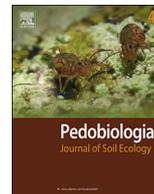




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Pedobiologia - Journal of Soil Ecology

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Forest edges reduce slug (but not snail) activity-density across Western Europe

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ARTICLE INFO

Keywords:

Edge effects
Forest fragmentation
Gastropoda
Terrestrial molluscs

ABSTRACT

Fragmentation strongly shapes the distribution of organisms within forest patches through contrasting environmental conditions between the edge and interior habitat. Edge-to-interior distribution patterns are, however, poorly studied for litter- and soil-dwelling fauna, such as terrestrial gastropods, despite their high densities and significant impact on ecosystem processes, as both herbivores and detritivores. Therefore, we investigated edge-to-interior abundance patterns of terrestrial gastropods in 224 fragmented forest patches across Western Europe. Catching over 15,000 gastropods, we found that slug abundance is reduced in forest edges, while snail abundance shows no response on the edge effect. We hypothesize that these patterns could be explained by higher drought tolerance of snails, since forest edges have reduced air and soil humidity and elevated temperatures compared to forest interiors. Reduced slug abundance in forest edges potentially has ecological consequences for herbivory in and outside forest patches and nutrient cycling.

Forest edge effects strongly alter the forest environment, resulting in pronounced abiotic gradients along forest edge-to-interior transects. Forest edges have, among others, higher temperatures, higher soil pH, receive more light, are subjected to higher wind speeds and have reduced air and soil moisture levels (Murcia, 1995; Ries et al., 2004). Along with the abiotic conditions, also the abundance and species composition of different forest biota may respond strongly to forest edges compared to the interior (see e.g. aboveground arthropods: Jokimäki et al., 1998 or plants: Chabrierie et al., 2013). These patterns are, however, poorly investigated for litter-dwelling and soil fauna (but see De Smedt et al., 2016). Terrestrial gastropods feed on dead organic material and living plant tissue and can reach high abundance in forests (Wolters and Ekschmitt, 1997). This makes them an important link in

the detrital food web, as well as important pest species for forest management and certain forest-neighbouring crops (Griffiths et al., 1998; Fritz et al., 2001; Meiners et al., 2002). Humidity is of critical importance in shaping distribution patterns of terrestrial gastropods (Prior, 1985), therefore, we can expect slugs and snail distribution to respond in similar direction. Snails have the ability to withdraw into their shells when humidity gets low, while slugs have to find suitable hiding places or retreat to areas with higher moisture (Prior, 1985). We hypothesise (1) that the abundances of terrestrial gastropods are reduced in forest edges relative to the interior and (2) that snails are less affected compared to slugs, because they can more easily bridge unfavourable periods by remaining inactive in their shells.

The study was carried out using data of the smallFOREST research

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<https://doi.org/10.1016/j.pedobi.2019.05.004>

Received 9 January 2019; Received in revised form 9 May 2019; Accepted 14 May 2019

