Tree functional diversity affects litter decomposition and arthropod community composition in a tropical forest

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ABSTRACT

Disturbance can alter tree species and functional diversity in tropical forests, which in turn could affect carbon and nutrient cycling via the decomposition of plant litter. However, the influence of tropical tree diversity on forest floor organisms and the processes they mediate are far from clear. We investigated the influence of different litter mixtures on arthropod communities and decomposition processes in a 60-year old lowland tropical forest in Panama, Central America. We used litter mixtures representing pioneer and old-growth tree species in experimental mesocosms to assess the links between litter types, decomposition rates, and litter arthropod communities. Overall, pioneer species litter decomposed most rapidly and old-growth species litter decomposed the slowest but there were clear non-additive effects of litter mixtures containing both functional groups. We observed distinct arthropod communities in different litter mixtures at six months, with greater arthropod diversity and abundance in litter from old-growth forest species. By comparing the decay of different litter mixtures in mesocosms and conventional litterbags, we demonstrated that our mesocosms represent an effective approach to link studies of litter decomposition and arthropod communities. Our results indicate that changes in the functional diversity of litter could have wider implications for arthropod communities and ecosystem functioning in tropical forests.

Keywords: soil fauna; pioneer; old-growth; Panama; carbon dynamics; mesocosm; non-additive effects.

THE DECOMPOSITION OF PLANT MATERIAL IS CENTRAL TO ECOSYSTEM FUNCTIONING because it underpins the cycling of carbon and nutrients (Swift et al. 1979, Cadish & Giller 1997), which in turn influences plant growth and carbon storage (Wardle 2002, Bardgett 2005). Much research has focused on understanding the interactions between plants and soil microbial communities, as these will be key to determining the effect of anthropogenic change on ecosystem processes (Hättenschwiler et al. 2005). However, soil and litter invertebrate communities also play an important role in litter decomposition but very little is known about how litter diversity and arthropod communities interact during decomposition processes – especially in tropical forests.

The activity of soil invertebrates indirectly affects the resources available to microorganisms and plants (Giller 1996, De Deyn et al. 2004, Ashford et al. 2013). The comminution of leaf litter by soil invertebrates stimulates decomposition by increasing leaching and exposing a greater leaf surface area to microbial attack (Ashford et al. 2013). The mineralization of organic matter is enhanced by arthropod species richness (Nielsen et al. 2011, Ashford et al. 2013) and previous work demonstrates that litter arthropod diversity is related to the concentrations of specific nutrients (Sayer et al. 2010, Ashford et al. 2013). However, interactions between arthropods and litter can be highly species-specific (Hättenschwiler & Gasser 2005) and changes in tree species composition or diversity are likely to be accompanied by changes in forest floor arthropod communities (Cole et al. 2016).

Disturbance could alter decomposition processes via cascading effects of altered tree species composition on litter and soil fauna. Disturbed or young secondary forests have high abundances of pioneer tree species, which are often characterised by fast growth, lower investment in leaf defences and higher foliar nutrient concentrations (Swaine & Whitmore 1988). In contrast, undisturbed mature forests are dominated by slow-growing shade-tolerant species

that invest a greater proportion of resources in belowground biomass, structural stability or defences against herbivores and pathogens (Swaine & Whitmore 1988, Chazdon et al. 2010). Extensive work on leaf herbivory in 41 tropical forest tree species showed that mature leaves of gap-colonising species were much more palatable than shade-tolerant plants (Coley 1983). Leaf traits related to herbivore defences are directly related to the rates of mass loss during litter decomposition (Cornelissen et al. 1999). Consequently, functional changes in tree species communities after disturbance have the potential to modify forest arthropod community composition (Lavelle et al. 1997) and alter decomposition processes. Given that around 50% of tropical forests worldwide are secondary regrowth or have been modified by human activities, we need to determine how the changes in tree functional diversity during secondary succession affect litter fauna and decomposition rates.

The rate of litter decomposition is governed by both the physical and chemical traits of leaf litter, which determine the quality of substrate available to decomposer organisms and the available habitat space in the forest floor (Berg et al. 1993, Perez-Harguindeguy et al. 2000). Heterogeneous litter mixtures provide a greater variety of resources and microhabitats, which can increase the diversity of decomposer organisms through niche partitioning (Hansen & Coleman 1998, Hättenschwiler et al. 2005). A number of experiments have demonstrated that litter mixtures decompose at a faster rate than single-species litter (Seastedt 1984, Gartner & Cardon 2004) but the species diversity of the litter does not explain these "non-additive" effects (Hättenschwiler et al. 2011). Decomposers preferentially break down high-quality litter first, resulting in the release of nutrients, particularly nitrogen (Hättenschwiler et al. 2005), which enables the transfer of nutrients to facilitate the decomposition of low-quality litter

(Hättenschwiler et al. 2005). Hence, litter functional diversity plays a greater role in decomposition processes than species diversity *per se*.

