



Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition

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ABSTRACT

Forest ecosystems have been widely fragmented by human land use. Fragmentation induces significant microclimatic and biological differences at the forest edge relative to the forest interior. Increased exposure to solar radiation and wind at forest edges reduces soil moisture, which in turn affects leaf litter decomposition. We investigate the effect of forest fragmentation, soil moisture, soil macrofauna and litter quality on leaf litter decomposition to test the hypothesis that decomposition will be slower at a forest edge relative to the interior and that this effect is driven by lower soil moisture at the forest edge. Experimental plots were established at Wytham Woods, UK, and an experimental watering treatment was applied in plots at the forest edge and interior. Decomposition rate was measured using litter bags of two different mesh sizes, to include or exclude invertebrate macrofauna, and containing leaf litter of two tree species: easily decomposing ash (*Fraxinus excelsior* L.) and recalcitrant oak (*Quercus robur* L.). The decomposition rate was moisture-limited at both sites. However, the soil was moister and decomposition for both species was faster in the forest interior than at the edge. The presence of macrofauna accelerated the decomposition rate regardless of moisture conditions, and was particularly important in the decomposition of the recalcitrant oak. However, there was no effect of the watering treatment on macrofauna species richness and abundance. This study demonstrates the effect of forest fragmentation on an important ecosystem process, providing new insights into the interacting effects of moisture conditions, litter quality, forest edge and soil macrofauna.

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1. Introduction

There have been many studies on the impacts of anthropogenic disturbance on diversity in forest ecosystems, particularly habitat degradation and fragmentation (reviewed by Saunders et al., 1991; Fahrig, 2003; Ewers and Didham, 2006; Watts, 2006). However, the consequences of forest fragmentation on ecosystem functions, such as litter decomposition and carbon and nutrient cycling, remain poorly understood, despite the important implications for forest conservation and management strategies (e.g. Saunders et al., 1991; Herbst et al., 2007). Temperate forest landscapes have been

substantially altered by human activity, with over half of broadleaf and mixed forests fragmented or removed in temperate regions, compared to one quarter of tropical rainforests and only 4% of boreal forests (Wade et al., 2003). Of all continents, Europe has the most human-caused fragmentation (Wade et al., 2003). In the UK, forest area has declined from around 75% of the land area 6000 years ago to less than 12% today, and 75% of the patches are now less than 2 ha (Watts, 2006). Such small forests effectively consist only of edge habitat (Young and Mitchell, 1994).

Due to increased solar radiation and wind, forest edges often have higher and more variable air and soil temperatures (Kapos, 1989; Saunders et al., 1991; Chen et al., 1995), higher evapotranspiration rates (Didham and Lawton, 1999; Herbst et al., 2007) and higher vapour pressure deficits (Young and Mitchell, 1994; Davies-Colley et al., 2000) compared with forest interiors. As a consequence of the higher evapotranspiration rates, soil and litter moisture content is lower at the forest edge than in the interior

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(Kapos, 1989; Didham and Lawton, 1999). Such edge effects have been shown to penetrate more than 50 m (Chen et al., 1995; Didham and Lawton, 1999; Davies-Colley et al., 2000; Herbst et al., 2007), depending on forest structure and the meteorological variable in question. In England, 32% and 65% of the forest area is within 30 m and 100 m from the nearest edge, respectively (T. Riutta, unpublished data), highlighting that edge habitats in fragmented landscapes form a considerable proportion of the total forest area.

Leaf litter decomposition is controlled by environmental factors (primarily moisture and temperature), litter chemistry and structure and the abundance, functional type and activity of soil organisms (Couteaux et al., 1995; Aerts, 1997; Gonzalez and Seastedt, 2001; Sariyildiz et al., 2005; Sariyildiz, 2008). Habitat fragmentation and climate change influence these biotic and abiotic controls of decomposition and, consequently, decomposition rates. Moisture limitation often overshadows the effect of temperature on litter decomposition rates in temperate regions (see Aerts, 2006 for review). However, despite these studies highlighting the importance of moisture there have been few studies which have actually tested the potential effects of changing moisture conditions on leaf litter decomposition processes (O'Neill et al., 2003; Taylor et al., 2004; Aerts, 2006).

In temperate forests, woodlice (Isopoda) and millipedes (Diplopoda) are the most abundant macro-decomposers, and they have been found to play a significant role in decomposition and nitrogen release (Hassall et al., 1987; Irmiler, 2000; David and Handa, 2010). While not directly responsible for the decomposition process *per se*, woodlice and millipedes provide important indirect effects through the breakdown of leaf litter into smaller particles, mixing of the leaf litter into a homogenous state, and moving it to more favourable microclimate conditions (Sutton, 1980; Hassall et al., 1987; David and Handa, 2010). They also increase the density and composition of the soil micro-flora and fauna responsible for fine-scale decomposition through the dispersal of microbial propagules, increasing the surface area through fragmentation of the litter, and through passage of litter through their guts (Hassall et al., 1987). Several studies have shown that in the absence of soil macrofauna litter disappearance is greatly reduced (e.g. Seastedt, 1984; Bradford et al., 2002; Hättenschwiler et al., 2005; Vasconcelos and Laurance, 2005).

