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Influence of fallen coarse woody debris on the diversity and community structure of forest-floor spiders (Arachnida: Araneae)

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ABSTRACT

Purely observational studies have documented differences in the abundance and diversity of several litter-dwelling arthropods between sites adjacent to, and far from, CWD, which suggests that reduction of fallen coarse woody debris (CWD) in temperate forests by traditional forestry practices may affect the litter arthropod community. As few field experiments have directly tested the impact of CWD on arthropods inhabiting the litter at different distances from CWD, we removed CWD from replicated open plots on the floor of a second-growth deciduous forest in order to reveal the causal connection between CWD and litter-dwelling spiders, often the most diverse and abundant predators among the litter macrofauna of temperate forests. We also documented the impact of the CWD manipulation on spider prey and several other major macroarthropod groups. Before removing CWD ($\varnothing = 14.3 \pm 0.7$ cm), we measured response variables as a function of distance (0.5–1.5 m) from CWD in both removal and control plots. In agreement with results of previous research that solely utilized this observational approach in temperate forests, volume and dry mass of litter, spider diversity, overall spider density, and densities of 8 of 16 major spider genera were higher adjacent to CWD before experimental manipulations. Removing CWD reduced the amount of litter and the density of spiders in litter close to where the CWD had been. Removing CWD also altered spider community structure, which had differed between litter sites adjacent to, and far from, CWD prior to the experimental removal of CWD. The patterns, though, were not completely congruent, as some of the taxa affected by the manipulation had not differed between sites prior to the removal of CWD, and vice-versa. Our findings suggest that complex interactions among structural, biotic and microclimatic factors underlie the observed responses to CWD removal by spiders and other arthropods in the litter layer. We also conclude that drawing inferences solely from observational studies is not a reliable approach for predicting the impact of changes in the amount of CWD on arthropods of forest-floor leaf litter. Further field experiments manipulating different volumes of CWD are needed in order to determine the minimum amount of CWD that should be kept on the forest floor of managed forests in order to maintain densities and diversities of major leaf-litter arthropods.

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1. Introduction

Managing the amount of fallen coarse woody debris (CWD) has implications for ecosystem functioning and also may be an essential element of conserving arthropod biodiversity in forests (Harmon et al., 1986; McMinn and Crossley, 1996; Vallauri et al., 2002; Mason et al., 2003; Tagliapietra, 2003; Matero and Saastamoinen, 2007).

Abbreviations: CWD, coarse woody debris.

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CWD usually is defined as all dead woody material more than 2.5–10 cm in diameter (Harmon et al., 1986; Enrong et al., 2006). In temperate forests CWD represents approximately half of the biomass of all fallen dead twigs, branches and trunks (pooled data from managed and old-growth forests [Chojnacky et al., 2004]); and more than two-thirds of the volume of all dead wood in harvested forests that have been allowed to regenerate for 40–70 years (Nordén et al., 2004a). CWD acts as a carbon sink (Manies et al., 2005; Woodbury et al., 2007), and immobilizes nutrients that are then gradually released to the soil (Idol et al., 2001; Hafner et al., 2005; Zhou et al., 2007). The importance of CWD for the conservation of saproxylic (dead-wood dependent) organisms is well established (Speight, 1989; McMinn and Crossley, 1996; Siitonen, 2001; Grove, 2002; English Nature, 2002; Mason et al., 2003; Tagliapietra, 2003; Nordén et al., 2004b; Vallauri et al., 2005;

Tikkanen et al., 2006). However, much less information exists on the impact of fallen CWD on the biological communities that inhabit the surrounding leaf litter.

Because of this gap in knowledge, recent research has focused on comparing the characteristics of the litter and associated fauna immediately adjacent to CWD with litter sites far from CWD. Litter adjacent to CWD is deeper (Marra and Edmonds, 1998), exhibits higher biomass (Kappes et al., 2006, 2007), has higher concentration of fine woody debris (Evans et al., 2003), and exhibits faster gross N mineralization rates (Spears et al., 2003). Litter adjacent to CWD has underlying soil with deeper organic horizons (Marra and Edmonds, 1998), different microclimatic conditions (Marra and Edmonds, 1998; Spears et al., 2003; Remsburg and Turner, 2006), and higher concentrations of water-soluble carbon (Spears et al., 2003) and several nutrients (Klinka et al., 1995; Kappes et al., 2006, 2007). Some studies have revealed that litter adjacent to CWD has higher densities of most arthropod taxa (Jabin et al., 2004; Ulyshen and Hanula, 2009a), and more diverse assemblages of Araneae (Varadi-Szabo and Buddle, 2006), and several major invertebrate taxa (Kappes, 2005, 2006; Topp et al., 2006a,b; Jabin et al., 2007; Kappes et al., 2007). In contrast, other research has found no differences between near and far litter sites in the diversity of most taxa (Marra and Edmonds, 1998; Andrew et al., 2000; Buddle, 2001; Déchêne and Buddle, 2010). This wide variability in the possible indirect effects of CWD on the fauna of surrounding litter may reflect differences between responses of various arthropod groups (Evans et al., 2003), or higher activity, rather than elevated densities, farther from CWD (Hanula et al., 2006, 2009). The sampling method may also affect the magnitude of the observed effects (Varadi-Szabo and Buddle, 2006).

Because removing CWD has been a widespread forestry practice, current levels of fallen CWD are usually far below natural levels in most of the world's managed forests (Siitonen, 2001; Butler et al., 2002; Vallauri et al., 2002). It has been hypothesized that the removal of CWD may profoundly affect forest-floor communities, which has led to proposing critical threshold densities of CWD on the forest floor (Müller et al., 2005; Kappes et al., 2009). Most studies of the impact of CWD on litter communities are purely observational. Two large-scale experiments carried out in loblolly pine forests (McCay et al., 2002; Hanula et al., 2006; Ulyshen and Hanula, 2009b) are an exception. One experiment revealed that removing dead wood leads to decreased activity of several arthropod taxa, a decrease in overall arthropod diversity, and changes in community composition (Hanula et al., 2006); in contrast, a later experiment (Ulyshen and Hanula, 2009b) found no effect of CWD removal on these variables.

Our study focused on spiders (Arachnida, Araneae) for several reasons. Spiders often are the most diverse and abundant taxa of the predator macrofauna in the litter layer of temperate forests (Blandin et al., 1980; Schaefer, 1991). They are sensitive to several types of environmental disturbances, leading to their being proposed as useful indicators for evaluating and monitoring the impacts of silvicultural practices (Pearce and Venier, 2006). Structural features of the litter can have large impacts on spider communities (Uetz, 1975, 1976, 1979, 1991; Stevenson and Dindal, 1982; Bultman and Uetz, 1982, 1984), as can changes in the abundance of major arthropod prey, such as Collembola and Diptera (Chen and Wise, 1999). Litter spiders can have major impacts on forest-floor food webs by depressing densities of major detritivores such as Collembola (Wise, 2004; Miyashita and Niwa, 2006), thereby indirectly altering rates of litter decomposition (Lawrence and Wise, 2000, 2004; Lensing and Wise, 2006).

Research to date suggests that the overall density of litter spiders is higher closer to CWD (Evans et al., 2003; Jabin et al., 2004; Varadi-Szabo and Buddle, 2006; Ulyshen and Hanula, 2009a). A coniferous forest was found to display a similar, but statistically

non-significant, trend (Marra and Edmonds, 1998). Pitfall trapping has not revealed differences in overall spider activity-density, although some taxa are trapped more frequently closer to CWD (Buddle, 2001; Hanula et al., 2006, 2009). Spider diversity measured by pitfall traps (Buddle, 2001) and litter sifting (Varadi-Szabo and Buddle, 2006) has also been observed to be higher closer to CWD, but only the last method yielded statistically significant results. To date, analyses of differences in community composition (i.e. identity of taxa, not richness or patterns of abundance) have been based only on pitfall-trap sampling, and no significant differences have been found (Buddle, 2001; Varadi-Szabo and Buddle, 2006). Pearce et al. (2004) found both negative and positive correlations of activity-density with the density of fallen CWD for several spider taxa. Another correlative study found that species richness of forest specialists was positively related to CWD cover, whereas the opposite correlation was found for species that prefer open spaces (Oxbrough et al., 2005). These studies have all been purely observational. With the exception of the aforementioned experiments in pine forests, intentional manipulation of CWD in replicated forest plots has not been utilized as a way to understand how CWD affects leaf-litter spiders.

Therefore, we conducted a field experiment by removing all CWD from replicated plots, and then comparing spider activity-densities, absolute densities, taxonomic diversity, and community structure in removal and non-manipulated control plots. Prior to manipulating CWD, we sampled spider densities and activity-densities adjacent to, and far from, CWD, in order to compare patterns with published results, and to strengthen the interpretation of changes caused by removing CWD. We also documented the impact of the CWD manipulation on two groups of spider prey, Collembola and Diptera (Foelix, 1996), and on other major groups of macroarthropods.

2. Methods

2.1. Study site

The experiment was conducted in the Berea College Forest (Madison County, Kentucky, USA), in a secondary oak-maple-hickory forest with scattered pine trees located at 37°34'N and 84°13'W ca. 285 m above sea level. Much of the forest had been cleared for grazing and farming prior to its acquisition by Berea College (Perry, 2000). Portions of the secondary forest that developed after the initial clearing were selectively logged 30–40 years ago, with the area in which our study was conducted (Horse Cove) not having been logged extensively for at least 70 years [John Perry (Berea College forester), personal communication]. Soils are primarily silt loams consisting of four series (Captina, Rockcastle, Shelocta, and Weikert), all of which are well-drained and acidic (USDA Soil Conservation Service, 1973). Mean annual temperature is 13 °C with a maximum average temperature in July of 23.9 °C and a minimum average temperature in January of 1.7 °C. Total mean annual precipitation is 1188 mm. June is the wettest month with 120.5 mm of rainfall on average, and October is the driest with an average of 70.6 mm (Kentucky Climate Center Data, <http://kyclim.wku.edu>).