Despite multiple lines of evidence for links between plant traits and invertebrate diversity, the role of larger soil arthropods in decomposition processes is often overlooked, partly due to methodological artefacts. Many decomposition experiments use mesh litterbags (Hättenschwiler et al. 2005), which often exclude macro-arthropods and can create unnatural conditions by changing the physical environment (Levings & Windsor 1996, Hättenschwiler et al. 2005). Consequently, it is unclear how changes in litter functional types will affect arthropod communities and decomposition rates in secondary tropical forests. We aimed to address this using a new approach to investigate how differences in broad tree functional groups (pioneer vs. old-growth) influence litter decomposition rates and arthropod communities in secondary tropical forests.

We used mesocosms to allow access by litter invertebrates during a 6-month decomposition experiment in a semi-deciduous lowland tropical forest in Panama. We compared the decomposition rates of litter mixtures from old-growth and pioneer species, and characterised litter arthropod communities within the mixtures to test the following hypotheses:

1. Litter from pioneer tree species represents a higher quality resource and will therefore decompose at a faster rate than litter from old-growth forest trees.
2. As a result of functional complementarity, litter mixtures containing both old-growth and pioneer species will decompose faster than expected.
3. Arthropod community composition will differ among litter mixtures with distinct chemical and physical properties.

In addition, we conducted a litterbag experiment using the same litter mixtures to establish whether the patterns of decomposition were comparable between our mesocosm approach and the conventional litterbag method.

METHODS

STUDY SITE AND LITTER MIXTURES — The study site was in a *c.* 3200 m^2 area of 60-year old secondary semi-deciduous lowland tropical forest on the Gigante Peninsula within the Barro Colorado Nature Monument, Panama. Tree species composition at the site includes both pioneer and old-growth forest species (Dent et al. 2013). The mean annual temperature on nearby Barro Colorado Island is 26ºC and the mean annual rainfall is 2600 mm, with a strong dry season from January to April (Leigh 1999). The soil is moderately fertile but has low concentrations of extractable phosphorus (Cavalier 1992, Sayer et al. 2006) and a pH of *c.* 5.5 (Cavalier 1992, Sayer et al. 2006). We started the experiment before the onset of the wet season in April 2015 to capture the end of the dry season and the pulse in decomposition at the start of the wet season (Wieder & Wright 1995). Due to the 2015 El Niño event, the dry season lasted longer than expected and there was no significant rainfall until late June; our experiment therefore spanned three months of 'dry season' and three months of 'wet season'.

To investigate differences in litter decomposition for broad functional groups of trees, we used litter mixtures containing an equal mass of litter from each of three pioneer species ('pioneer litter') or three old-growth species ('old-growth litter'), and a mixture containing an equal mass of litter from all six species ('mixed litter'; Table 1). All species were common throughout the forest at the study site (Dent et al. 2013). As a control, we used natural mixed-species litter from the study site ('control litter'). Leaf litter for the other three mixtures was collected from up to four different individual trees in the same forest type on Barro Colorado

111 Island, *c*. 2-km from the study site. All litter was collected from litter traps within a week of leaf
112 abscission *c*. one month before the start of the experiment and dried to constant weight at 35ºC
113 immediately after collection.
114 For all constituent species in the litter mixtures, we measured specific leaf area (SLA)
115 using a leaf area meter (LI-3100C, LiCor Biosciences, Nebraska, USA), and leaf toughness using
116 a Pesola spring scale (Pesola AG, Baar, Switzerland), which measures the maximum force
117 needed to punch through leaves with a 1-mm diameter plunger. We measured total foliar
118 concentrations of carbon and nutrients in the litter of each constituent species, the control litter
119 and the litter mixtures (Table 2). Elemental analyses were carried out at the Smithsonian
120 Tropical Research Institute in Panama, where total carbon (C) and nitrogen (N) were measured
121 on a CN-analyser (FlashEA 1112, Thermo Fisher Scientific, Massachusetts, USA).
122 Concentrations of foliar phosphorus, potassium, calcium, and magnesium were measured by
123 spectrometry (Optima 7300 DV, PerkinEla Inc., Massachusetts, USA).
124
125 MESOCOSM EXPERIMENTS — To test our hypotheses about the decomposition of different litter
126 mixtures, we installed 16 mesocosms in each of five replicate blocks (80 mesocosms in total).
127 We applied the four different litter mixtures (Table 1) to the mesocosms. Within each replicate
128 block, there were four sets of mesocosms for each mixture to allow destructive sampling of two
129 sets after three months; the remaining sets were harvested after six months.
130 The mesocosms consisted of plastic tubes (20-cm diameter; 12-cm height) with four 5-cm
131 diameter holes drilled into the side at equal intervals to allow access by arthropods (Figure 1).
132 The mesocosms were inserted into the soil to *c.* 2-cm depth so that the access holes for
133 arthropods were at ground level. Leaf litter from inside the mesocosms was removed and the soil
134 gently cleared of debris. A pre-weighed 19-cm diameter mesh disc was placed on the soil surface