Woodlice and millipedes are sensitive to temperature and moisture conditions, and species differ in their tolerance to dry conditions (Sutton, 1980; David and Handa, 2010; Hassall et al., 2010). Macro-decomposer abundance, diversity, functional type and distribution are therefore likely to differ between forest edges and interiors, and fragments of different sizes, and are predicted to vary with changing climatic conditions that will result in altered decomposition rates and changes in the functioning of the ecosystem. Responses of macro-decomposers and decomposition to climatic and land use changes have been little studied in the field (Hättenschwiler and Bretscher, 2001; Aerts, 2006; David and Handa, 2010).

The objective of this study was to experimentally investigate the interactions between soil moisture and the presence of macroarthropods on the decomposition of easily decomposing and recalcitrant leaf litter to determine the potential impact of edge effects and forest fragmentation on this important ecosystem processes. To our knowledge there are no studies that have investigated the interaction of edge effects, soil moisture and soil macrofauna on litter decomposition rates in temperate deciduous forests.

Specifically, we addressed the following hypotheses:

- Microclimatic differences at the forest edge and interior will cause differences in the rate of leaf litter decomposition.
- Differences between rates of leaf litter decomposition at the edge and interior of forest fragments are mainly driven by

moisture limitation at the forest edge. Thus, addition of water to the edge will reduce differences in decomposition rates between the forest edge and interior.

- Soil macrofauna will respond to edge effects and moisture conditions. Therefore, changes in the abundance of soil macrofauna will influence the decomposition rates of leaf litter.
- Easily decomposable vs. recalcitrant leaf litter will respond differently to changes in soil moisture and the presence of soil macrofauna.

2. Material and methods

2.1. Site description and experimental design

The study site was situated in Wytham Woods, Oxfordshire, UK (51° 46' N, 001° 20' W). Wytham is a mixed deciduous temperate forest of approximately 400 ha (see Savill et al., 2010). The study site was located in mature, naturally regenerated secondary forest on the northern edge of the 400 ha forest, dominated by ash (*Fraxinus excelsior* L.) and, to a lesser extent, common oak (*Quercus robur* L.) in the canopy and hazel (*Corylus avellana* L.) in the shrub layer. The area is *Fraxinus-Acer campestre-Mercurialis* woodland with *Geranium robertianum* sub-community (W8e) in the National Vegetation Classification (Rodwell, 1991).

The soil is a surface water gley of the Denchworth series in the England and Wales Soil Survey Classification (Clayden and Hollis, 1984), and Stagni-vertic Cambisol in the FAO system. Mean annual temperature (1993–2009) of the site is 10.1 °C and average precipitation is 730 mm (measured approximately 1 km from the site by an automatic weather station in an open location, as part of the UK Environmental Change Network monitoring program at Wytham; www.ecn.ac.uk).

We established an experiment to determine the effect of soil moisture and soil macrofauna on the decomposition of ash and oak leaves at the forest edge and interior. The experimental design consisted of a row of ten plots, located 7 m from the forest edge (known hereafter as edge plots), and another in the forest interior at 107 m from the forest edge (interior plots). The rows of plots were parallel to the forest edge. Variations in soil and vegetation between plots were minimal. The distance used to distinguish between edge and interior was based on previous studies in Wytham (Herbst et al., 2007) and other forests (Kapos, 1989; Young and Mitchell, 1994; Didham and Lawton, 1999) that indicated that edge effects on water loss penetrate less than 100 m from the edge. In each row, plots were arranged in five pairs; one control and one watering treatment plot in each pair. Each individual plot was 3 m × 3 m. The distance between the plots within each pair was 2 m and the distance between adjacent pairs was 5 m.

2.2. Watering treatment

To test the moisture limitation hypothesis we applied a water addition treatment based on the assumption that if the differences in decomposition rates between the forest edge and the interior are mainly driven by moisture conditions adding water will make the decomposition processes at the edge more similar to those at the forest interior. A weekly watering treatment was carried out 13 times between 1st June and 3rd September 2009, and 138 L of water was added to each watered plot each week. This amount represented an extra 200 mm of rainfall, which is more than double the average summer rainfall (165 mm from June to August, Environmental Change Network data 1993–2009) and would overcompensate for any potential differences in evapotranspiration and

evaporation from the soil between the forest edge and interior (Herbst et al., 2007).

Volumetric soil moisture content was measured with hand held time delay reflectometry (TDR) probes (HydroSense, Campbell Scientific Ltd., Shepshed, UK) at five locations in every plot, to a depth of 12 cm. Soil temperature was measured to a 10 cm depth with a hand held sensor. The measurements were taken on each watering day before water was added, that is, one week after the previous watering. Therefore, the data show the minimum impact of the watering treatment. Due to a sensor malfunction there was a gap in the soil moisture records for August.