Before setting up the experiment we estimated the density of CWD in our study area. In the autumn of 2005 we randomly located thirty 50-m transects throughout approximately 75 ha of forest in Horse Cove, and then used the Line Intercept Sampling method (LIS; Marshall et al., 2000) to estimate the density of fallen CWD. The average volume of fallen CWD ($\varnothing > 5$ cm) was estimated to be $32.6 \pm 4.7 \text{ m}^3 \text{ ha}^{-1}$, which is within the range expected for a broadleaf forest with patches around 45–100 years old (Vallauri et al., 2002).

2.2. Experimental design

All woody debris with a maximum diameter > 5 cm was considered CWD. This threshold was selected after a survey of the density and frequency of all size classes of fallen dead wood in this forest (Castro and Wise, 2009) revealed that CWD > 10 cm, the more frequently used threshold for CWD (Enrong et al., 2006), was not sufficiently abundant for executing a properly replicated experiment.

We selected twenty-two 12 × 12-m open plots at least 30 m apart that we judged to contain similar amounts of CWD. Before initiating the experiment we counted and measured all the fallen CWD > 5 cm inside all plots in order to determine the actual pattern. We then randomly assigned each plot to either a Removal or Control treatment (11 replicates/treatment). All CWD was removed from the Removal plots 4–10 August 2006. Because CWD continually falls onto the forest floor, CWD was taken from the Removal plots again on 3 November and 15 December, and in 2007 on 23 February, 30 May and 17 July. Because removing CWD can be disruptive to the litter, a similar disruption was simulated by walking through the Control plots on each date CWD was taken from the Removal plots.

2.3. Sampling techniques

Response variables (densities and/or activity-densities of spiders and their potential prey) were measured twice before manipulation of CWD commenced (initial conditions), and three times post-CWD removal. Initial conditions were evaluated in spring and summer of 2006. Post-manipulative estimates were made two months after initial CWD removal in August 2006 in order to check for short-term effects, and after 8 and 12 months (spring and summer of 2007) to detect longer-term effects. Samples were taken in a 10 × 10-m central area inside the plot in order to reduce possible edge effects. Four different sampling techniques were used:

2.3.1. Litter extraction

Used to estimate densities of Collembola and to obtain accurate estimates of densities of smaller spiders (carapace length < ca. 1.1 mm). Two 0.05-m² samples of leaf litter (upper and fragmented layers, not including the humus) from each plot were placed for 1 week in a temperature-humidity extraction apparatus (Kempson et al., 1963). Invertebrates were first extracted into 50% ethylene glycol, then washed and finally stored in 70% EtOH for later identification and counting. Litter-extraction samples were taken 9 May, 14 July and 13 October 2006, and 21 March and 30 July 2007. The litter was weighed after animals had been extracted.

2.3.2. Litter sifting

For larger spiders (carapace length > 1.1 mm), estimating population density by litter extraction is not as accurate as sifting and searching the litter in the field (Chen and Wise, 1999). Therefore, two 0.2-m² litter samples per plot were taken 23 May–3 June, 24 July–1 August, and 6–16 October in 2006; and 30 March–17 April and 2–9 August 2007. Encountered spiders were collected with a manual aspirator and preserved in 70% EtOH. Mass and volumes of leaf litter, and volume of fine woody debris, were determined for pre-treatment samples. Because there were no statistically significant differences in initial amounts of fine woody debris in Control and Treatment plots, this variable was not measured after treatment because its measurement is so time consuming.

2.3.3. Pitfall traps

Used to estimate activity-density of spiders. Traps were made of plastic cups 8.5 cm in diameter and 11-cm deep inserted in a plastic

sleeve and covered when not in use, two traps per plot. Traps were open and filled to a depth of ~5 cm with ethylene glycol diluted 50% with water during the following periods: 12–16 May, 15–20 July and 5–12 October 2006; and 22–26 March and 3–8 August 2007.

2.3.4. Sticky traps

Used to estimate the activity-density of potential insect prey active immediately above the litter layer (Diptera and Hymenoptera). Traps (Chen and Wise, 1999) were vertically oriented 10 × 10-cm pieces of metal insect screening coated on both sides with a tree-banding compound (Tanglefoot Company, Grand Rapids, Michigan, USA). Two sticky traps, set parallel to each other and perpendicular to a piece of CWD, were placed on each plot for 24 h. Traps were set 19 May and 18 July 2006, and 18 March and 31 July 2007. Sticky traps were not used in the third sampling period because cool temperatures in the autumn reduce activity of most flying insects.

2.3.5. Location of the samples

For each sampling technique the two samples taken per plot on each sampling occasion were paired samples. One sample (the “focal” sample) was taken immediately adjacent to a piece of CWD; the other sample was taken 50–150 cm from the focal CWD. The distance separating the paired samples varied between plots because the second sample was located as far as possible from the focal CWD and other pieces of CWD in the plot. This sampling procedure was followed in the Removal plots even after the CWD had been removed, made possible because the location of each removed piece of CWD was marked by flags. Pitfall and sticky traps remained in the same location throughout the experiment. Other types of samples were taken at different locations but the same near-far separation was maintained. The average diameter of pieces of CWD where the focal samples were taken was 14.3 ± 0.7 cm (14.6 ± 1.2 cm for Removal plots, and 14.0 ± 0.7 for Control plots). All pieces were in Stage II or III of decomposition (Marshall et al., 2000).

2.4. Identification of spiders

Spiders were identified to genus following the keys and nomenclature of Ubick et al. (2005). Accurate spider identification to species level usually requires adult specimens with developed genitalia. Because juveniles accounted for two-thirds of all spiders in the samples, individuals were not identified to species level in order to avoid a considerable loss of information. Because juveniles can usually be identified to genus, several abundant genera that were represented by two or more species (*Phrurotimpus*, *Drassyllus*, *Schizocosa*, *Agyrota*) could be identified accurately to genus but not to species. In all samples combined, 96% of all spiders were identified to genus level, yielding a negligible loss of information in terms of individuals collected.

2.5. Statistical analyses

2.5.1. Overview

Several specific requirements motivated the statistical approaches taken: (1) incorporating initial conditions (obtained by pooling data for the two sampling dates prior to CWD removal) into the analysis of how removing CWD affects litter arthropods; (2) determining differences in arthropod populations in litter adjacent to, and far from (i.e., not immediately adjacent to) CWD in non-manipulated plots (“distance effect”); (3) evaluating the impact of removing CWD on densities and activity-densities of specific arthropod taxa, spider diversity, and spider community composition as a function of distance from CWD in order to (a)

uncover how the presence of CWD directly impacts litter-dwelling arthropods, and (b) to interpret more fully any “distance effects” uncovered by the pre-manipulation sampling. Thus, a range of statistical tests was employed, briefly summarized below.

2.5.2. Student's *t*-test

Used to test for initial differences between Control and Removal plots in several CWD properties: total volume, number of pieces, and fraction of forest floor covered.

2.5.3. Paired-treatment (“repeated-measures”) ANOVA on initial conditions

In these analyses the within-subject factor is the distance (close or far) of the sample from CWD within the plot; the between-subject factor reflects any statistically significant initial difference between Control and Removal treatment plots (not yet manipulated). A significant distance effect would be consistent with two categories of hypothesis: CWD only affects either the adjacent or “distant” litter community, or that there are effects both near and far that differ in sign and/or magnitude. A treatment effect would reveal an initial bias between Control and Removal plots that would have to be taken into account when analyzing the impact of the experimental manipulation of CWD. If the distance by treatment interaction was statistically significant, planned contrasts were conducted to reveal the nature of the initial bias. This statistical model was used to analyze the following variables: litter mass and volume; fine woody debris volume; abundances of major arthropod taxa and major spider genera; and four estimators of spider diversity.

2.5.4. Repeated-measures MANOVA

Because initial values of some response variables differed significantly ($P < 0.05$) between Control and Removal plots, the criterion for a significant effect of removing CWD was the P value of the time \times treatment interaction term in a repeated-measures multivariate analysis of variance (rm-MANOVA; two within-subject factors – distance and time). Planned-comparisons contrasts were performed to analyse (a) the treatment effect through time for each level of the factor “distance from CWD” and (b) the change over time in the distance effect for each treatment level (i.e. CWD Removal or Control). If significant results were found, *a posteriori* contrasts were performed to elucidate on which date(s) the differences were statistically significant. Low counts for some response variables [Rarefied taxonomic richness, Diplopoda and Hymenoptera densities (Kempson samples), activity-densities of major taxa of flying insects (sticky traps) and several major spider genera (pitfall traps)] dictated that we pool the last two sampling dates. Densities estimated from litter-sifting samples of sixteen spider genera (87% of all spiders collected) were analyzed using this model because they exhibited a low number (<one-third) of sampling units with zero values; these genera also were those with densities $> 1 \text{ m}^{-2}$. Repeated-measures ANOVA was also performed for spider genera that met this condition in Kempson (litter extraction) samples and pitfall traps, but these results are more limited because a lower number of genera could be included in the statistical analyses.

2.5.5. Estimators of spider diversity

Four indices – Taxonomic Richness, Shannon Index, Simpson Index (expressed as its complement), and rarefied taxonomic richness (standardized to the least number of individuals observed in the less numerous sample) – were selected as descriptors of spider diversity because of their widespread use, well-known properties, and the complementary information that they provide (Magurran, 2004). The first three indices indicate diversity density (per sample or unit area), and the last one taxa richness (Gotelli and

Colwell, 2001). The analysis of spider diversity was based on the litter-sifting samples because this sampling technique yielded the greatest range of taxa, was less biased towards any specific taxon, and resulted in the highest number and frequency of specimens collected.

