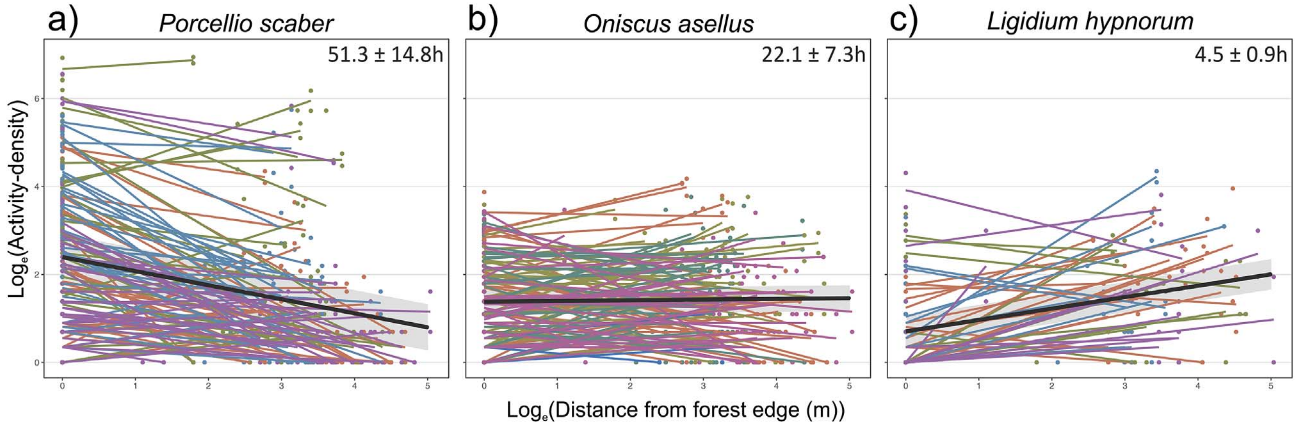


Fig. 2. Species-specific activity-density (log-transformed) in relation to the distance (log-transformed) from the forest edge towards the forest interior for a) *Porcellio scaber*, b) *Oniscus asellus* and c) *Ligidium hypnorum.* Displayed are data per sampling point summed for two trapping periods of fourteen days. The solid black line represents the global average across all regions and forest patches with 95% confidence interval (grey shaded area). Coloured lines represent edge-to-interior patterns within individual forest patches with dots being individual sampling points of forest patches 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). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

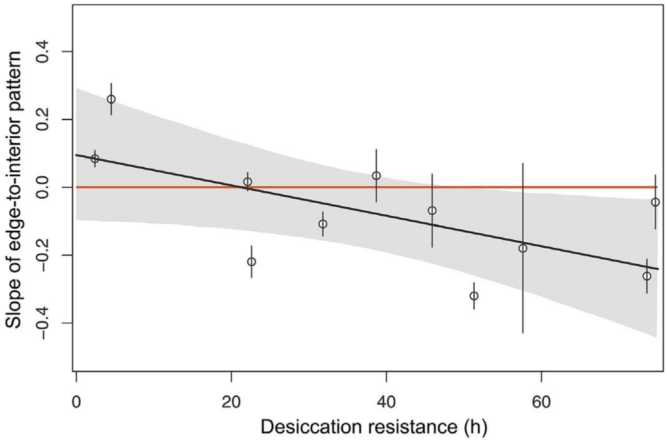


Fig. 3. Relationship between desiccation resistance of the eleven most common isopod species and the average slope of the regression between the species' activity-density and distance to the forest edge (cf. Fig. 2). The shaded area represents the 95% confidence interval of the relationship and the red 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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 A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ejsobi.2017.12.002.