2.3. Leaf litter bags and mesh size treatment

Leaf litter decomposition was studied using the litter bag method. Two leaf species were used, easily decomposable ash (*F. excelsior*) and decomposition resistant oak (*Q. robur*) (Howard and Howard, 1974). Recently fallen leaves were collected in the autumn of 2008 and air-dried. A known amount (approximately 2.5 g) of each of air dried ash and oak leaves were put in each nylon mesh 20 × 20 cm litter bag. Additional replicate samples were oven-dried to determine the initial oven-dried mass in the litter bags. The initial moisture content of the air-dried samples was 5.7% ± 0.51% (SE) for ash and 6.4% ± 0.68% for oak. Two mesh sizes were used: large mesh of 5 mm aperture that allowed soil macrofauna to access the litter and small mesh of 1 mm that excluded the macrofauna.

Two bags of each mesh size were placed in each plot on 30th May 2009. Before putting the bags in the plots the air-dried litter in the bags was remoistened using distilled water to restore natural moisture levels. One set of bags was retrieved after three months and a second set after twelve months. After return to the laboratory the contents were carefully cleaned, remaining oak and ash litter separated and then dried at 75 °C for 48 h and weighed. Mass loss in each bag was calculated as a proportion of the initial dry mass at the beginning of the study. Mass loss in the small mesh bags was taken as an estimate of the contribution of the microbes, microfauna and mesofauna to decomposition while the difference in mass loss between large and small mesh bags was taken as an estimate of the contribution of the macrofauna (Seastedt, 1984; Irmiler, 2000).

2.4. Macrofauna surveys

To determine the species composition and abundance of the macro-decomposers, woodlouse and millipede surveys were conducted one week before the watering treatment started and again one week after the treatment ended. The vegetation, dead wood, litter and the litter–soil interface were hand-searched in two 25 cm × 25 cm quadrats next to the litter bags in each plot. All large woodlice and millipede species (>2 mm) were collected using forceps and pooters, identified in the field, and released back to the same quadrat.

Most woodlice and millipedes are epigeal, living in the top layer of soil and leaf litter. Although most species are nocturnal, and some of the larger and common species can be arboreal, during the summer months many species are active during the day and arboreal species come down to the ground (Brereton, 1957; Banerjee, 1967; Sutton, 1980). We were restricted to sampling during the day and only at ground level. To try and overcome this problem hand-searching was used as it is not as reliant on the activity patterns of the animals as alternative methods, such as pitfall trapping, and is the method currently recommended by the British Myriapod and Isopod Group (S. Gregory, pers. comm.) for larger species, although we acknowledge that numbers may have been underestimated. However, as the purpose of the research was to compare treatments and sites rather than establishing absolute densities, we feel that hand-searching is adequate.

2.5. Statistical analyses

2.5.1. Soil moisture

Soil moisture data were analysed with mixed effects models, using location, watering treatment and time as fixed effects, and plot pair (control and watered) as the random effect. The dependent variable was the mean value of the five soil moisture measurements per plot recorded each week. The data were log-transformed to meet model assumptions. Temporal dependence of errors was modelled with a first order autoregressive correlation structure. The best model was selected using the AIC score, by stepwise removal of terms from the saturated model. In addition, edge watered and control plots and interior watered plots were compared with the interior control plots using major axis regression, to examine how soil moisture varied among habitats.

2.5.2. Soil macrofauna

The abundance and species richness of woodlice and millipedes were analysed using mixed effects models with location, watering treatment and survey time (May and September) treated as fixed effects, and plot pair as a block (random effect). Abundances were log-transformed prior to analysis to stabilize the variance. The full models were fitted, and then non-significant interaction terms dropped from the model until the minimal adequate model was obtained as described above. The simpler models had lower AIC values than the more complex models in all cases.

2.5.3. Mass loss

The experiment was analysed as block design, i.e. one measurement made per treatment × plot combination. There were 2 locations (forest edge and interior) with 5 replicates of 2 watering treatments (unwatered control and extra water) × 2 mesh sizes × 2 litter species. The response variable was mass loss during the first three months of decomposition, calculated as the proportion of the original mass lost and arcsine square-root transformed prior to analysis to stabilize the variance. Treatments (location, watering level, mesh size and species) were treated as fixed effects, with pair as a block (random effect). We hypothesized that the effect of watering, mesh size and location might differ between species, so interactions with species were modelled for these three factors. We also looked for an interaction between the location (edge vs. interior) and the watering treatment. The full models were fitted, and then non-significant interaction terms dropped from the model until the minimal adequate model was obtained. The simpler models had lower AIC values than the more complex models in all cases.

The main emphasis of the analyses was to look at the decomposition rates during the three month watering period. However, as we were also interested in whether the summer watering treatment continued to have an effect on decomposition rates during the winter, when water was no longer being added, we ran similar models including the data from the second retrieval (at 12 months), with retrieval time (3 and 12 months) as an additional fixed factor.