2.5.6. Composition and structure of the spider community

Effects of CWD removal on spider community composition and structure were tested by analyzing data from sifting samples, for the same reasons that these samples were used to examine effects on spider diversity. Treatment effects were evaluated by comparing pre-treatment (initial conditions) with post-treatment [last two sampling dates (year 2007) pooled] communities. The small numbers of many of the major taxa on single sampling dates made pooling of the last two sampling dates necessary in order to satisfy assumptions, and to increase the power, of the statistical tests employed. Changes in community composition (i.e. simple membership in the community) were estimated by means of Jaccard's coefficient, and changes in community structure (i.e. relative abundances of each species) by using the Bray-Curtis coefficient (Legendre and Legendre, 1998; Magurran, 2004). In order to visualize changes in community composition, principal coordinates diagrams were created for pre- and post-treatment communities [PCO (Principal Coordinates Analysis)] ordination using the PAST statistical package (version 1.81; Hammer et al., 2001). Statistical significance of apparent changes due to removing CWD was evaluated by permutational analysis of variance (PERMANOVA; Anderson, 2001, 2005) for treatment effects. The DISTLM extension of the PERMANOVA package (distance-based multivariate analysis for a linear model; McArdle and Anderson, 2001; Anderson, 2004a) was used to analyze differences associated with distance from CWD because this extension of PERMANOVA accommodates within-subject designs.

2.5.7. Data structure

For all statistical analyses the initial condition of each variable was defined as the average of the values for the two pre-treatment sampling dates. Statistical analyses based upon Kempson extractions and litter sifting were conducted on the “raw” values, and then repeated with values expressed per unit litter mass or per unit litter volume, respectively; the results of the second analysis are reported only when they differ from the analysis based upon simple counts. Data were log-transformed when necessary to satisfy assumptions of homoscedasticity, multivariate normality, and homogeneity of covariances (multivariate analysis). Because PERMANOVA is sensitive to differences in dispersion among groups, PERMDISP (Anderson, 2004b) was used to test for differences in multivariate dispersion; no statistically significant differences were found. All *t*-tests and repeated-measures analyses were performed with STATISTICA 6.0. (Statsoft, 2001). Unless stated otherwise, results are presented as mean \pm standard error.

3. Results

3.1. Initial amounts of CWD

CWD parameters were similar between assigned treatments before CWD removal commenced. Initial conditions of several parameters characterizing Removal and Control plots, respectively, were: volume – 30.0 ± 3.0 and $27.6 \pm 2.3 \text{ m}^3 \text{ ha}^{-1}$ ($t_{20} = -0.63$, $P = 0.534$); number of pieces per plot – 36.3 ± 2.8 and 38.8 ± 2.7 ($t_{20} = 0.65$, $P = 0.521$); and percentage of forest floor covered by CWD – 3.4 ± 0.1 and 3.5 ± 0.1 ($t_{20} = 0.89$, $P = 0.383$). The mean volume per unit area of CWD was close to that estimated by the LIS method (Methods section).

3.2. Effects of CWD on leaf litter biomass and volume

3.2.1. Proximity to CWD: “Distance Effect” for initial conditions

Before CWD was removed, litter dry mass was 1.3x greater, and litter volume was 1.2x greater, closer to CWD in both Removal and Control plots [Table 1; $P(F_{1,20}; \text{distance})'s < 0.001$ for both response variables in Control and Removal plots). The magnitude of the distance effect did not differ between Removal and Control plots for litter mass or volume [$P(F_{1,20}; \text{treatment} \times \text{distance interaction})'s > 0.87$]. In contrast to the distance effects for leaf litter, the volume of fine woody debris did not vary with distance from CWD [$P(F_{1,20}) = 0.27$].

3.2.2. Removal of CWD

Removing CWD reduced both the mass and volume of leaf litter adjacent to CWD [Table 1; $P(F_{3,18}; \text{treatment} \times \text{time interaction})'s = 0.068, 0.013$, respectively]. Removing CWD had no effect on litter mass or volume for sites far from CWD [$P(F_{3,18}; \text{treatment} \times \text{time interaction})'s > 0.22$].

The distance effect for litter dry mass and volume remained constant throughout the experiment in Control plots ($P_s > 0.38$ for rm-MANOVA, multivariate test for planned contrasts of date \times distance interaction). In Removal plots the starting differences in litter volume between adjacent and far sites disappeared after the first CWD removal (multivariate $F_{3,18} = 5.19, P = 0.009$). A similar but slightly weaker pattern occurred for litter dry mass by the first post-treatment date (univariate contrast $F_{1,20} = 4.22, P = 0.053$) and at the end of the experiment ($F_{1,20} = 4.39, P = 0.049$).

3.3. Effects of CWD on density and activity-density of spiders, genera pooled (“total spiders”)

3.3.1. Overall catch

5113 spiders representing 29 families and 81 genera were collected, from which 3365 individuals from 66 genera were obtained by litter sifting, 1081 individuals from 7 genera by Kempson samples and 667 individuals representing 51 genera by pitfall traps

3.3.2. Proximity to CWD: “Distance Effect” for initial conditions

In the litter-sifting samples, total spider density was 1.8x and 1.5x higher in litter adjacent to CWD than in litter farther away in Control ($F_{1,20} = 37.78, P < 0.001$) and Removal plots ($F_{1,20} = 10.39, P = 0.004$), respectively. The distance \times treatment interaction ($F_{1,20} = 4.27, P = 0.052$) suggests that the magnitude of the distance effect differed initially between Control and Removal plots, before CWD was removed from the latter. Nevertheless, there was a clear interaction effect, as initial differences between treatments in litter samples taken adjacent to CWD were clearly different ($F_{1,20} = 8.51, P = 0.009$), whereas there were no treatment difference for sites far from CWD ($F_{1,20} = 0.33, P = 0.574$) (Table 1). The distance effect disappeared in the Removal plots when total spider density was corrected for litter volume ($F_{1,20} = 2.13, P = 0.160$), whereas control plots exhibited a clear effect of distance from CWD on total number of spiders per unit of litter volume ($P < 0.001$). The Kempson samples exhibited higher densities of spiders close to CWD only in Removal plots, but the magnitude of the effect was less pronounced (Table 1; $F_{1,20} = 3.12, P = 0.092$). In contrast to these patterns, activity-density of spiders estimated from pitfall trapping did not exhibit any correlation with distance from CWD (Table 1).

3.3.3. Removal of CWD

In the litter-sifting samples, removing CWD had no effect on total spider density far from CWD, but did affect spider numbers in litter near CWD (Table 1). The difference between Control and Removal treatments in spider density in litter adjacent to CWD

Table 1

Variation in the mass (dry weight; 0.05–m² Kempson samples) and volume (0.2–m² sifting samples) of litter; density (estimated by sifting and Kempson methods) and activity-density (pitfall traps) of spiders, and three diversity indices throughout the experiment. Statistically significant ($P < 0.05$) and marginally significant ($P < 0.10$) F values for the date \times treatment interaction (rm-MANOVA) are indicated in bold (last column). Asterisks indicate on which dates the difference between Removal and Control differed significantly from the difference for initial conditions (* $P < 0.05$, ** $P < 0.01$).

		Initial Conditions				Second post-treatment date		Third post-treatment date		Time \times treatment interaction			
		Removal		Control		Removal	Control	Removal	Control	$F_{3,18}$	P		
		Far	Close	Far	Close	Far	Close	Far	Close				
Litter weight g sample ⁻¹		44 ± 2	56 ± 4	41 ± 2	54 ± 3	31 ± 2	36 ± 4	31 ± 2	35 ± 3	34 ± 2	39 ± 3	1.62	0.220
Kempson samples						29 ± 2*	45 ± 4	42 ± 3*	42 ± 3*	33 ± 3	47 ± 4	2.82	0.068
Litter volume dm ³ sample ⁻¹		11.5 ± 0.7		11.4 ± 0.8		9.3 ± 0.6	10.1 ± 0.4	14.5 ± 0.6	13.9 ± 0.6	12.4 ± 0.7	12.8 ± 0.8	0.95	0.439
Sifting samples		14.0 ± 0.6		13.9 ± 0.7		8.9 ± 0.4	10.8 ± 0.6	13.2 ± 0.6*	16.0 ± 0.6*	11.0 ± 0.7**	14.2 ± 0.5**	4.29	0.013
Spiders m²		53 ± 8		60 ± 8		76 ± 10	82 ± 14	52 ± 6	63 ± 6	69 ± 9	83 ± 15	0.05	0.984
Sifting samples		78 ± 8		106 ± 5		59 ± 10**	145 ± 19**	47 ± 9	84 ± 11	53 ± 6*	122 ± 18*	3.68	0.032
Spiders m²		66 ± 8		73 ± 9		96 ± 17	96 ± 17	76 ± 13	85 ± 19	111 ± 26	129 ± 23	0.07	0.977
Kempson samples		92 ± 11		85 ± 8		147 ± 23	169 ± 21	95 ± 25	116 ± 10	85 ± 10	125 ± 22	0.72	0.551
Spiders trap⁻¹		2.5 ± 0.4		3.5 ± 0.5		1.4 ± 0.5	1.2 ± 0.3	4.0 ± 0.6	5.8 ± 0.6	2.6 ± 0.5	3.2 ± 0.4	0.36	0.781
Pitfall samples		3.4 ± 0.4		3.3 ± 0.4		0.8 ± 0.2	1.7 ± 0.4	3.9 ± 0.7	5.0 ± 0.7	2.7 ± 0.5	3.0 ± 0.5	1.21	0.336
Number of genera		6.1 ± 0.7		6.2 ± 0.5		8.5 ± 0.9	7.9 ± 0.9	6.4 ± 0.8	7.5 ± 0.7	7.5 ± 0.7	8.4 ± 0.9	0.35	0.790
Sifting samples		6.9 ± 0.5		9.7 ± 0.4		7.3 ± 1.1	11.5 ± 0.8	6.1 ± 0.9	7.5 ± 0.7	6.7 ± 0.5	10.7 ± 0.9	1.41	0.273
Shannon Index		1.58 ± 0.12		1.62 ± 0.07		1.92 ± 0.12	1.77 ± 0.15	1.63 ± 0.18	1.80 ± 0.10	1.84 ± 0.08	1.93 ± 0.14	0.40	0.752
Sifting samples		1.66 ± 0.08		2.04 ± 0.05		1.73 ± 0.15	2.11 ± 0.07	1.57 ± 0.14	1.71 ± 0.09	1.79 ± 0.07	2.10 ± 0.08	0.48	0.700
Simpson Index		0.74 ± 0.04		0.77 ± 0.01		0.81 ± 0.03	0.77 ± 0.04	0.74 ± 0.07	0.80 ± 0.02	0.81 ± 0.01	0.82 ± 0.03	0.52	0.672
Sifting samples		0.76 ± 0.02		0.84 ± 0.01		0.78 ± 0.03	0.84 ± 0.01	0.74 ± 0.04	0.77 ± 0.02	0.81 ± 0.01	0.84 ± 0.01	0.76	0.533

increased after CWD had been removed. When data for sifting samples were analysed as number of spiders per unit volume, the treatment effect for litter adjacent to CWD remained only for the first post-treatment date ($F_{1,20} = 6.92, P = 0.016$). There is no hint of an effect of CWD removal on total spider density for either Kempson samples or pitfall traps (Table 1).