within each mesocosm, and 16.1g of leaf litter from one of the four mixtures (Table 1) was spread on top of the mesh disc. The mass of litter was chosen to represent the litterfall at the study site in February 2015, which was estimated from existing litter traps.

Mesocosms were installed in March 2015 and left undisturbed for at least two weeks. We applied the leaf litter mixtures on the 6th of April 2015 and took initial soil temperature and soil water content measurements for each mesocosm. Mean soil water content at 0-6 cm depth was determined from three measurements taken within a 1-m radius around each mesocosm using a Thetaprobe (Delta-T Devices, Cambridge, UK) and soil temperature was measured at 0-10-cm depth using a soil temperature probe (Fisher Scientific, Leicestershire, UK).

ARTHROPOD DIVERSITY AND ABUNDANCE — To test whether arthropod communities differed among litter mixtures, we collected arthropods from the litter within the mesocosms of eight mesocosms per block (n = 10 per mixture) after three months and again at the end of the study after six months. The mesh discs with litter were carefully removed from the mesocosms and placed into plastic bags. Immediately upon returning from the field, all litter samples were placed in Berlese funnels lined with 10-mm wire mesh. The litter was moistened regularly to prevent desiccation. Arthropods were extracted during 48 hours and stored in 95% ethanol. Subsamples of litter were taken and examined under a microscope to monitor the efficacy of the extraction. After 48 hours, all litter samples were oven-dried to constant weight at 40ºC and weighed to determine mass loss.

To assess whether the presence of mesocosms altered arthropod communities, we also determined the abundance and diversity of litter arthropods at the study site by collecting two samples of the litter standing crop in each block after the first three months. We placed a 20-cm

158 diameter tube on the forest floor, cut around the inside walls of the tube and collected the litter;
159 arthropods were then extracted as described above. We extracted samples from additional control
160 mesocosms to make a direct comparison with the forest floor arthropod communities.
161 Arthropods were identified at least to order following Gibb & Oseto (2006), and body length was
162 measured to the nearest 0.02-mm using a dissecting microscope with an optical micrometer.
163
164 LITTERBAG EXPERIMENT — To compare decomposition rates in the mesocosms with the
165 conventional litterbag method, we installed four litterbags per litter mixture within each block.
166 Litterbags were constructed of 2.5-mm nylon mesh and measured 17.7-cm × 17.7-cm, to give the
167 same total area as the mesocosms (314.16 cm^2), and each received 16.1 g of litter. The bags were
168 placed on bare soil and, to maintain similar conditions to the litter in the mesocosms, any leaf
169 litter that had fallen onto the litterbags was carefully removed every 2-4 weeks. We collected two
170 bags per litter mixture and block after three and six months and stored them in the fridge until
171 they could be processed. The leaf litter was carefully separated from the bag and washed for 75
172 seconds under a continuous stream of water. All litter samples were oven-dried to constant
173 weight at 40ºC and weighed to determine mass loss.
174

175 DATA ANALYSIS — All statistical analyses were performed in R version 3.2.2 (R Core Team,
176 2015) using the lme4 package (Bates et al. 2015) for linear mixed effects models and the vegan
177 package (Oksanen et al. 2007) for multivariate analyses. Non-normally distributed data were log-
178 transformed prior to analysis where appropriate and all analyses are based on one mean value per
179 litter mixture, block, and time point.
180 The decay rate *k* for all litter mixtures in litterbags and mesocosms was calculated from total
181 mass loss at 6 months according to Olson (1963):

182 $$\ln\left(\frac{X}{X_0}\right) = -kt \qquad \text{(Eq. 1)}$$

183 Where *t* is time (yr), *X* is litter dry mass (g) at collection and X_o is the litter dry mass at time zero
184 (g).