The *lme* function of the *nlme* package for R 2.10.1 (R Development Core Team, 2006; Pinheiro et al., 2008) was used for all of the above analyses.

3. Results

3.1. Moisture and temperature conditions

June–August rainfall sum in 2009 (208 mm) was higher than the long term (1993–2009) average (165 mm ± 63 SD) at the study site, although not exceptional. June and July 2009 were wetter than average whereas August was slightly drier. Mean air temperature

Table 1

Coefficients for mixed effects model of log-transformed soil moisture. Date is number of days after 31 May 2009. The intercept refers to soil moisture level at the interior control plots at the beginning of the experiment. The final model was selected using the Akaike Information Criterion by stepwise removal of terms from the saturated model. Temporal autocorrelation of errors between successive measurements was 0.04. The error variance attributable to plot pairs was 0.004, and residual error variance was 0.03.

| Term | Coefficient | SE | F | DF | P |
|---|-------------|-------|--------|--------|--------|
| Intercept | 4.36 | 0.049 | 21,105 | 1, 186 | <0.001 |
| Treatment (watered) | 0.11 | 0.035 | 39.8 | 1, 186 | <0.001 |
| Location (edge) | -0.79 | 0.070 | 180.4 | 1, 8 | <0.001 |
| Date | -0.01 | 0.006 | 545.4 | 1, 186 | <0.001 |
| Treatment (watered)* Location (edge) | 0.09 | 0.050 | 3.2 | 1, 186 | 0.075 |
| Location (edge)* Date | 0.0018 | 0.008 | 4.3 | 1, 186 | 0.038 |

during June and August, 15.6 °C, was similar to the long term average (16.0 °C ± 0.81 SD).

The soil moisture level was significantly higher in the forest interior compared to the forest edge (Table 1, Fig. 1). The temporal variation in soil moisture was larger in the interior than at the edge, but this relative difference varied over the course of the experiment. The edge plots showed only around half the amount of change over the course of the experiment compared to the interior plots (Fig. 1). The watering treatment significantly increased the soil moisture level at both the interior and edge (Table 1, Fig. 1). It should be noted that the data show the smallest possible difference between the watered and control plots, as the measurements were taken a week after the previous watering. The relative difference between watered and control plots stayed the same over the course of the experiment (watering treatment × date interaction $P > 0.3$); variation in soil moisture content in control plots were matched by parallel changes in watered plots. Weekly soil temperature measurements showed no difference (<0.1 °C throughout the course of the study) between the edge and the interior, or between the watered and control plots.

3.2. Soil macrofauna

Five woodlice species and six millipede species were recorded. The most abundant species was the common striped woodlice

(*Philoscia muscorum* (Scopoli, 1763)). The abundance and species richness of both woodlice and millipedes was markedly higher in May than September (month was significant, $P < 0.001$ in all models). Total woodlice abundance was significantly lower at the interior ($F_{1,67} = 6.62$ $P = 0.012$) compared to the edge and the difference was most pronounced in May at the start of the experiment (Fig. 2a). Woodlice species richness did not differ between the interior and edge ($P > 0.05$) (Fig. 2b). There was no significant interaction between watering treatment and month ($P > 0.05$), indicating that the watering treatment did not have an effect on woodlice abundance or species richness (Fig. 2a and b).

Millipede abundance did not differ between forest interior and edge or between watered and control plots ($P > 0.05$) in either May or September (Fig. 2c). However, millipede species richness was higher in the interior than edge plots in both May and September ($F_{1,8} = 7.15$, $P = 0.028$); but there was no effect of watering treatment ($P > 0.05$) (Fig. 2d).

3.3. Leaf litter decomposition

After three months of decomposition on average 87% ± 1.9% (SE) and 71% ± 3.0% (SE) of ash had been lost in the large and small mesh bags respectively. The corresponding values for oak were 57% ± 4.3% (SE) and 25% ± 2.3% (SE). Mass loss was dependent on location (forest interior or edge), watering treatment, mesh size (presence or absence of soil macrofauna) and litter species (ash or oak). We first fitted the full model with litter species as a factor, however the significant three-way interactions among location × watering treatment × species ($F_{1,62} = 4.7$, $P = 0.033$) meant that simple interpretation of the results was not possible. However, the dominant effect of species was to be expected because the two species were chosen for the study based on their markedly different rates of decomposition. We therefore ran the model for each species separately to allow us to fully understand the effects of location, watering and mesh size on decomposition.