The distance effect did not change over time in Control plots in either sifting, Kempson or pitfall samples (distance \times date interaction $P_s > 0.22$). However, in litter-sifting samples in Removal plots, the difference in spider density between near and far samples weakened after CWD-removal (multivariate $F_{3,18} = 2.70, P = 0.076$). Separate univariate distance \times date interactions for the three post-treatment dates were consistently close to statistical significance at the 0.05 level ($F_{1,20} = 3.88, P = 0.063$; $F_{1,20} = 4.04, P = 0.058$; and $F_{1,20} = 5.19, P = 0.034$; for first to final post-treatment dates, respectively). In the Removal plots there were no changes over time in distance effects for either Kempson or pitfall-trap samples ($P_s > 0.22$).

3.4. Effects of CWD on diversity of spiders

3.4.1. Proximity to CWD: "Distance Effect" for initial conditions

In Control plots, spider diversity was higher in litter adjacent to CWD as measured by genera richness [1.6x; $P(F_{1,20}) < 0.001$], the Shannon Index [1.3x; $P(F_{1,20}) < 0.001$], and the Simpson Index [1.1x; $P(F_{1,20}) = 0.036$] (Table 1). Although these diversity indices initially were also ~ 1.1 x higher near CWD in the Removal plots, apparent distance effects were not statistically significant [$P(F_{1,20})'s > 0.23$]. Genera richness, standardized to individuals, exhibited distance effects only in Removal plots (adjacent - 5.43 ± 0.21 , far - 5.91 ± 0.08 ; distance \times treatment interaction $F_{1,20} = 6.08, P = 0.023$).

Congruent with the above pattern, separate univariate ANOVAs showed that Control and Removal plots differed initially for genera richness ($F_{1,20} = 19.73, P < 0.001$), the Shannon index ($F_{1,20} = 14.92, P < 0.001$), and the Simpson Index ($F_{1,20} = 11.54, P = 0.003$) in sites

adjacent to CW. Litter far from CWD showed no differences between treatments ($P_s > 0.18$).

3.4.2. Removal of CWD

No significant effects on genera richness, the Shannon Index or the Simpson Index were detected when the CWD-treatment effect was examined for samples that were the same distance from CWD [$P(F_{3,18})'s$ for treatment \times time interaction > 0.27] (Table 1). However, removing CWD affected rarefied genera richness (post-treatment dates pooled, distance \times date \times treatment interactions $F_{1,20} = 1.25, P = 0.006$) by increasing the number of genera in litter close to CWD in Removal (6.09 ± 0.23) compared to Control (5.69 ± 0.16) plots ($F_{1,20} = 6.61, P = 0.018$).

In the Removal plots the relationship of rarefied genera richness between litter located far and close to CWD changed from 1.09x in initial conditions to 0.97x after CWD removal (both post-treatment dates pooled, distance \times date interaction $F_{1,20} = 5.68, P = 0.027$). All other spider diversity indices exhibited no shifts in distance effects in either Control or Removal plots (multivariate planned contrasts, distance \times date interaction $P_s > 0.12$).

3.5. Effects of CWD on the composition and structure of the spider community

3.5.1. Proximity to CWD: "Distance Effects" for initial conditions

Within both Removal and Control plots, spider communities initially differed in both composition and structure as a function of distance of the litter from CWD (Removal plots - Jaccard's *Pseudo* $F_{1,10} = 2.43, P = 0.004$, Bray-Curtis's *Pseudo* $F_{1,10} = 2.92, P = 0.004$; Control plots - Jaccard's *Pseudo* $F_{1,10} = 2.09, P = 0.011$; Bray-Curtis's *Pseudo* $F_{1,10} = 2.38, P = 0.008$).

3.5.2. Removal of CWD

Principal coordinates ordination (PCO) based on Bray-Curtis dissimilarities reveals a quantitative change in the structure

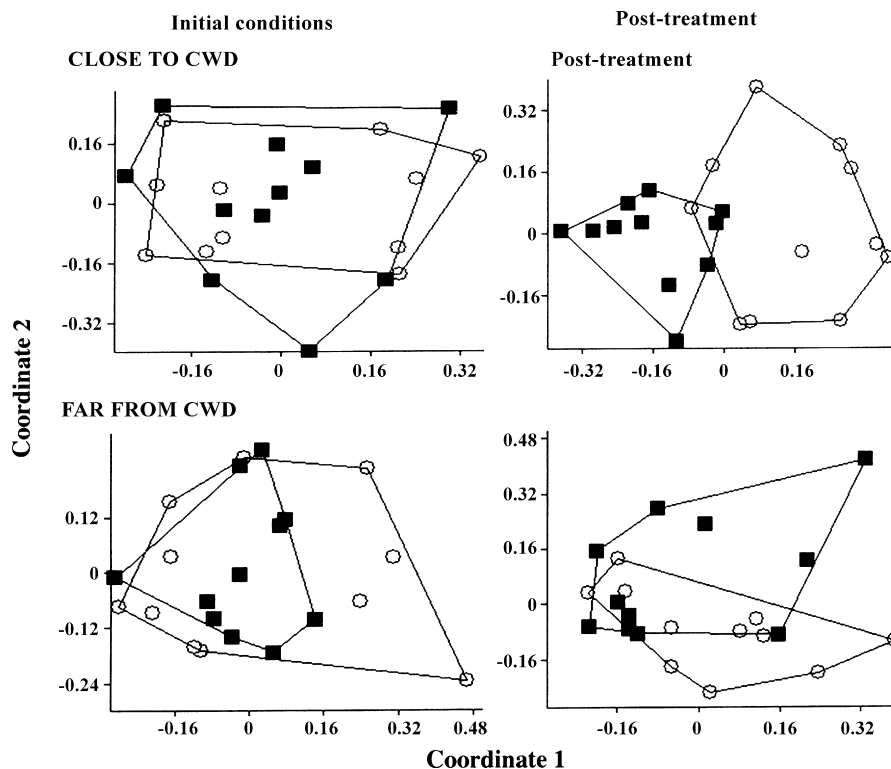


Fig. 1. Changes in community composition (Bray - Curtis distance) of spiders displayed by principal coordinates ordination. Data displayed come from the two first pretreatment (left) and the two last post-treatment (right) dates. Symbols: (■) - Control plots, (○) - Removal plots.

of the litter spider community between initial and post-CWD removal conditions (Fig. 1). This shift occurs primarily because of changes in the spider community in litter close to CWD. PERMANOVAs for Bray-Curtis dissimilarity show an effect close to the $P=0.05$ level of CWD-removal for samples far from CWD ($Pseudo-F_{1,21} = 1.64, P=0.055$), but a highly significant effect for litter close to CWD ($Pseudo-F_{1,21} = 4.35, P<0.001$); no differences were observed between Control and Removal plots in initial conditions ($P_s > 0.28$). Analysis of Bray-Curtis dissimilarity for data expressed as spiders per unit volume shows a similar pattern. An analysis based on Jaccard dissimilarities reveals a parallel shift in the “qualitative structure” – the composition by genera – of the spider community. For litter close to CWD, there is a clear change in community composition between initial ($Pseudo-F_{1,21} = 1.03, P=0.43$) and post-CWD removal ($Pseudo-F_{1,21} = 2.13, P=0.006$) conditions. In contrast, litter samples far from CWD exhibit no qualitative changes in the community, as Control and Removal plots differed neither for initial ($Pseudo-F_{1,21} = 1.06, P=0.40$), nor post-CWD removal ($Pseudo-F_{1,21} = 1.34, P=0.15$) conditions.

After the date on which CWD was removed from the Removal treatment, distance effects on both community composition and community structure remained statistically significant in Control plots (Jaccard's $Pseudo F_{1,10} = 1.76, P=0.027$, Bray-Curtis's $Pseudo F_{1,10} = 2.32, P=0.012$). In contrast, the original differences in community composition and structure between near and far litter samples disappeared in the Removal plots (Jaccard's $Pseudo F_{1,10} = 1.49, P=0.12$; Bray-Curtis's $Pseudo F_{1,10} = 1.41, P=0.18$).

3.6. Effects of CWD on abundances of major spider genera

3.6.1. Proximity to CWD: “Distance Effect” for initial conditions

Six spider genera emerged as having been initially more abundant near fallen CWD ($P(F_{1,20})'s < 0.050$) in either Control (*Cicurina*, *Agyseta*), Removal (*Origanates*) or both plots (*Lepthyphantes*, *Phrurotimpus*, *Anahita*). Results are also statistically significant ($P<0.05$) for all these genera when numbers are expressed per unit volume of litter (with the exception of *Origanates*, for which the P value for pooled samples increases to 0.098). Two genera showed possibly negative effects of CWD, but only in one treatment ($P_s > 0.035$; Table 2).