185 To assess mixture effects on mass loss during decomposition, we used Generalised Linear
186 Models (GLMs) with a quasi-binomial error distribution to account for over-dispersion (Gelman
187 & Hill, 2007). We assessed mixture effects on the litter decay rate (*k*) using linear models and as
188 preliminary analyses showed that decomposition rates varied among replicate blocks, block was
189 retained as an error term in all models. The maximal models included litter mixture, experiment
190 type (mesocosms or litterbags), and their interaction. The models were simplified by sequentially
191 dropping terms until a minimal adequate model was identified, following procedures
192 recommended by Crawley (2007). To identify patterns in decomposition during the dry season
193 and the wet season, we performed separate analyses for mass loss during the first three months
194 and the final three months of the experiment. To identify potential non-additive effects of the
195 litter mixture containing both functional groups, we calculated the mean decay rate across the
196 pioneer and old-growth litter mixtures (expected decay rate; *k*) in litterbags and mesocosms after

six months and used a paired t-test to compare the expected decay rate to the measured decay rate of the mixed litter.

We calculated total arthropod abundance, Shannon's diversity (*H*), and Simpson's evenness (*D*) for each sample, and used GLMs as above to model each variable as a function of litter mixture. Changes in arthropod community composition were visualised using non-metric multidimensional scaling (NMDS) based on Jaccard similarity (*MetaMDS* function); stable solutions with stress scores < 0.2 and $r^2 > 0.95$ were used for subsequent analyses. Differences in arthropod community composition among mixtures were assessed by permutational multivariate analysis of variance (PerMANOVA; *adonis* function) after testing for homogeneity of dispersions among mixtures (*betadisper* and *permutest* functions). Models were tested with 999 permutations constrained within replicate blocks. Separate analyses were conducted to assess i) the effect of mesocosm installation, by comparing arthropod communities in forest floor samples and control mesocosms (at the three-month collection only), and ii) differences among litter mixtures, collection time, and their interaction.

RESULTS

LITTER DECOMPOSITION AND LITTER PROPERTIES — Litter decay rate (*k*) was best explained by litter mixture and experiment type. In support of our first hypothesis, *k* differed significantly among mixtures, whereby *k* for pioneer litter > control litter > mixed litter > old-growth litter regardless of the type of experiment (Table 2). Although the measured litter properties of individual species showed no consistent pattern within functional groups (Table 2a), the pioneer litter mixture had the lowest C:N:P ratio and the old-growth litter had the highest (Table 2b).

The greatest proportion of mass loss occurred in the first three months, even though this was during the dry season (Figure 3). Mass loss of the old-growth litter mixture was significantly lower than any of the other mixtures during the dry season (0-3 months: $t = -3.77$, $p < 0.001$), whereas mass loss of the pioneer litter mixture was significantly greater than the mixed litter and old-growth litter mixtures during the wet season (3-6 months pioneer litter: $t = 2.17$, $p = 0.041$; Figures 2 and 3). The pattern of mass loss over time differed between the two types of experiment. In the dry season (months 0-3), litter mass loss from bags was significantly higher compared to mesocosms ($t = -7.29$, $p < 0.001$), whereas in the wet season (months 3-6), mass loss was greater in mesocosms ($t = 3.72$, $p = 0.001$; Figure 2). Accordingly, k was *c.* 20% lower for litter mixtures in mesocosms compared to litterbags across all mixtures ($F_{1,28} = 13.3$, $p = 0.001$).

In partial support of our second hypothesis, we observed a significant non-additive effect of the litter mixture containing pioneer and old-growth species. However, the expected decay rate based on the individual pioneer and old-growth mixtures (1.16 ±0.06) was significantly higher than the decay rate measured in the mixed litter (0.88 ±0.09; $t = 2.67$, $p = 0.02$), indicating antagonistic effects of litter mixtures on decomposition processes.

ARTHROPOD COMMUNITIES — Arthropod abundance did not differ between samples collected at three months and those collected at six months (Table 3) but the diversity and evenness of the arthropod community was significantly greater at six months than at three months (H: $t = -2.06$, $p = 0.049$; D: $t = -2.57$, $p = 0.016$). Litter mixture alone had no significant effect on evenness but the diversity and abundance of arthropods was significantly greater in the old-growth litter compared to the other litter mixtures (H: $t = -2.11$, $p = 0.044$; abundance: $t = 2.26$, $p = 0.029$).