Mass loss of both leaf litter types was faster in the forest interior compared with the forest edge (ash: $F_{1,8} = 14.3$, $P = 0.005$; oak: $F_{1,8} = 7.6$, $P = 0.025$), in the watered plots compared with the control plots, (ash: $F_{1,28} = 8.26$, $P = 0.008$; oak: $F_{1,28} = 4.4$,

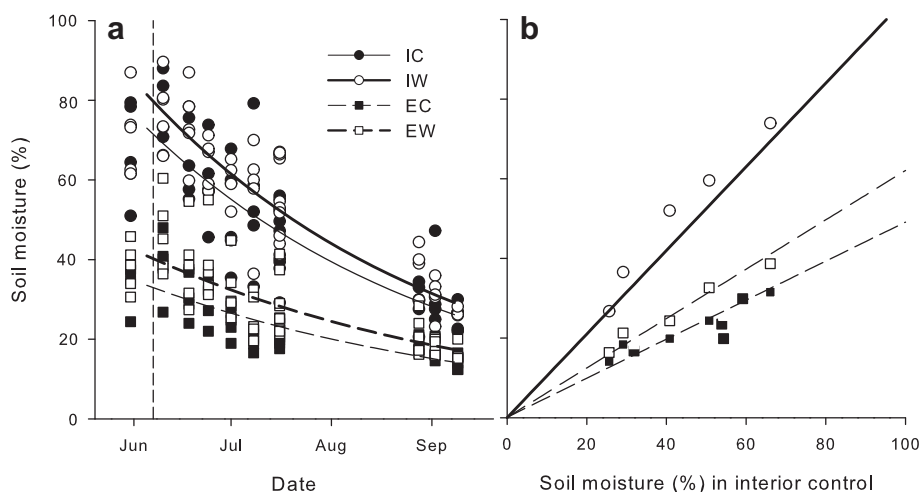


Fig. 1. (a) Soil moisture (%) over the duration of the experiment. Points are means of five readings for each interior control (IC), interior watered (IW), edge control (EC) and edge watered (EW) plot. Points for watered plots are offset slightly for visual clarity. Curves show population fitted values for a mixed effects model on log-transformed data, for edge control, edge watered, interior control and interior watered. The horizontal dashed line marks the start of the watering treatment. (b) Soil moisture in edge control, edge watered and interior watered plots against the reference conditions in the interior control plots at each measurement day. Points are mean values for five plots on each sample date. Curves show fitted values of a Major Axis regression, back-transformed to percentage values from arcsine transformation, for edge control, edge watered, and interior watered plots against the interior control plots. Slopes differ significantly among locations (permutation test, $P < 0.001$), but not between watering treatments within a location ($P > 0.5$).

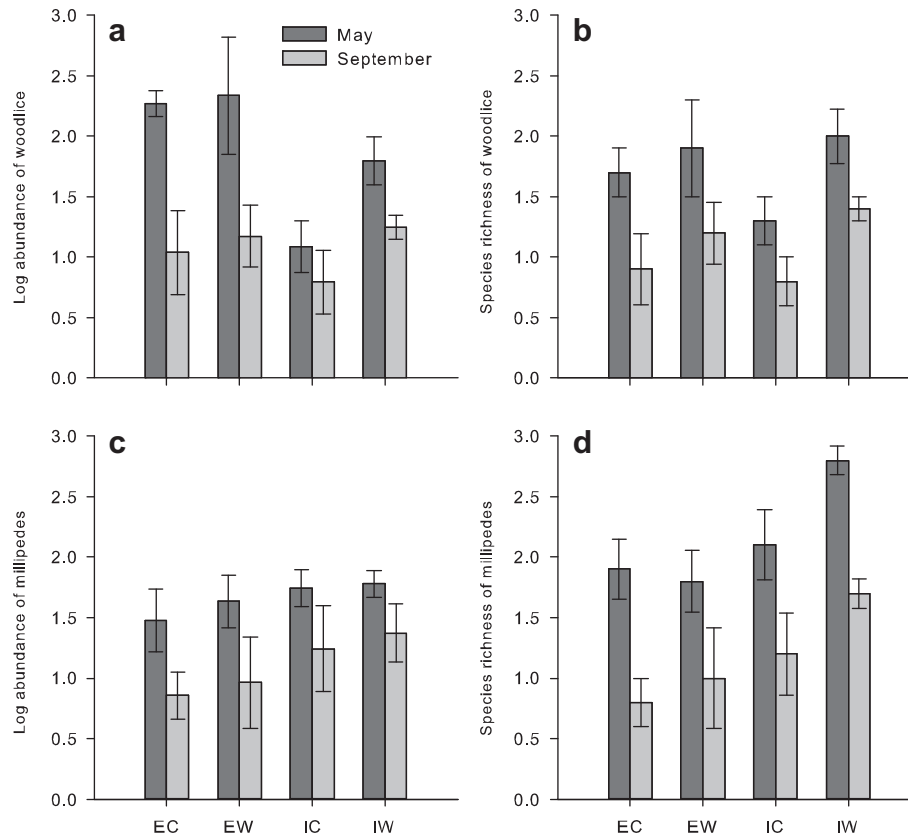


Fig. 2. (a) The abundance and (b) species richness of woodlice and (c) the abundance and (d) species richness of millipedes in each treatment (EC – edge control, EW – edge watered, IC – interior control, IW – interior watered) during May and September. Means \pm 1 SE, $n = 5$.