Data from Kempson (number m^{-2} and also number per unit litter weight) and pitfall trap samples were adequate for evaluating the possible effect of distance from CWD for *Cicurina*, *Origanates*, *Lathys*, *Phrurotimpus*, *Drassyllus*, *Schizocosa* and *Xysticus*. No F values were close to statistical significance ($P_s > 0.11$) except for *Origanates* Kempson samples [$P=0.059$ (number m^{-2})].

3.6.2. Removal of CWD

The complex pattern of responses to CWD removal by major genera in the sifting samples (Table 3) is best understood by first focusing on the responses of the three genera that exhibited the clearest effects of distance from CWD before CWD was removed (*Phrurotimpus*, *Anahita* and *Lepthyphantes*; preceding section and Table 2). Among these genera only the two cursorial spiders, *Phrurotimpus* and *Anahita*, responded to CWD removal, and only in litter adjacent to CWD ($P_s < 0.044$; Table 3). Their densities in the Close samples decreased over time in the Removal plots compared to the Control treatment. Densities of the web-builder *Titanoeca* also clearly declined with respect to Control plots in the Close samples ($P=0.004$; Table 3), although this spider exhibited no hint of an effect of distance from CWD under initial conditions (Table 2). The cursorial genus *Xysticus*, which also exhibited no distance effect from CWD (Table 2), exhibited a positive, not negative, response to the removal of CWD in the Close samples (Table 3). In contrast to these genera, *Ariadna* and *Gnaphosa* responded more clearly to CWD removal in the Far, not Close, samples (Table 3),

Table 2

Effect of distance from CWD on densities (no. m^{-2} in litter-sifting samples) of major spider genera based upon rm-ANOVA before CWD removal (initial conditions). Differences between close and far litter samples with $P<0.05$ are marked in bold (no values fell between 0.10 and 0.05). “Cursorials” are spiders that do not use webs to capture prey.

Genera	Plots	Close-Far differences (no. m^{-2})	Distance effect	
			$F_{1,20}$	P
Web-builders				
<i>Cicurina</i>	Removal	1.1 ± 0.9	1.77	0.198
	Control	2.3 ± 0.8	7.09	0.015
<i>Lathys</i>	Removal	−0.9 ± 2.4	0.09	0.762
	Control	4.1 ± 3.4	1.91	0.183
<i>Ceratinopsis</i>	Removal	−0.7 ± 1.0	0.29	0.598
	Control	−0.2 ± 1.4	0.03	0.860
<i>Origanates</i>	Removal	7.7 ± 3.5	4.40	0.049
	Control	3.9 ± 3.9	1.10	0.307
<i>Tapinocyba</i>	Removal	0.7 ± 0.9	0.60	0.448
	Control	1.6 ± 1.1	2.41	0.136
<i>Agyseta</i>	Removal	1.8 ± 1.7	1.38	0.254
	Control	4.3 ± 1.4	7.78	0.011
<i>Lepthyphantes</i>	Removal	2.0 ± 1.1	4.79	0.041
	Control	3.4 ± 1.1	8.88	0.007
<i>Ariadna</i>	Removal	−2.3 ± 0.9	5.04	0.036
	Control	1.8 ± 1.5	0.96	0.339
<i>Titanoeca</i>	Removal	0.7 ± 1.4	1.07	0.313
	Control	−0.9 ± 1.4	0.01	0.929
Cursorials				
<i>Phrurotimpus</i>	Removal	11.4 ± 2.7	13.08	0.002
	Control	13.6 ± 2.8	24.37	<0.001
<i>Anahita</i>	Removal	2.0 ± 0.6	11.74	0.003
	Control	2.7 ± 0.6	20.87	<0.001
<i>Drassyllus</i>	Removal	0.0 ± 1.6	0.01	0.999
	Control	1.4 ± 1.6	0.75	0.395
<i>Gnaphosa</i>	Removal	0.2 ± 0.4	0.02	0.895
	Control	−1.8 ± 1.1	4.50	0.047
<i>Schizocosa</i>	Removal	−0.5 ± 0.8	0.44	0.514
	Control	0.5 ± 1.0	0.51	0.483
<i>Marpissa</i>	Removal	−0.2 ± 0.7	0.09	0.763
	Control	0.9 ± 0.8	1.50	0.236
<i>Xysticus</i>	Removal	0.2 ± 1.1	0.03	0.868
	Control	2.3 ± 1.6	2.85	0.107

although interpreting this pattern is complicated by the fact that these genera initially exhibited a “positive” distance effect (i.e. densities were higher farther from CWD) in the Removal or Control plots, respectively. Data from Kempson samples and pitfall traps did not reveal responses by any genera to CWD removal ($P_s > 0.13$).

In Control plots distance effects were maintained throughout the experiment, with the possible exception of *Ariadna* (planned comparison $F_{1,20} = 4.32, P=0.051$), with the Far/Close density ratio changing from 0.38 to 1.86, although statistical significance disappears when *Ariadna* density is expressed as number per unit volume ($F_{1,20} = 2.13, P=0.16$). Activity-densities and densities of genera estimated by pitfall traps and the Kempson method, respectively, did not exhibit statistically effects ($P_s > 0.22$). In Removal plots the effect of distance from CWD on density (no. m^{-2}) in litter-sifting samples declined over the experiment for the cursorial spiders *Phrurotimpus* ($F_{1,20} = 8.00, P=0.010$) and *Anahita* ($F_{1,20} = 18.29, P<0.001$), for the web-builder *Cicurina* ($F_{1,20} = 8.58, P=0.008$), and possibly for the web-builder *Origanates* ($F_{1,20} = 3.84, P=0.064$). Data expressed as number per unit litter volume yielded slightly higher P values for *Origanates* ($F_{1,20} = 2.53, P=0.127$) and *Phrurotimpus* ($F_{1,20} = 3.78, P=0.066$). In contrast to the aforementioned four genera, *Ariadna* became more abundant in the Close samples, compared to Far samples, in the CWD-removal treatment [Far/Close density ratio decreased from 4.33 to 0.50 for no. m^{-2} ($F_{1,20} = 3.76, P=0.067$), and from 5.71 to 0.37 for density expressed as number per unit litter volume ($F_{1,20} = 6.17, P=0.022$)]. Data from Kempson samples and pitfall traps in Removal plots did not exhibit

Table 3

Effect of removing CWD on densities of major spider genera in litter-sifting samples as indicated by the interaction term [treatment (CWD Removal) × date] in rm-ANOVA. Statistically significant ($P < 0.05$) and marginally significant ($P < 0.10$) probabilities of the F for interaction are indicated in bold (last column). The analysis was performed separately for both distances from CWD (Far and Close) in order to uncover patterns suggesting whether or not the effect of CWD removal varied with proximity of the litter to CWD.

Taxa	Distance	Initial Conditions		Post-treatment		Treatment × date interaction	
		Removal	Control	Removal	Control	$F_{1,20}$	P
Web-builders							
<i>Cicurina</i>	Far	0.7 ± 0.4	0.2 ± 0.2	1.8 ± 0.6	0.5 ± 0.3	1.25	0.277
	Close	1.8 ± 0.8	2.5 ± 0.8	–	0.9 ± 0.4	0.03	0.856
<i>Lathys</i>	Far	7.7 ± 2.3	7.7 ± 2.3	4.3 ± 0.9	9.8 ± 2.0	2.54	0.127
	Close	6.8 ± 1.5	11.8 ± 3.2	3.4 ± 1.3	9.1 ± 2.0	0.05	0.828
<i>Ceratinopsis</i>	Far	2.0 ± 0.7	3.0 ± 1.1	1.1 ± 0.4	3.6 ± 1.0	0.82	0.375
	Close	1.4 ± 0.9	2.7 ± 0.9	2.0 ± 0.5	3.2 ± 0.5	0.06	0.806
<i>Origanates</i>	Far	5.0 ± 1.6	5.7 ± 2.0	3.4 ± 1.0	3.9 ± 1.7	0.01	0.951
	Close	12.7 ± 3.6	9.5 ± 2.5	2.7 ± 0.7	8.2 ± 1.8	4.02	0.059
<i>Tapinocyba</i>	Far	0.9 ± 0.5	1.4 ± 0.7	1.6 ± 0.5	0.9 ± 0.7	1.04	0.320
	Close	1.6 ± 0.7	3.0 ± 0.9	1.1 ± 0.4	2.5 ± 0.9	0.00	1.00
<i>Agyneta</i>	Far	2.5 ± 1.0	1.1 ± 0.5	1.6 ± 0.7	0.7 ± 0.4	0.02	0.889
	Close	4.3 ± 1.2	5.5 ± 1.5	0.5 ± 0.3	3.0 ± 0.8	1.61	0.219
<i>Lepthyphantes</i>	Far	1.8 ± 1.2	3.0 ± 1.3	0.9 ± 0.6	0.7 ± 0.4	0.85	0.367
	Close	3.9 ± 1.5	6.4 ± 1.9	1.1 ± 0.8	2.0 ± 0.9	0.32	0.575
<i>Ariadna</i>	Far	3.0 ± 0.8	1.1 ± 0.4	1.1 ± 0.5	3.0 ± 0.7	7.19	0.014
	Close	0.7 ± 0.4	3.0 ± 1.3	2.3 ± 0.7	1.6 ± 0.6	3.00	0.099
<i>Titanoeca</i>	Far	2.3 ± 1.2	2.3 ± 1.4	5.5 ± 2.0	4.1 ± 1.5	0.02	0.887
	Close	3.0 ± 1.0	1.4 ± 0.7	3.6 ± 1.4	5.5 ± 1.6	10.27	0.004
Cursorials							
<i>Phrurotimpus</i>	Far	7.0 ± 1.6	8.9 ± 2.6	13.0 ± 2.00	14.1 ± 2.8	0.02	0.881
	Close	11.4 ± 3.8	22.5 ± 2.6	10.0 ± 1.7	28.2 ± 5.3	6.17	0.022
<i>Anahita</i>	Far	–	0.5 ± 0.3	1.8 ± 0.9	2.0 ± 0.7	0.01	0.939
	Close	2.0 ± 0.6	3.2 ± 0.6	0.9 ± 0.5	7.7 ± 2.4	4.68	0.043
<i>Drassyllus</i>	Far	4.8 ± 1.2	5.5 ± 1.5	5.7 ± 0.9	5.7 ± 1.5	0.08	0.777
	Close	4.8 ± 1.1	6.8 ± 0.8	4.8 ± 0.7	8.6 ± 1.3	1.11	0.304
<i>Gnaphosa</i>	Far	0.9 ± 0.5	3.4 ± 1.1	4.3 ± 1.3	3.0 ± 0.7	4.68	0.043
	Close	1.1 ± 0.7	1.6 ± 0.7	3.0 ± 0.5	1.6 ± 0.6	2.41	0.137
<i>Schizocosa</i>	Far	1.6 ± 0.6	1.4 ± 0.7	2.5 ± 0.6	3.9 ± 0.9	1.21	0.285
	Close	1.1 ± 0.6	1.8 ± 0.6	1.8 ± 0.7	3.2 ± 0.9	0.05	0.834
<i>Marpissa</i>	Far	1.6 ± 0.5	1.1 ± 0.5	1.4 ± 0.6	2.3 ± 0.6	2.09	0.163
	Close	1.4 ± 0.4	2.0 ± 0.7	3.4 ± 0.9	2.3 ± 0.6	2.37	0.139
<i>Xysticus</i>	Far	3.6 ± 0.9	5.9 ± 1.4	3.2 ± 0.9	3.9 ± 0.9	0.81	0.380
	Close	3.9 ± 0.9	8.2 ± 0.8	2.7 ± 0.8	3.9 ± 0.7	4.83	0.040