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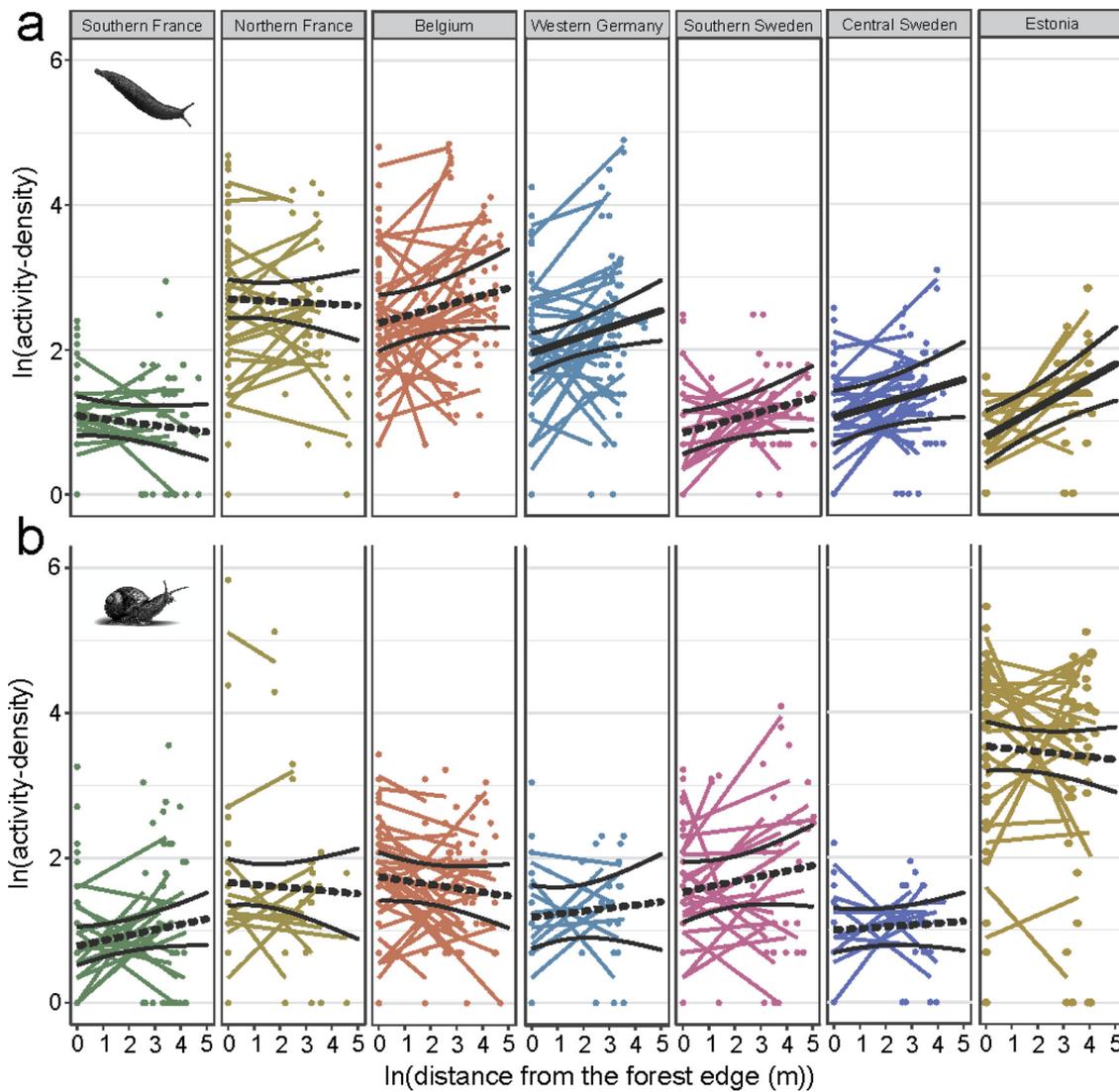


Fig. 1. Activity-density (log-transformed) of a) slugs and b) snails along forest edge-to-interior gradients (log transformed distance from the forest edge from 0 up to 148 m ($\ln(5)$)) in seven European regions. In each of 224 forest patches, two sampling points were located at the edge and two were located in the centre. These sampling points are represented as dots, with coloured lines representing the modelled trend between edge and centre within the individual patches. The bold black lines represents the overall trend \pm 95% confidence interval (thin black lines). Solid black lines are significant trends ($p < 0.05$).

network (Valdés et al., 2015). In each of seven regions distributed along a latitudinal gradient in Western Europe (southern France to Estonia), two 5 x 5 km landscapes with contrasting land-use intensity were investigated (Supplementary material Appendix 1). In each landscape, we selected 16 forest patches, from diverse size (0.08–28.19 ha, median 1.39 ha) and age (12–326 years, median 52 years; weighted average of the different stands) classes, resulting in 224 patches. Terrestrial gastropods were captured using pitfall traps (\varnothing 10 cm). This is not a standard method for sampling slugs and snails, but the catch was a result of by-catch from a large sampling campaign on litter dwelling arthropods (see De Smedt et al., 2019). The catch is expressed as activity-density, since pitfall trap data is a result of both activity and abundance of animals rather than true abundances. The pitfall traps contained ethylene glycol and water (200 ml, 1/1 mixture). In each forest patch, we sampled at two locations: at the forest centre and at the south facing forest edge (between the first row of trees) neighbouring agricultural land. In cases where south-facing edges were bordered by man-made structures such as roads, larger ditches etc., east- (16%), west- (18%) and north- (4%) facing forest edges were used instead. At each 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 patch (two in the centre and two in the edge). A sampling point consisted of two coupled pitfall traps (about 1 cm from each other) separated by a plastic barrier to assess arthropod fluxes (Supplementary material Appendix 2). The traps were covered with an aluminium roof (leaving a gap of \pm 3 cm) to prevent larger vertebrates from entering the traps. This design resulted in 896 sampling points with a total of 1792 pitfall traps. Pitfall traps were emptied twice, every time after a fourteen days trapping period between April and August 2013. Precise timing was adjusted to the regional temperature sum (i.e. more northern regions were sampled later in the year to match phenology with more southern regions). For example, sampling of the first trapping period started at the 29th of April in Southern France, 23th of May in Western Germany and the 13th of June in Central Sweden (see Lindsey and Newman (1956) for the calculation of Growing Degree Hours). All terrestrial gastropods were counted, separating slugs from snails.