$P = 0.044$) and was greater in the presence of the soil macrofauna (large mesh bags) (ash: $F_{1,28} = 31.3$, $P < 0.001$; oak: $F_{1,28} = 9.8$, $P < 0.001$) (Table 2; Fig. 3). There were no significant interactions among locations, watering treatment or mesh size ($P > 0.05$ in all cases). The contribution of the soil macrofauna to litter mass loss was similar in the forest interior and edge, and also in the watered and control plots (Fig. 3, solid grey bars). Ash litter decomposed faster than the oak litter in all conditions, but the presence of the soil macrofauna had a greater effect on the decomposition of the oak (Fig. 3). Approximately 18% of the mass loss of ash litter and 55% of oak litter can be attributed to the soil macrofauna.

Table 2

Coefficients for mixed effects model of arcsine square-root transformed mass loss (proportion of initial mass) during three months of decomposition (June–August). Location (edge vs. interior), watering treatment (watered vs. control) and mesh (large vs. small) were modelled as fixed effects and plot pair (consisting of a watered and a control plot) as a random effect. The intercept is the reference mass loss through decomposition in large mesh bags in the interior control plots. The two litter species, ash (*Fraxinus excelsior*) and oak (*Quercus robur*) were modelled separately. The variance attributable to variation among plot pairs was much smaller than the residual variance among samples in all cases (oak: 0.00045 vs. 0.02368; ash: <0.00001 vs. 0.01313).

| Species | Term | Coefficient | SE | <i>t</i> | DF | <i>P</i> |
|---------|---------------------|-------------|-------|----------|----|----------|
| Ash | Intercept | 1.234 | 0.036 | 34.056 | 28 | <0.001 |
| | Location (edge) | -0.137 | 0.036 | -3.786 | 8 | <0.005 |
| | Treatment (watered) | 0.104 | 0.036 | 2.875 | 28 | <0.008 |
| | Mesh (small) | -0.203 | 0.036 | -5.593 | 28 | <0.001 |
| Oak | Intercept | 0.884 | 0.050 | 17.821 | 8 | <0.001 |
| | Location (edge) | -0.139 | 0.050 | -2.765 | 28 | 0.025 |
| | Treatment (watered) | 0.103 | 0.049 | 2.107 | 28 | 0.044 |
| | Mesh (small) | -0.343 | 0.049 | -7.059 | 28 | <0.001 |

After 12 months of decomposition on average $95\% \pm 1.4\%$ (SE) and $86\% \pm 3.4\%$ (SE) of ash had been lost in the large and small mesh bags respectively. The corresponding values for oak were $74\% \pm 6.7\%$ (SE) and $43\% \pm 5.4\%$ (SE). The ash in the control bags decomposed at a faster rate than in the watering treatment bags between the first (September 2009) and second (May 2010) retrieval (watering treatment \times retrieval interaction $F_{1,66} = 10.442$, $P = 0.002$). This may be an artefact due to the small amount of ash left, particularly in the bags in the watered plots, after the first retrieval. Similar to the results after three months, the decomposition rate of ash was faster in the interior than in the edge ($F_{1,8} = 26.771$, $P < 0.001$) and faster in the large mesh bags than in the small mesh bags ($F_{1,66} = 10.442$, $P < 0.001$).

For oak, the twelve-month decomposition results followed the pattern of the results after three months. There were no interactions between treatments and time of retrieval for oak (P -values > 0.1 in all cases). Decomposition rate was higher in the interior plots than in the edge plots ($F_{1,8} = 16.798$, $P = 0.003$), in watered plots than in the control plots ($F_{1,67} = 12.283$, $P < 0.001$) and in large mesh bags than in small mesh bags ($F_{1,67} = 116.900$, $P = 0.001$).

4. Discussion

4.1. Edge and moisture effects on leaf litter decomposition

To the best of our knowledge, this study is the first to experimentally investigate the effect of moisture conditions at the forest edge on the key ecosystem process of leaf litter decomposition. The results demonstrate that decomposition is faster in the interior of the forest compared to the edge, and that this is consistent with