clearly statistically significant variation in distance effects for any genera ($P_s > 0.069$).

3.7. Effects of CWD on abundances of potential prey of spiders and other major arthropod taxa

3.7.1. Proximity to CWD (initial conditions)

Densities (no. m^{-2}) of the Collembola family Hypogastruridae in Kempson samples, and activity-densities from sticky traps of Hymenoptera, and Nematocera and Brachycera Diptera, were higher closer to CWD in at least one of the treatments to be applied (Table 4). Likewise, epigeal pitfall traps detected distance effects for total macroarthropods, Dictyoptera and Orthoptera, but in this case activity-densities were higher farther from CWD. The number of flying non-Formicidae Hymenoptera caught by sticky traps was higher closer to CWD in the Removal plots. A few other statistically significant effects appear in Table 4. The patterns remained similar when Kempson samples were analysed as number of individuals per unit of litter biomass.

3.7.2. Removal of CWD

Removing CWD had no clear or consistent effects on densities or activity-densities of potential spider prey and other arthropods (Table 5). Only one significant interaction term appears among all the taxa (Pseudoscorpiones far from CWD). Taxa such as Tomoceridae, Symphyla, Formicidae, larvae, and non-Formicidae Hymenoptera exhibit P values between 0.05 and 0.10 for the effect of CWD removal on density as no. m^{-2} from Kempson samples

(Table 5), which become clearly insignificant ($P_s > 0.30$) when density is expressed per unit of litter biomass. Given the absence of a clear response to CWD for most non-spider taxa, there is no value in examining evidence for the interaction between distance effects and CWD removals as was done for previous response variables.

4. Discussion

The most striking result of our experiment is that removing CWD did not always affect the spider community in ways predicted from static patterns based upon comparisons of litter near and far from CWD. According to the initial effects of distance from CWD that we observed, and those of related research, removal of fallen CWD should have decreased spider diversity, and caused a decline in densities of the major genera of web-builders that were initially more abundant near CWD. However, this expected response to CWD removal did not occur. Furthermore, some spider genera that did not show initial distance effects reacted to the removal of CWD. These results support the cautious claims of Evans et al. (2003) who warn about the uncertain consequences of harvesting CWD on forest-floor invertebrates. Below we first discuss the “distance effects” of CWD we observed in the context of other research, and then evaluate what these apparent effects of CWD mean when interpreted in the light of our experimental results.

4.1. Distance effects – comparisons with other studies

Our results agree with previous research that has found higher densities of spiders in litter adjacent to CWD in other forests:

Table 4
Effect of distance from CWD on densities (no. m⁻² in Kempson samples) or activity-densities (no. caught in sticky traps or pitfall traps) of Collembola families and major macroarthropod taxa based upon rm-ANOVA of numbers in plots before CWD removal (initial conditions). ANOVA was performed separately for plots categorized by whether or not they were to have CWD removed or were to serve as Controls. Differences between Close and Far litter samples with $P < 0.05$ are marked in bold.

Taxa	Method	Removal		Control	
		F _{1,20}	p	F _{1,20}	p
Collembola					
Overall (families pooled)	Kempson	1.09	0.310	0.31	0.587
Hypogastruridae	Kempson	6.78	0.017	3.57	0.074
Onychiuridae	Kempson	0.26	0.617	0.91	0.351
Tomoceridae	Kempson	2.28	0.146	3.10	0.094
Entomobryidae	Kempson	0.31	0.582	0.47	0.502
Isotomidae	Kempson	0.01	0.969	0.15	0.707
Sminthuridae	Kempson	2.23	0.151	0.03	0.866
Macroarthropods					
Overall (taxa pooled)	Kempson	0.06	0.812	0.57	0.457
	Pitfall traps	4.24	0.053	6.90	0.016
	Sticky traps	8.19	0.010	21.89	<0.001
Opiliones	Pitfall traps	0.36	0.553	5.46	0.030
Pseudoscorpiones	Kempson	0.16	0.696	0.22	0.641
Chilopoda	Kempson	0.44	0.513	0.14	0.715
Diplopoda	Kempson	4.03	0.058	2.58	0.124
	Pitfall traps	0.93	0.347	0.88	0.360
Symphyla	Kempson	2.33	0.142	0.36	0.553
Protura	Kempson	0.74	0.401	3.05	0.096
Psocoptera	Kempson	4.18	0.054	0.22	0.644
Dictyoptera	Pitfall traps	2.59	0.123	12.29	0.002
Orthoptera	Pitfall traps	7.58	0.012	34.56	<0.001
Thysanoptera	Kempson	0.05	0.822	0.06	0.814
Coleoptera	Kempson	0.23	0.638	1.08	0.312
	Pitfall traps	2.33	0.143	1.49	0.236
Diptera	Kempson	3.34	0.082	0.54	0.470
	Pitfall traps	4.02	0.059	0.67	0.424
	Sticky traps	6.51	0.019	21.08	<0.001
Diptera Nematocera	Sticky traps	1.78	0.197	20.48	<0.001
Diptera Brachycera	Sticky traps	8.34	0.009	3.99	0.059
Hymenoptera (no ants)	Kempson	8.52	0.008	2.75	0.113
	Pitfall traps	0.28	0.602	1.99	0.173
	Sticky traps	5.40	0.031	0.99	0.331
Hymenoptera: Formicidae	Kempson	0.01	0.909	0.01	0.913
	Pitfall traps	2.03	0.169	0.71	0.410
Larvae	Kempson	0.07	0.799	0.44	0.514

red and silver beech (*Nothofagus fusca* and *N. menziesii*) in New Zealand (Evans et al., 2003), oak-beech (*Quercus petraea*-*Fagus sylvatica*) in Germany (Jabin et al., 2004), sugar maple (*Acer saccharum*) in Canada (Varadi-Szabo and Buddle, 2006), and loblolly pine (*Pinus taeda*) in USA (Ulyshen and Hanula, 2009a). These studies uncovered distance effects 1.5 to 5 m from fallen trunks > 20 cm in diameter. Our research reveals an effect for smaller diameter CWD (14 ± 1 cm) for distances of 0.5–1.5 m. We found higher spider genera richness closer to CWD, as did Varadi-Szabo and Buddle (2006) for species richness. We found that litter adjacent to CWD also has a different spider community compared to that of the open forest floor, in contrast to earlier results suggesting no difference in Canadian deciduous forests (Buddle, 2001; Varadi-Szabo and Buddle, 2006). This disparity may partly reflect the different sampling methods employed. The spider community analyses of Buddle and Varadi-Szabo was based on activity-densities determined by pitfall trapping, whereas we utilized density data from litter sifting.

We found no effects of distance from CWD on spider activity-densities, in agreement with the findings of Buddle and Varadi-Szabo. In a quite different forest type, longleaf pine (*Pinus palustris*) in Florida (USA), Hanula et al. (2009) found that 17 genera of spiders showed distance effects, with only three exhibiting greater activity-densities closer to CWD. It is difficult to relate their study of distance effects to our study and others, however, for several reasons: (1) most importantly, they sampled pieces of CWD that had been added to the plots, a manipulation that may not have

allowed sufficient time for a stable assemblage of spiders and prey to develop; (2) several of their results were due to complex interactions between fire regime and trap location; (3) their traps were designed differently, having a wedge-shaped aluminum sheet on one side in order to reduce the possibility that arthropods would bypass the trap through the gap between the pitfall trap and the log.

4.2. Distance effects – possible explanations hypothesized prior to results obtained by removing CWD from the forest floor

It has been hypothesized that distance effects caused by CWD may be due to several factors: increased structural complexity of the litter adjacent to CWD, higher abundance of potential prey, and more favorable microclimatic conditions near CWD (Evans et al., 2003; Jabin et al., 2004; Varadi-Szabo and Buddle, 2006). These hypotheses are evaluated below.