We fitted two separate multilevel models (one for slugs and one for snails) with total activity-density per sampling point as a response. Distance to the forest edge, region and their interaction were used as predictors. To account for the paired nature of the sampling points within patches, we added a group-level effect for forest patch and

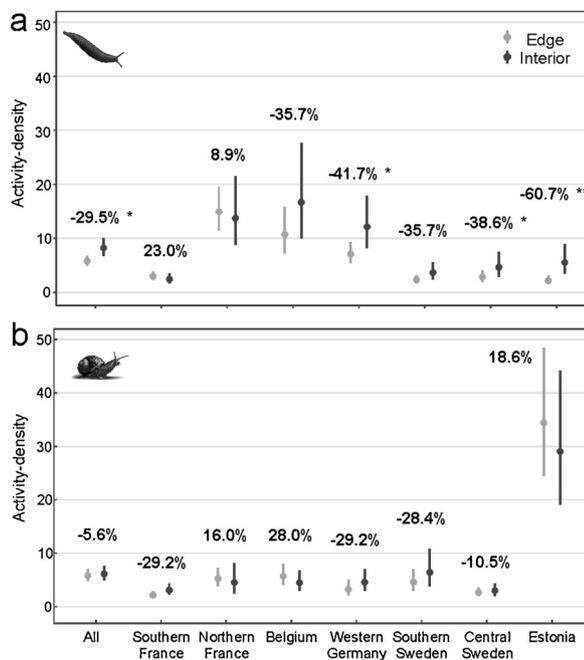


Fig. 2. Expected mean activity density (\pm 95% confidence interval) of a) slugs and b) snails in forest edges (grey) and 100 m inside the forest (black). Estimates were derived from multilevel models (cf. Fig. 1) and are given for all regions combined and each region separately. Percentage indicate the relative change in activity-density between 100 m inside the forest and the forest edge. Stars (*) indicate a significant difference in activity-density between forest edge and forest interior.

allowed the activity-density at the forest edge (intercept) and its relationship with distance (slope) to vary between forest patches (random intercepts and slopes model). We only included forest patches where at least five slugs (149 patches) or snails (114 patches) were sampled. Secondly, we fitted similar models for slug and snail distribution per region, to explore possible region-specific distribution patterns. Additionally, we performed a Tukey post-hoc test to test for differences in activity-density between the regions. Models were fitted in R 3.4.0 (R Core Team, 2017), using the *lme4* package for fitting the multilevel models (Bates et al., 2017) and *lsmeans* for the post-hoc tests (Lenth and Love, 2018). Both the activity-density and distance were transformed by taking their natural logarithm before analyses.