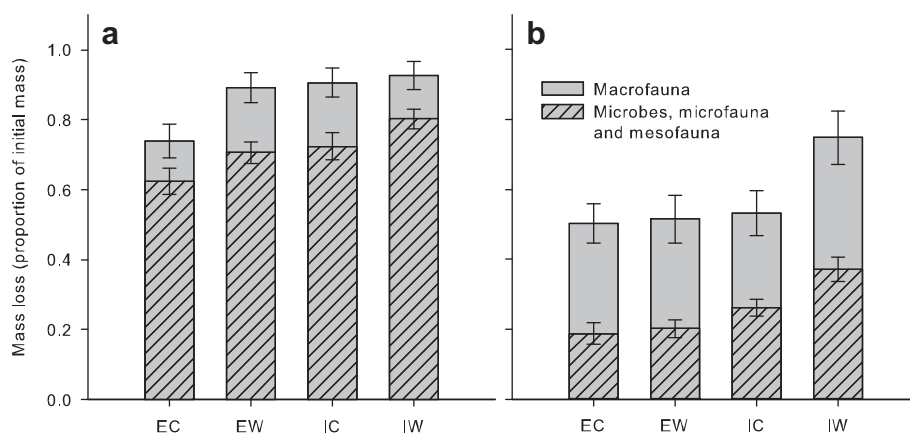


Fig. 3. The contribution of macrofauna and microbes, microfauna and mesofauna to leaf litter breakdown and decomposition of (a) ash and (b) oak in each treatment (EC – edge control, EW – edge watered, IC – interior control, IW – interior watered), measured as mass loss from leaf litter bags. Mass loss in small mesh bags is taken as an estimate of the contribution of the microbes, microfauna and mesofauna. The difference in mass loss between large and small mesh bags is taken as an estimate of the contribution of the macrofauna. Means \pm 1 SE, $n = 5$.

lower water availability at the forest edge. Watering throughout the summer increased litter mass loss at both the edge and interior compared to control plots, indicating that decomposition was moisture-limited at both the edge and interior of the forest. The summer of 2009 was wetter than average; thus our results show that moisture is a limiting factor for decomposition even during wet years. Although the moisture conditions in the watered plots at the edge of the forest never reached the levels in the forest interior the watering treatment does appear to have compensated for the edge effect, as the decomposition rates were similar in the watered edge and interior control plots. Our findings are consistent with several studies that have shown that low precipitation reduces the rate of mass loss of leaf litter (Austin and Vitousek, 2000; O'Neill et al., 2003; Taylor and Wolters, 2005; Staley et al., 2007), in part due to slower decomposition rate but also because leaching losses are lower in the absence of precipitation (Salamanca et al., 2003). A dry season irrigation experiment in Amazonia also showed that moisture deficits limited decomposition (Vasconcelos et al., 2007), however, abiotic edge gradients did not correlate with litter decomposition rates in studies at edges and interiors of other tropical forests (Didham, 1998; Vasconcelos and Laurance, 2005). Forest fragmentation was nevertheless found to increase the variability and unpredictability of litter decomposition rates at the forest edge and was slower in smaller fragments (Didham, 1998).

Many studies have failed to find a positive response of leaf litter decomposition to warming due to moisture being the limiting factor (see Aerts, 2006 for review). In this study we did not control for the effect of temperature between the forest edge and interior. However, weekly soil temperature measurements showed no difference between the edge and the interior plots or between the watered and the control plots. Thus, it is unlikely that the differences in decomposition were temperature driven, providing further support for the hypothesis that decomposition rates in this system were limited by moisture.

When generalising the results over wider landscapes, the differences between the forest edge and the interior has the potential to be even more pronounced than in this study, due to the possibility of more severe moisture deficits in south facing compared to north facing edges (Chen et al., 1993, 1995). However, previous work conducted in our study site on soil moisture and soil fauna feeding activity showed similar edge effects in both north and south facing edges (Simpson et al., 2012). An additional factor that our study did not consider is the possible difference in the litter

quality between the edge and the interior, due to a higher ratio of sun leaves at the forest edge, which in general decompose slower than shade leaves (Heath and Arnold, 1966; Sariyildiz and Anderson, 2003).

4.2. Macrofaunal effects on leaf litter decomposition

The presence of macrofauna accelerated the decomposition rate, but there was no effect of moisture treatment on macrofauna abundance or species richness. Moreover, the contribution of the soil macrofauna to litter mass loss was similar in the forest interior and edge, and also in the watered and control plots. This suggests that the moisture limitation of decomposition is not mediated by macrofauna, but is mainly driven by the changes in microbial and/or mesofauna activity. However, the macrofauna were particularly important in the decomposition of oak leaves, with 55% of the mass loss being attributable to the macrofauna. Faunal effects on decomposition have also been found in other studies to be strongest in species with more recalcitrant litter, such as *Quercus* species (Taylor et al., 1989; Gonzalez and Seastedt, 2001; Yang and Chen, 2009). Although ash decomposed faster than oak the majority of the mass loss of ash was due to microbial and/or mesofaunal decomposition. The faunal effect on leaf litter decomposition has been found to vary from 1.6% to 66% depending on litter type and climate (Gonzalez and Seastedt, 2001; Vasconcelos and Laurance, 2005).