CWD enhances the structural complexity of the adjacent forest floor by trapping and accumulating leaf litter (Marra and Edmonds, 1998; Kappes, 2005; Kappes et al., 2006, 2007; Jabin et al., 2007; and our results), by serving as a source of fine woody debris (Evans et al., 2003), and by providing large surfaces for web-spinning spiders to attach their webs (Varadi-Szabo and Buddle, 2006). Higher structural complexity usually results in a higher abundance and diversity of spiders (Uetz, 1991). Earlier research has found that there is 1.3–1.8x higher litter biomass closer to CWD in European temperate oak-beech forests (Kappes, 2005; Kappes et al., 2006; Topp et al.,

Table 5

Effect of removing CWD on densities (no. m⁻² in Kempson samples) or activity-densities (no. caught in sticky traps or pitfall traps) of Collembola families and major macroarthropod taxa as indicated by the interaction term [treatment (CWD Removal) × date] in rm-ANOVA; probabilities of the *F* for interaction < 0.05 are marked in bold. The analysis was performed separately for both distances from CWD (Far and Close) in order to uncover patterns suggesting whether or not the effect of CWD-removal varied with proximity of the litter sample to the fallen CWD. All rm-ANOVA's included initial conditions, and most utilized all post-treatment (CWD Removal) sampling dates (rm-MANOVA *F*_{3,18}) with the exception of those marked (1) only the last two dates pooled (rm-ANOVA's *F*_{1,20}); (2) the first post-treatment date and the last two dates pooled (rm MANOVA *F*_{2,19}); and (3) only the last two sampling dates (rm MANOVA *F*_{2,19}).

Taxa	Method	Treatment × date interaction			
		Far		Close	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Collembola					
Overall (families pooled)	Kempson	0.87	0.475	1.34	0.294
Hypogastruridae	Kempson	0.30	0.826	1.30	0.304
Onychiuridae	Kempson	0.23	0.874	1.46	0.258
Tomoceridae	Kempson	1.19	0.341	2.51	0.091
Entomobryidae	Kempson	1.06	0.390	2.64	0.080
Isotomidae	Kempson	1.70	0.203	0.89	0.466
Sminthuridae	Kempson	1.72	0.199	1.07	0.386
Macroarthropods					
Overall (taxa pooled)	Kempson	1.30	0.304	1.32	0.298
	Pitfall traps	0.44	0.725	0.72	0.551
	Sticky traps (3)	0.55	0.588	0.80	0.462
Opiliones	Pitfall traps	2.16	0.129	0.90	0.462
Pseudoscorpiones	Kempson	3.90	0.026	0.56	0.651
Chilopoda	Kempson	0.59	0.633	0.36	0.783
Diplopoda	Kempson (1)	0.86	0.364	2.05	0.168
	Pitfall traps (2)	0.53	0.598	0.64	0.541
Symphyla	Kempson	0.92	0.449	2.59	0.085
Protura	Kempson	0.34	0.796	0.97	0.430
Psocoptera	Kempson	0.18	0.911	0.16	0.922
Dictyoptera	Pitfall traps (2)	0.44	0.652	0.63	0.545
Orthoptera	Pitfall traps (2)	0.47	0.633	0.07	0.933
Thysanoptera	Kempson	0.56	0.649	0.27	0.844
Coleoptera	Kempson	0.55	0.656	0.23	0.874
	Pitfall traps	0.25	0.860	0.81	0.506
Diptera	Kempson	0.70	0.562	0.62	0.612
	Pitfall traps	1.17	0.348	2.29	0.113
	Sticky traps (1)	0.03	0.858	1.79	0.196
Diptera Nematocera	Sticky traps (1)	0.01	0.907	1.22	0.283
Diptera Brachycera	Sticky traps (1)	0.19	0.664	0.21	0.653
Hymenoptera (no ants)	Kempson (1)	0.01	0.858	0.05	0.624
	Pitfall traps	2.60	0.084	1.39	0.278
	Sticky traps (1)	3.37	0.081	0.12	0.730
Hymenoptera: Formicidae	Kempson	2.72	0.075	0.77	0.523
	Pitfall traps	1.71	0.202	0.35	0.793
Larvae	Kempson	1.00	0.416	1.55	0.235

2006; Kappes et al., 2007), and that the litter layer (including the topsoil humus-mineral layer) can be 2x deeper in North American western hemlock-Douglas-fir forests (Marra and Edmonds, 1998). An exception to this trend was found in an old-growth red beech forest of New Zealand (Evans et al., 2003), where distance from CWD had no effect on litter biomass. In the forest we studied, litter close to CWD had 1.3x the dry mass and 1.2x the volume of litter farther away, in agreement with that of European temperate forests. The influence of CWD on litter mass explains the pattern found in our Kempson samples, where distance effects on density of spiders disappeared after analyzing data as number of spiders per dry litter mass. Likewise, Marra and Edmonds (1998), whose data were expressed as density of spiders per unit volume, did not find any difference in abundance of spiders between samples taken far from and close to CWD. However, the impact of CWD on litter amount does not explain our finding of higher density and taxonomic richness of spiders in our litter-sifting data. When abundance and richness are normalized to number of individuals per unit volume of litter, the distance effect still remains, although partially reduced. This pattern is similar to that in red beech (*Nothofagus*) forests, where Evans et al. (2003) found that spiders were more abundant closer to fallen logs even though litter mass did not vary with distance from CWD. These investigators discovered a positive

correlation between proximity to CWD and amounts of fine woody debris. Although in our study forest higher biomass of fine woody debris (FWD) affects spider community structure by increasing the densities of some taxa (Castro and Wise, 2009), we observed that the volume of FWD did not change with proximity to CWD; hence, changes in FWD with distance from CWD cannot explain the patterns we found. Evans et al. (2003) likely found that CWD affected the accumulation of FWD because the CWD in their study was 4–5x larger in diameter with seedlings growing on top. These two attributes could contribute to higher inputs of fine woody debris next to CWD in the *Nothofagus* forest. Providing additional attachment sites for webs is probably more important than increased FWD as an explanation of CWD effects on spiders. The fact that CWD has more of a positive effect on web-builders than on cursorials supports this hypothesis. A more complex litter structure is associated with higher numbers of the web-building linyphiid *Lepthyphantes* (Bultman and Uetz, 1982). This genus was found to be the only one more abundant in pitfall catches next to CWD in a deciduous forest in Canada (Buddle, 2001). Varadi-Szabo and Buddle (2006) found that species richness of web-building spiders was higher closer to CWD, whereas richness of cursorial spiders showed no distance effects. In German beech forests, where spiders were 1.7x more abundant close to CWD, the major genera consisted of the web

builders *Coelotes* (Agelenidae) and *Drapetisca* (Linyphiidae) (Jabin et al., 2004).

Collembola and Diptera are major prey of litter spiders (Foelix, 1996). Activity-density of Diptera and the density of Hypogastruridae (Collembola) were higher in the proximity of CWD. A previous field experiment in this forest found that elevated activity-density of Diptera and increased Collembola densities in open plots led to a doubling of densities of the web-building Amaurobiidae, Dictyniidae and Linyphiidae, as well as an increase in densities of the cursorial Gnaphosidae and Lycosidae (Chen and Wise, 1999). Therefore, elevated prey numbers may also contribute to the higher abundance of spiders observed in the proximity of CWD. More prey rather than increased litter near CWD may have been a more important factor for *Phrurotimpus*, since an earlier study showed that cursorial spiders such as *Phrurotimpus* respond more to nutritional content than structural features of leaf litter (Bultman and Uetz, 1982).

CWD may also increase the density and diversity of spiders by providing more favorable or more stable microclimatic conditions. Soil under CWD holds more moisture in warmer seasons (Marra and Edmonds, 1998; Remsburg and Turner, 2006) and moderates temperature fluctuations (Spears et al., 2003; Remsburg and Turner, 2006). Previous research in Berea College Forest demonstrated that small web-builders such as Linyphiidae tend to colonize the lower litter layers (Wagner et al., 2003). This behavior may characterize the most abundant linyphiid genera that responded to CWD in our experiment (*Agyneta*, *Lepthyphantes* and *Origanates*), spiders that prefer higher moisture and lower temperatures (Huhta, 1971). Wind can also affect the presence of spiders. After combining laboratory experiments with field observations in a temperate forest of Belgium, Jocqué (1973) concluded that Linyphiidae were able to build webs both just above or in the litter close to fallen trunks opposite the prevailing winds, but only below the litter surface when colonizing the windward side.

The hypotheses and patterns just discussed suggest that web-building spiders are more affected than cursorials by ecological gradients on the forest floor created by the presence of CWD. However, effects of experimentally removing CWD demonstrate that so-called “distance effects” cannot easily be explained by many of the proposed hypotheses. The results of our removal experiment provide new insights and aid in evaluating which hypotheses to explain the distance effects are more likely true.

4.3. Effects of CWD removal on spiders near and far from CWD

Our experimental results agree with those of McCay et al. (2002) for a loblolly-pine plantation (*Pinus taeda*, South Carolina, USA), in the sense that removal of CWD (logs and snag) had not influenced overall spider activity-density one year after experimental manipulations. Most spiders in temperate latitudes show annual or biennial life cycles (Schaefer, 1987), which means that the full response by the spider community might not stabilize until more than one or two years after removal of CWD has started. Therefore, our results could have underestimated the effect of removing CWD. This possibility is supported by the fact that further depletion of CWD in loblolly-pine stands for five years (Hanula et al., 2006) caused a decline in the activity-densities of three spider families. However, subsequent research in loblolly-pine plantations, which involved removal of CWD monitored for four years (Ulyshen and Hanula, 2009b), found no effects of removing CWD on either overall spider activity-density or the activity densities of specific families, indicating that other factors (discussed in Sections 4.3.1–4.3.3) were influencing the spider community. We also measured spider densities in the litter, which was not done in the experiments in loblolly pine. The lack of agreement between our overall activity-density

and density data may be related to an interaction between the size of our open plots (12 × 12 m) and the dispersal capacity of spiders, which could migrate from the nearest concentrations of fallen CWD into the Removal plots. Movement of spiders across open-plot boundaries might have diluted some of the effects of CWD removal on the whole spider community. We judge this not to have been a major problem for two reasons: (1) other field experiments in the same forest in which resources were manipulated in smaller open plots have yielded marked effects on spider densities (2 × 5 m; Chen and Wise, 1999; 2 × 2 m; Lawrence, 2000); (2) strong distance effects were observed in the open 12 × 12-m plots before CWD was removed.