We collected 15,534 terrestrial gastropods of which 46.9% were slugs and 53.1% were snails. Slug activity-density was influenced by distance from the forest edge ($F_{(1,122)} = 14,470$, $p < 0.001$) and region ($F_{(6,154)} = 25.855$, $p < 0.001$). There was no significant distance \times region interaction ($F_{(6,123)} = 2.022$, $p > 0.05$). Models showed that slug activity-density is expected to increase by 29.5%, from 5.8 individuals at the edge to 8.2 at 100 m inside the forest (Fig. 1a). Within region patterns of change between the edge and 100 m inside the forest were significant for Western Germany ($F_{(1,29)} = 4.467$, $p < 0.05$), Central Sweden ($F_{(1,75)} = 6.812$, $p < 0.05$) and Estonia ($F_{(1,75)} = 12.064$, $p < 0.01$), showing an increase in activity-density of 41.7%, 38.6% and 60.7%, respectively (Fig. 2a). Slug activity-density per forest patch was highest in Belgium (80.4 ± 86.9) and Northern France (72.2 ± 64.3), followed by Western Germany (53.0 ± 67.7) and lowest in Central Sweden (13.6 ± 8.7), Southern France (11.5 ± 6.4), Estonia (11.8 ± 6.2) and Southern Sweden (9.9 ± 3.4). Snail activity-density did not change with distance from the forest edge ($F_{(1,139)} = 0.279$, $p > 0.05$) and there was no interaction with region ($F_{(6,126)} = 0.887$, $p > 0.05$), but the activity-density between regions differed significantly ($F_{(6,134)} = 26.223$, $p < 0.001$). Snail activity-density per forest patch was highest in Estonia (216.1 ± 118.7) followed by Northern France (47.0 ± 144.8), Southern Sweden

(30.8 ± 28.6) and Belgium (24.1 ± 17.7) and was lowest in Southern France (14.1 ± 10.0), Western Germany (14.0 ± 7.3) and Central Sweden (9.2 ± 2.3) (Figs. 1b and 2 b).

In our study, activity-density of terrestrial gastropods across Europe is reduced at forest edges for slugs but not for snails, but variability in edge-to-interior patterns is high between regions and between individual forest patches. As hypothesised, slugs show a stronger response compared to snails, which can be related to their lower drought tolerance (Prior, 1985). Drought tolerance was also found to be a good predictor for the forest edge-to-interior distribution of isopods (De Smedt et al., 2018). In another study on slug and snail distributions in forests, Kappes et al. (2009) found most slug and all snail species to be decreasing from 75 m from the forest edge towards the forest interior. We show the strongest decrease in activity-density of slugs close to the forest edge (exponentially declining; the linear decline in Fig. 1 is due to the log-scale) and the changes at distances higher than 75 m are less pronounced. To fully understand the established distribution patterns in our study, a detailed species-specific study could shed more light on the underlying mechanisms (e.g. De Smedt et al., 2018). This was unfortunately impossible in our study since the samples were by-catch from pitfall traps, preventing identification of slugs to species level due to disintegration of the animals in the trapping fluid. Important to notice is that in northern countries like Sweden and Estonia, there is a large expansion of invasive slug and snail species with unknown effects on the observed patterns e.g. *Arion vulgaris* in Sweden and *Arianta arbutorum* in Estonia. Studying the importance of invasive slug and snail species in forest (edge) ecology and their effects on native slug and snail populations should be an important focus of future research.

We found an overall reduction in slug activity-density within forest edges of 35% compared to 100 m inside the forest across all regions (up to 60% in Western Estonia). Such substantial decrease potentially results in lower herbivory by slugs in forest edges. Nystrand and Granström (2000) showed, for instance, that slug herbivory on seedlings was much higher in closed unlogged forest compared to more open forest types, which have a more comparable microclimate to forest edges. Apart from their role as herbivores, slugs and snails are also important links in the detrital food web. Although forest edges store more carbon and nutrients compared to forest interiors and have a faster nutrient cycling (Remy et al., 2016; Reinmann and Hutrya, 2017), the role of slugs and snails in these ecosystem processes remains unstudied. They are also known as prey for arthropods such as carabids (see Symondson et al., 2002) or other vertebrate predators, and predation pressure has been shown to increase in forest edges. Finally, forest edges are at the interface between different land-use types, that is, forest and, in most cases, agricultural land. Slugs are known to be pest species for agricultural crops and, therefore, forest edges can buffer spill-over of slugs from the forest towards agricultural areas. The assessment of the effects of the observed patterns for ecosystem functioning is an important next step to understand the processes induced by forest edges in fragmented patches. Besides, future research should focus on the context dependency of the observed patterns like forest patch characteristics, edge orientation, adjacent agricultural field management and landscape context.

Declarations of interest

None.

Acknowledgements

P.D.S. holds a postdoctoral fellowship of the Research Foundation-Flanders (FWO). 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 A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.pedobi.2019.05.004>.

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