Although woodlice and millipedes are known to be sensitive to temperature and moisture conditions (Sutton, 1980; David and Handa, 2010; Hassall et al., 2010), some experimental studies found soil fauna abundances to be relatively unaffected by moisture treatments (Taylor et al., 2004; Staley et al., 2007) and habitat fragmentation (David and Handa, 2010 and references therein) and noted that changes in responses to abiotic conditions may take several years (David et al., 1991). Previous studies on British millipedes and woodlice did not find consistent patterns between abundance and either rainfall or temperature (Brereton, 1957; Banerjee, 1967). There may be several reasons why we did not see any differences in soil macrofauna abundance and species richness between the edge and interior or with watering. It may be that woodlice and millipedes do not respond at the temporal and spatial scale at which the experiment was conducted. Woodlice and millipedes are thought to have relatively low dispersal abilities and many have life-cycles of several years (Brereton, 1957; David and

Handa, 2010), thus the duration of this experiment may have been too short to observe changes in abundance. Woodlice and millipedes have developed both behavioural and physiological adaptations to deal with short-term seasonally dry conditions; for example sheltering and aggregation behaviour, rolling into a ball, and reduced metabolism (Hassall and Tuck, 2007; David and Handa, 2010; Hassall et al., 2010). The summer of 2009 had higher rainfall than average, meaning that even the control plots received regular moisture and providing there were enough damper micro-habitats within drier plots in which to shelter abundances may not have been affected. Whether such adaptations will allow woodlice and millipedes to survive severe, prolonged periods of drought is unknown.

Resistance of macrofauna to desiccation differs among species and so changes in community composition are likely with changes in climate and at drier forest edges (David and Handa, 2010; Hassall et al., 2010). However, due to the low numbers of individuals and species collected we were unable to test for differences in macrofauna community composition between watering treatments or forest edge and interior. Thus, whether changes in abundance, species richness or composition of these macro-decomposers had an effect on decomposition rates could not be tested. In a study in Amazonian forests, however, differences in abundance, species richness and composition of soil invertebrates did not translate into altered decomposition rates, despite the key role they were found to play in the system overall (Vasconcelos and Laurance, 2005).

One of the biggest criticisms of litter bag experiments that use different mesh sizes to study the effects of arthropods on decomposition rates is that the difference between the decomposition rates in the treatments is not a pure arthropod effect but is the additive effect of the mesh size and the 'true' arthropod effect (Bradford et al., 2002; Kampichler and Bruckner, 2009). The mass lost from large mesh bags is thought to overestimate the actual mass lost through decomposition processes due to 'fall-through' of litter. However, it is assumed that any biases are standard across the plots, allowing direct comparisons between treatments and as such this method is considered adequate for studies comparing species, sites or experimental manipulations on decomposition (Wieder and Lang, 1982). Moreover, the loss of small fragments of litter from the mesh bags with large apertures, to which the macroarthropods have access, represents the effect of the macroarthropods, as their role in the decomposition process is as 'fragmenters'. Thus, following Bradford et al. (2002), we consider that mass loss from litter bags includes fragmentation of the litter as a functional role of macrofauna, facilitating litter movement down the soil profile, and as such is not an artefact of the litter bag technique. Moreover, as has been found in other studies (e.g. Taylor et al., 2004; Cotrufo et al., 2010) no significant interaction between mesh size and watering treatment was found indicating that the size of the mesh did not affect the moisture conditions inside the litter bags.

4.3. Implications for temperate forest ecosystem functioning

Our study emphasises the importance of moisture on decomposition processes, even when rainfall is relatively high, suggesting that altered moisture conditions related to habitat fragmentation or changes in climate will have a large impact on the functioning of forest ecosystems. Summer temperatures in the south of England are expected to rise by 2.2–6.9 °C and precipitation is likely to decrease in the summer and increase in the winter (Jenkins et al., 2009). The changes in summer precipitation are likely to have the strongest effect on decomposition, as moisture limitation overshadows the effect of increases in temperature (Aerts, 2006). Our study demonstrates the importance of the moisture conditions

through the edge effect: decomposition is markedly slower at the forest edge as a direct effect of water loss, and we predict that as a result the forest edges will be more susceptible to desiccation under current climate change scenarios. In regions where forests are highly fragmented, such as in large parts of the temperate zone, such edge effects must be taken into account if the aim is to quantify ecosystem processes, and the effect of climate change on them, at a landscape level.

Several studies have highlighted the differences in decomposition rates among litter species (Sariyildiz et al., 2005; Cornwell et al., 2008; Zhang et al., 2008; Roufied et al., 2010) and that interspecific differences in litter quality and decomposability may be larger than phenotypic responses to rising temperatures (Aerts, 2006). Our study shows that not only is the rate of decomposition species-specific, but that the role of soil organisms also varies between plant species. Therefore, changes in tree species composition and litter quality, either through forest management or in response to habitat fragmentation or climate, may have knock-on effects for the decomposer community. For example, changes in isopod densities and food preferences under elevated CO₂ have been shown to result in changes in rates of decomposition and nutrient mineralisation (Hättenschwiler and Bretscher, 2001; David and Handa, 2010).

This study demonstrates the effect of forest fragmentation on an important ecosystem process, providing new insights into the interacting effects of moisture conditions, litter quality, forest edge and soil macrofauna.

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