Apart from the above aforementioned experiments in loblolly pine, there are no other removal experiments with CWD comparable to ours. Therefore, we focus on our experiment in interpreting the unexpected results of the CWD removal with respect to the distance effects initially observed. Because natural history traits of different spiders may be most directly related to which groups exhibited unexpected results, we focus below on the responses of particular spider genera to CWD removal.

4.3.1. Cursorial Spiders

Phrurotimpus and *Anahita* responded according to prediction. Both were initially more abundant closer to CWD, and removing CWD reduced their densities in litter adjacent to the removed CWD. Litter was deeper near CWD before CWD removal, and litter depth favors *Phrurotimpus* (Uetz, 1977), but other factors also play a role because the effect of removing CWD (i.e. declines in *Phrurotimpus* and *Anahita* densities) remains when densities are calculated per unit volume of litter. Removing CWD may have decreased litter complexity, i.e. number of interstitial spaces inside litter layers. There is evidence that *Phrurotimpus* is more abundant in more complex litter (Uetz, 1977; Bultman and Uetz, 1982). In response to CWD removal, densities of the cursorial crab spider *Xysticus* genus increased in litter adjacent to removed CWD. *Xysticus* does not require deep, complex litter (Uetz, 1977), and may have responded positively to lowered numbers of *Phrurotimpus* and *Anahita* as potential predators or competitors. More difficult to explain is the marginal response of *Gnaphosa*, which, like *Phrurotimpus*, is known to be more abundant in deeper and more complex litter (Uetz, 1977). Surprisingly, *Gnaphosa* was more abundant far from CWD in Control plots, and showed no distance effect initially in the Removal treatment. Hence other factors, possibly biotic interactions, had a greater influence on *Gnaphosa* densities in our study site.

4.3.2. Web-building spiders

The responses of web-building spiders to CWD removal are surprising and their interpretation presents a challenge. No genera responded in a manner predicted from observed distance effects, with the possible exception of the linyphiid *Origanates*, whose density likely decreased in litter next to CWD after its removal ($P=0.059$). Unexpectedly, genera that were initially more abundant closer to CWD, such as *Lepthyphantes*, *Agyneta* and *Cicurina*, did not react to the removal of CWD; and densities of *Titanoeca*, which exhibited no distance effect, declined in litter close to CWD after it was removed. In contrast to these patterns, *Ariadna*, which was initially more abundant far from CWD, decreased in numbers at this distance in response to CWD removal. Thus, *Ariadna* responded as predicted, but the original distance effect was opposite to what one might predict for a web-builder. This clear pattern of results is striking, particularly when it is recognized that web-builder densities in litter are generally thought to be more sensitive to litter amount and complexity than densities of cursorial spiders (Bultman and Uetz, 1982; Uetz, 1991).

4.3.3. Implications for mechanisms by which CWD influences densities of litter-dwelling spiders

The spectrum of responses exhibited by spider genera to CWD removal, and the absence of a tight correspondence of the responses to simple hypotheses predicted from distance effects, suggest that (1) direct effects of removing CWD on structural complexity of the forest floor (via direct effects related to CWD itself plus indirect effects on adjacent litter) altered densities of certain genera, which then altered numbers of other genera in unexpected ways due to biotic interactions among the spiders, such as intraguild predation and competition (these interactions also likely affect densities of certain genera in litter farther from CWD, i.e. *Ariadna*); and (2) effects of CWD on spiders via changes in the structural complexity of the forest floor are more complex than expected due to the importance of litter stratification.

In the Berea College Forest different guilds of spiders are more active or abundant at different litter depths (Wagner et al., 2003). These authors distinguished three different litter layers: an upper layer consisting of curled leaves fallen one year before (thickness depended on the season), a middle layer formed by compressed leaves from several years (1–2 cm thick), and a bottom layer primarily consisting of humus (1–2 cm). Small web-building spiders (Linyphiidae and Dictynidae) were more abundant in the middle and bottom layers, and cursorials and large web-builders (*Ariadna*) were more numerous in the top layer. Spider preferences for each stratum can help explain some of our results. It is possible that after removal of CWD, the top layer could have been thinned, structurally simplified, and dried by wind action. This change would negatively affect spiders from the top layer that are favored by litter complexity, such as *Phrurotimpus*, and positively affect taxa not influenced by this factor, such as *Xysticus* (Uetz, 1977; Bultman and Uetz, 1982). In the same way, the hypothesized drying effect of the wind after removing CWD could benefit *Gnaphosa*. A previous field experiment in this forest found that desiccation of the litter increases gnaphosid activity-density (Lensing et al., 2005). Finally, and perhaps most importantly, since most web-builders inhabit deeper layers, they would not be affected by changes in the top layer. The distance effect observed for these genera (*Lepthyphantes*, *Agyreta* and *Cicurina*) is most likely due to the accumulation of long-term alterations in the structure and moisture-retention properties of the deeper litter layers, which would not change appreciably after a year of CWD removal.

Our results suggest that effects caused by removing CWD are due largely to structural and subsequent microclimatic changes in the litter system, but changes in spider-spider interactions cannot be ruled out as an important contributing factor. The variety of genera responses generates several, and not necessarily exclusive, hypotheses about the mechanisms by which CWD affects litter-dwelling spiders. This wide range of possible explanations is in line with those reviewed in the meta-analysis of Langellotto and Denno (2004), who conclude that interactions between habitat structure and prey-predator systems are complex and still poorly understood.

5. Conclusions

5.1. Overview of the common effects of CWD on the distribution of litter invertebrates

Research done so far (see Section 4.1) reveals that litter adjacent to CWD shows higher densities of invertebrates, and that there are far more litter taxa positively than negatively correlated with the presence of CWD in their surroundings. This localized effect is produced by CWD as small as 14 cm in diameter, and starts to decline significantly at distances between 0.5–1.5 m (reviewed in Section

4.2). Whether these size and distance thresholds are the true limits requires further research. There is evidence that litter accumulations next to CWD can favor the aggregation of certain taxa, but no doubt other abiotic and biotic factors may also be involved.

5.2. Implications of our findings for the management of CWD as it affects forest biodiversity and ecosystem functioning

Litter invertebrates play a significant role in soil ecosystem processes (Swift et al., 1979; Lavelle et al., 2006). Not only microbiodetritivores, but also predators can exert substantial indirect effects on rates of litter decomposition. Trophic cascades initiated by spiders can range from acceleration to retardation of decomposition, depending upon factors such as moisture (Lawrence and Wise, 2000, 2004; Lensing and Wise, 2006). This complexity leads to imprecise predictions of the consequences of changes in spider diversity on forest ecosystem processes. Nevertheless, it is reasonable to predict that variation in the composition of the spider community across the forest floor (beta diversity) has a greater influence than alpha diversity (species richness or heterogeneity measures of diversity) on ecosystem processes such as decomposition (e.g. Wardle, 2002). Hence, determining the overall impact of CWD requires integration over the entire forest floor of CWD's localized effects on the leaf-litter spider community both near and far from CWD. As the direction (positive or negative) of localized effects of CWD differed even among spider genera in our experiment, it is inevitable that effects will be even more variable when higher taxonomic categories are considered.

Another factor complicating our ability to make precise predictions of the consequences of changes in CWD is the fact that effects on litter adjacent to CWD depend upon the overall density of CWD on the forest floor, because organisms move between these litter patches, but at different rates. Correlative observational studies conducted in 18 European oak-beech forests reveal that the motility of the taxonomic group influences the minimum volume of CWD predicted to be necessary to create homogeneous communities in the litter adjacent to CWD (Kappes et al., 2009). Highly mobile invertebrates such as Isopoda and Diplododa would require at least $5 \text{ m}^3 \text{ ha}^{-1}$ of CWD in order for homogeneous communities associated with litter adjacent to CWD to develop, whereas slower dispersers, such as Gastropoda, would require $> 20 \text{ m}^3 \text{ ha}^{-1}$ of CWD to do so. As a comparison, we found that removing around $30 \text{ m}^3 \text{ ha}^{-1}$ of CWD changed the litter spider community as measured by shifts in the relative abundances of several genera, sometimes in different directions. Quantitative changes in the entire macroarthropod community (based on morphospecies analysis) have been caused by removing $\sim 6.5 \text{ m}^3 \text{ h}^{-1}$ of fallen CWD (McCay et al., 2002; Hanula et al., 2006). In all the aforementioned works, more taxa were negatively than positively affected by lower densities (observational studies), or removal (experiments), of fallen CWD.

Because of the impact that depletion of CWD may have on litter invertebrates and ecosystem processes, some investigators have suggested retaining minimum densities of CWD ranging from $20 \text{ m}^3 \text{ h}^{-1}$ (Kappes et al., 2009) to $50 \text{ m}^3 \text{ h}^{-1}$ (Muller et al., 2005) in exploited European temperate forests. These thresholds, however, are based on patterns revealed by purely observational studies. Predictions based upon purely observational studies must be tempered by our finding that removal of CWD does not always result in changes in arthropod litter communities that would have been predicted from static distance effects. Therefore, we argue that recommendations for specific forests should also take into account the results of manipulative experiments in which effects of different volumes of CWD on litter invertebrate communities are measured directly.

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