241 The comparison of arthropods in control mesocosms and forest floor litter samples after
242 three months showed a minor effect of mesocosm installation on community composition
243 (PerMANOVA, main treatment effect: $F_{1,24} = 1.77$, $p = 0.061$; Figure 4A). Arthropod community
244 composition did not differ among litter mixtures at three months (Figure 4B) but there was a
245 significant effect of litter mixture at six months (PerMANOVA, main treatment effect: $F_{3,15} =$
246 1.66, $p = 0.011$; Figure 4C), which partially supports our third hypothesis. Comparison of the
247 arthropod communities in decomposing litter at three and six months showed that community
248 composition differed among mixtures and diverged over time, but the time × mixture
249 interaction was not significant (PerMANOVA, treatment effect: $F_{3,34} = 1.98$, $p = 0.002$; time
250 effect: $F_{1,34} = 7.17$, $p = 0.001$; Figure 4D).
251
252 **DISCUSSION**
253 Our mesocosm experiments allowed us to study litter decomposition and arthropod communities
254 within the same experimental arena. Our results demonstrate non-additive effects and diverging
255 arthropod communities during the decomposition of mixtures containing litter from broad tree
256 functional types.
257
258 INFLUENCE OF LITTER MIXTURES ON DECOMPOSITION — As hypothesised, the litter from pioneer
259 species decomposed faster than the old-growth forest litter, with the control and mixed litter
260 taking an intermediate position (Figure 2). Litter of pioneer species generally has low mass per
261 leaf area, high concentrations of nutrients, and low fibre and lignin contents (Arnone et al. 1995,
262 Hirschel et al. 1997). Thus, it is considered a high-quality resource, which decomposers
263 preferentially break down (Hirschel et al. 1997). By contrast, old-growth species generally have

high dry-mass investment per leaf area, low nutrient concentrations and high fibre and lignin contents, and are therefore considered to be a low-quality resource for decomposers (Hättenschwiler et al. 2011). Although, the litter chemical traits of the individual species we measured did not conform to these expected patterns, the C:N:P ratio of the mixtures could explain the decay rates in our study (Table 2b). Other traits such as lignin and polyphenol concentrations are also likely to be important in determining substrate availability or palatability for decomposer organisms (Berg et al. 1993, Perez-Harguindeguy et al. 2000). In our study, leaf toughness was greater in old-growth compared to pioneer species litter (Table 2a) and as leaf toughness represents plant investment in structural carbon and herbivore defences (Westbrook et al. 2011), it is strongly related to litter decomposition rates (Perez-Harguindeguy et al. 2000).

Our results suggest antagonistic non-additive effects of litter mixtures because the decay rate for the mixed litter was lower than would be expected from the decay rates of the individual pioneer and old-growth mixtures. A number of studies have demonstrated synergistic non-additive effects during the decomposition of litter mixtures (Hättenschwiler et al. 2005, Gessner et al. 2010), whereby the transfer of nutrients and secondary compounds from high-quality litter can facilitate the decomposition of low-quality litter (Fyles & Fyles 1993). However, the presence of low-quality litter can also decrease the overall decay rate of mixtures (Gartner & Cardol 2004) and increase the immobilization of nutrients (Meier & Bowman 2010), which could be beneficial to nutrient retention in tropical forests, as the gradual release of nutrients from decomposing litter can minimise losses due to leaching (Sayer et al. 2012).

Few other studies have investigated non-additive effects of litter mixtures of different functional groups, although non-additive effects were demonstrated in litter mixtures of dicot herbs, grasses and trees (Wardle et al. 1997). Although most studies of non-additive effects have

287 focused on comparing single-species litter to mixtures (Gartner and Cardon 2004), we show that
288 the same considerations apply to mixed litter from broad functional groups, suggesting that
289 complementary litter traits of pioneer and old-growth species alter decomposition processes.
290
291 ARTHROPOD ABUNDANCE AND DIVERSITY IN LITTER MIXTURES — There was a visible separation
292 of arthropod communities in litter from pioneer species compared to old-growth litter at six
293 months and the diversity and abundance of arthropods was greater in old-growth litter by the end
294 of the study (Figure 4), which partially supports our third hypothesis. The differences in
295 arthropod communities may be a result of greater litter mass and habitat structure in the old-
296 growth litter relative to rapidly decomposing litter mixtures (Sayer et al. 2010). Despite this, we
297 found no relationship between litter decay rates and arthropod abundance or diversity. Previous
298 studies show that there is a degree of redundancy in taxonomic richness as decomposition rates
299 plateau at low species richness (Setala & McLean 2004, Hedde et al. 2010). However, the
300 separation of arthropod communities in different mixtures over time could partly result from the
301 differences in chemical and physical properties of the litter, suggesting that certain leaf traits
302 may play a greater role in shaping arthropod community composition during the later stages of
303 decay, once high-quality substrates and labile compounds have been depleted.
304 We had expected greater effects of litter mixtures on arthropod abundance, diversity,
305 evenness, or community composition. Our identification of arthropods to order or family level
306 may not provide sufficient taxonomic resolution to detect changes in arthropod community
307 composition (Walter & Ikonen 1989) but as we found differences among litter mixtures after six
308 months, we propose that the unusually long dry season probably had an overriding effect on
309 arthropod community composition during the first half of the study. Many arthropods are