References

[1] T.G. Wade, K.H. Riitters, J.D. Wickham, F.B. Jones, Distribution and causes of global forest fragmentation, Conserv. Ecol. 7 (2003) 7.
[2] N.M. Haddad, L.A. Brudvig, J. Clobert, K.F. Davies, A. Gonzalez, R.D. Holt, T.E. Lovejoy, J.O. Sexton, M.P. Austin, C.D. Collins, W.M. Cook, E.I. Damschen, R.M. Ewers, B.L. Foster, C.N. Jenkins, A.J. King, W.F. Laurance, D.J. Levey, C.R. Margules, B.A. Melbourne, A.O. Nicholls, J.L. Orrock, D.X. Song, J.R. Townshend, Habitat fragmentation and its lasting impact on Earth's ecosystems, Sci. Adv. 1 (2015) e1500052.
[3] M.A. Bradford, G.M. Tordoff, T. Eggers, T.H. Jones, J.E. Newington, Microbiota, fauna, and mesh size interactions in litter decomposition, Oikos 99 (2002) 317–323.
[4] S. Hättenschwiler, A.V. Tiunov, S. Scheu, Biodiversity and litter decomposition in terrestrial ecosystems, Annu. Rev. Ecol. Evol. S 36 (2005) 191–218.
[5] C.E. Prescott, Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochem 101 (2010) 133–149.
[6] J. Chen, J.F. Franklin, T.A. Spies, Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests, Ecol. Appl. 5 (1995) 74–86.
[7] S. Gehlhausen, M.W. Schwartzand, C.K. Augspurger, Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments, Plant Ecol. 147 (2000) 21–35.
[8] J.-F. David, I.T. Handa, The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change, Biol. Rev. 85 (2010) 881–895.
[9] E. Hornung, Evolutionary adaptation of oniscidean isopods to terrestrial life: structure, physiology and behaviour, Terr. Arthropod Rev. 4 (2011) 95–130.
[10] B.V. Purse, S.J. Gregory, P. Harding, H.E. Roy, Habitat use governs distribution patterns of saprophagous (litter-transforming) macroarthropods – a case study of British woodlice (Isopoda: oniscidae), Eur. J. Entomol. 109 (2012) 543–552.
[11] P. De Smedt, K. Wuyts, L. Baeten, A. De Schrijver, W. Proesmans, P. De Frenne, E. Ampoorter, E. Remy, M. Gijbels, M. Hermy, D. Bonte, K. Verheyen, Complementary distribution patterns of arthropod detritivores (woodlice and millipedes) along forest edge-to-interior gradients, Insect Conserv. Diver 9 (2016) 456–469.
[12] K.T. Tuff, T. Tuff, K.F. Davies, A framework for integrating thermal biology into fragmentation research, Ecol. Lett. 19 (2016) 361–374.
[13] A.T.C. Dias, E.J. Krab, J. Mariën, M. Zimmer, J.H.C. Cornelissen, J. Ellers, D.A. Wardle, M.P. Berg, Traits underpinning desiccation resistance explain distribution patterns of terrestrial isopods, Oecologia 172 (2013) 667–677.
[14] S. Jeffery, C. Gardi, A. Jones, L. Montanarella, L. Marmo, L. Miko, K. Ritz, G. Peres, J. Römbke, W.H. van der Putten (Eds.), European Atlas of Soil Biodiversity, European Commission, Publications Office of the European Union, Luxembourg, 2010.
[15] A. Valdés, J. Lenoir, E. Gallet-Moron, E. Andrieu, J. Brunet, O. Chabrerie, D. Closset-Kopp, S.A.O. Cousins, M. Deconchat, P. De Frenne, P. De Smedt, M. Diekmann, K. Hansen, M. Hermy, A. Kolb, J. Liira, J. Lindgren, T. Naaf, T. Paal, I. Prokofieva, M. Scherer-Lorenzen, M. Wulf, K. Verheyen, G. Decocq, The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across Europe, Glob. Ecol. Biogeogr. 24 (2015) 1094–1105.
[16] B.A. Woodcock, Pitfall trapping in ecological studies, in: S.R. Leather (Ed.), Insect Sampling in Forest Ecosystems, Methods in Ecology Series, Blackwell Science Ltd, Oxford, 2004, pp. 37–57.
[17] R. Core Team, R: a Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria (2017) URL https://www.R-project.org/.
[18] D. Bates, M. Maechler, B. Bolker, S. Walker, R.H. Bojesen Christensen, H. Singmann, B. Dai, G. Grothendieck, P. Green, lme4: Linear Mixed-effects Models Using ‘Eigen’ and S4, (2017) R package version 1.1-13 https://cran.r-project.org/web/packages/lme4/.
[19] J. Hadfield, MCMCglmm: MCMC Generalised Linear Mixed Models, (2016) R package version 2.24 https://cran.r-project.org/web/packages/MCMCglmm.
[20] B. Dixie, H. White, M. Hassall, Effects of microclimate on behavioural and life history traits of terrestrial isopods: implications for responses to climate change, ZooKeys 515 (2015) 145–157.
[21] E. Remy, K. Wuyts, L. Van Nevel, P. De Smedt, P. Boeckx, K. Verheyen, Driving factors behind litter decomposition and nutrient release at temperate forest edges, Ecosystems (2017) 1–17.