sensitive to dry conditions and a study on nearby Barro Colorado Island found that population levels of only two major arthropod groups increased in the dry season, compared to nine in the wet season (Levings & Windsor 1996). In our study, there was a marked shift in arthropod community composition between the dry and the wet season (Figure 4). Taxa that were only found at the three-month collection during the dry season were all either predators or parasitoids (*Dermaptera*, *Phoridae*, *Geophilamorpha*, *Chalicoidae* and *Scolopendromorpha*; Appendix 2), whereas those present only at the six month collection feed on plant material (*Isoptera*, *Gelechiidea, Symphypleona* and *Gryllidae*; Appendix 2, Petersen & Luxton 1982). This could indicate that conditions are more favourable for litter decomposers during the wet season.

There was a minor difference in arthropod community composition between forest floor samples and the control litter in the mesocosms at the three-month collection (Figure 4A), which could be attributed to the physical barrier created by mesocosm installation, or because we added a single amount of litter that was much less than the surrounding litter standing crop. However, our ordinations revealed substantial overlap between the arthropod communities in the mesocosms and the forest floor (Figure 4A) and they may more closely resemble the natural forest floor community with a longer installation period and larger or repeated litter inputs.

COMPARISON OF DECOMPOSITION IN LITTERBAGS AND MESOCOSMS — Our mesocosm approach represents a viable alternative to litterbags, which allowed us to integrate measurements of decomposition and arthropod communities. Our method comparison showed the same pattern of decay among different litter mixtures in litterbags and mesocosms over the six-month study period (Figure 2B,C). Although mass loss from mesocosms was lower than litterbags in the dry season and greater during the wet season, this difference in initial mass loss, and the lower

333 overall decay rate, could be explained by the distinct microenvironments in litterbags and
334 mesocosms. A major critique of the litterbag method is that the bags retain more moisture than
335 the surrounding forest floor (Tanner 1981, Sayer et al. 2006) and as the first three months of the
336 study took place during the dry season, the litterbags could have stayed moister for longer after
337 brief periods of rainfall. In this case, the litterbags would have presented a more favourable
338 environment for decomposers. By contrast, the microenvironment in the mesocosms is more
339 representative of natural litter on the forest floor and was hence more likely to dry out during the
340 dry season. The wet season started approximately halfway through the experiment and here, the
341 mesocosms may have represented the more favourable environment, as the litter was less
342 compressed compared to litterbags.

343 Regardless of season, the initial stages of decomposition are generally rapid as the readily
344 available carbon and nutrients are leached or used by decomposers (Maraun & Scheu 1996a,b).
345 Once most of the labile carbon has been depleted, decay rates tend to decrease (Olson 1963,
346 Wieder & Lang 1982). The litter in bags will have reached this point more rapidly because of the
347 faster decomposition in the first three months, which also partially explains the slower
348 decomposition rates during the remaining three months. Nonetheless, the two methods produced
349 comparable mass loss at six months (Figure 2) and revealed the same distinct patterns of
350 decomposition among litter mixtures.

351

352 **CONCLUSIONS**

353 Our study highlighted distinct decomposition rates among mixtures of leaf litter from different
354 tree functional groups and changes in the associated litter arthropod communities. We
355 demonstrate antagonistic non-additive effects during the decomposition of mixed litter from

356 broad tree functional groups. As litter represents a major pathway for nutrient cycling in tropical
357 forests, modified decomposition processes due to changes in tree species composition could have
358 wider implications for carbon and nutrient cycling. Further research is needed to determine how
359 non-additive effects could modify nutrient immobilisation and release during decomposition in
360 tropical forests. In our study, the decomposition of different litter mixtures in mesocosms and
361 litterbags was highly comparable. Thus, our mesocosm experiments represent an effective
362 method to measure litter decomposition and arthropod communities in a single system. This
363 approach enables future research into the mechanisms of non-additive effects and the role of
364 arthropod functional diversity during litter decomposition.
365

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375 **AVAILABILITY STATEMENT**

376 Data availability: The data used in this study are archived on Dryad (doi supplied upon
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378

LITERATURE CITED

ARNONE, J. A., ZALLER, J. G., ZIEGLER, C., ZANDT, H. & KÖRNER, C. 1995. Leaf quality and insect herbivory in model tropical plant-communitites after long-term exposure to elevated atmospheric CO_2. *Oecologia,* 104, 72-78.

ASHFORD, O. S., FOSTER, W. A., TURNER, B. L., SAYER, E. J., SUTCLIFFE, L. & TANNER, E. V. J. 2013. Litter manipulation and the soil arthropod community in a lowland tropical rainforest. *Soil Biology & Biochemistry,* 62, 5-12.

BARDGETT, R. G. 2005 Ectomycorrhizal fungi challenged by saprotropic basidiomycetes and soil microfungi under different ammonium regimes in vitro. *Mycological Research,* 104, 691-97.

BATES, D., MACHLER, M., BOLKER, B. M. & WALKER, S. C. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software,* 67, 1-48.

BERG, B., BERG, M. P., BOTTNER, P., BOX, E., BREYMEYER, A., DEANTA, R. C., COUTEAUX, M., ESCUDERO, A., GALLARDO, A., KRATZ, W., MADEIRA, M., MALKONEN, E., MCCLAUGHERTY, C., MEENTEMEYER, V., MUNOZ, F., PIUSSI, P., REMACLE, J. & DESANTO, A. V. 1993. Litter Mass-Loss Rates in Pine Forests of Europe and Eastern United-States - Some Relationships with Climate and Litter Quality. *Biogeochemistry,* 20**,** 127-159.

CADISH, G. & GILLER, K. E. 1997. Driven by nature: plant litter quality and decomposition. Wallingford: CAB Int. 432 pp.

CAVALIER, J. 1992. Fine-root biomass and soil properties in a semi-deciduous and a lower montane rain forest in Panama. *Plant and Soil,* 142**,** 187-201.

401 CHAZDON, R. L., FINEGAN, R. S., CAPERS, R. S., SALGADO-NEGRET, B., CASANOVES, F., BOUKILI,
402 V. & NORDEN, N. 2010. Composition and dynamics of functional groups of trees during
403 tropical forest succession in northeastern Costa Rica. *Biotropica,* 42, 31-40.
404 COLE, R. J., HOLL, K. D., ZAHAWI, R. A., WICKEY, P. & TOWNSEND, A. R. 2016. Leaf litter
405 arthropod responses to tropical forest restoration. *Ecology and Evolution*, *6*, 5158-5168.
406 COLEY, P. D. 1983. Herbivory defensive characteristics of tree species in a lowland tropical
407 forest. *Ecological Monographs*, 53, 209-234.
408 CORNELISSEN, J. H. C., PÉREZ-HARGUINDEGUY, N., DÍAZ, S., GRIME, J. P., MARZANO, B.,
409 CABIDO, M., VENDRAMINI, F. & CERABOLINI, B. 1999. Leaf structure and defence control
410 litter decomposition rate across species and life forms in regional floras on two
411 continents. *New Phytologist*, 143, 191-200.
412 CRAWLEY, M. J. 2007. *The R book,* Chichester, Wiley-Blackwell.
413 DE DEYN, G. B., RAAIJMAKERS, C. E. & VAN DER PUTTEN, W. H. 2004. Plant community
414 development is affected by nutrients and soil biota. *Journal of Ecology,* 92**,** 824-834.
415 DENT, D. H., DEWALT, S. J., & DENSLOW, J. S. 2013. Secondary forests of central Panama
416 increase in similarity to old-growth forest over time in shade tolerance but not species
417 composition. Journal of Vegetation Science, 24(3), 530-542.

418 FYLES, J. H. & FYLES, I. H. 1993. Interactions of Douglas-fir with red alder and salal foliage litter
419 during decomposition. *Can J For Res,* 23, 358-361.
420 GARTNER, T. B. & CARDON, Z. G. 2004. Decomposition dynamics in mixed-species leaf litter.
421 *Oikos,* 104**,** 230-246.
422 GELMAN, A. & HILL, J. 2007. Data analysis using regression and hierarchical/multilevel models.
423 Cambridge University Press: Cambridge, UK. 110-118 pp.

GESSNER, M. O., SWAN, C. M., DANG, C. K., MCKIE, B. G., BARDGETT, R. D., WALL, D. H. & HATTENSCHWILER, S. 2010. Diversity meets decomposition. *Trends in Ecology & Evolution,* 25**,** 372-380.

GIBB, T. J. & OSETO, C. Y. 2006. Arthropod collection and identification*,* Oxford, Academic Press.

GILLER, P. S. 1996. The diversity of soil communities, the 'poor man's tropical rainforest'. *Biodiversity and Conservation,* 5**,** 135-168.

HANSEN, R. A. & COLEMAN, D. C. 1998. Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acari: Oribatida) in litterbags. *Applied Soil Ecology,* 9**,** 17-23.

HATTENSCHWILER, S., COQ, S., BARANTAL, S. & HANDA, I. T. 2011. Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis. *New Phytologist,* 189**,** 950-965.

HÄTTENSCHWILER, S. & GASSER, P. 2005. Soil animals alter plant litter diversity effects on decomposition. *Proc Natl Acad Sci,* 102, 1519-1524.

HÄTTENSCHWILER, S., TIUNOV, A. V. & SCHEU, S. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics.* Palo Alto: Annual Reviews, 36, 191-218.

HEDDE, M., BUREAU, F., CHAUVAT, M. & DECAENS, T. 2010. Patterns and mechanisms responsible for the relationship between the diversity of litter macro-invertebrates and leaf degradation. *Basic and Applied Ecology,* 11**,** 35-44.

HIRSCHEL, G., KORNER, C. & ARNONE, J. A. 1997. Will rising atmospheric CO2 affect leaf litter quality and in situ decomposition rates in native plant communities? *Oecologia,* 110**,** 387-392.

LAVELLE, P., BIGNELL, D., LEPAGE, M., WOLTERS, V., ROGER, P., INESON, P., HEAL, O. W. & DHILLION, S. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology,* 33**,** 159-193.

LEIGH, E. G., JR. 1999. *Tropical Forest Ecology: A View from Barro Colorado Island,* New York, Oxford University Press.

LEVINGS, S. C. & WINDSOR, D. M. 1996. *Seasonal and annual variation in litter arthropod populations*. Smithsonian Institution Press. 355-388 pp.

MARAUN, M. & SCHEU, S. 1996a. Changes in microbial biomass, respiration and nutrient status of beech (*Fagus sylvatica*) leaf litter processed by millipedes (*Glomeris marginata*). *Oecologia,* 107**,** 131-140.

MARAUN, M. & SCHEU, S. 1996b. Seasonal changes in microbial biomass and activity in leaf litter layers of beech (*Fagus sylvatica*) forests on a basalt-limestone gradient. *Pedobiologia,* 40**,** 21-31.

MEIER, C. L. & BOWMAN, W. D. 2010. Chemical composition and diversity influence non-additive effects of litter mixtures on soil carbon and nitrogen cycling: implications for plant species loss. *Soil Biology and Biochemistry,* 42, 1447-1454.

NIELSEN, U. N., AYRES, E., WALL, D. H. & BARDGETT, R. D. 2011. Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity-function relationships. *European Journal of Soil Science,* 62, 105-116.

OKSANEN, J. F., BLANCHET, G., KINDT, R. LEGENDRE, P., MINCHIN, P. R., O'HARA, R. B., SIMPSON, G. L., SOLYMOS, P., STEVENS, M. H. H., AND WAGNER, H. 2015. vegan: Community Ecology Package. R package version 2.3-1.

OLSON, J. S. 1963. Energy-Storage and Balance of Producers and Decomposers in Ecological-Systems. *Ecology,* 44**,** 322-331.

PEREZ-HARGUINDEGUY, N., DIAZ, S., CORNELISSEN, J. H. C., VENDRAMINI, F., CABIDO, M. & CASTELLANOS, A. 2000. Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant and Soil,* 218**,** 21-30.

PETERSEN, H. & LUXTON, M. 1982. A Comparative-Analysis of Soil Fauna Populations and Their Role in Decomposition Processes. *Oikos,* 39**,** 287-388.

SAYER, E. J., SUTCLIFFE, L. M. E., ROSS, R. I. C. & TANNER, E. V. J. 2010. Arthropod abundance and diversity in a lowland tropical forest floor in Panama: the role of habitat space vs. nutrient concentrations. *Biotropica,* 42**,** 194-200.

SAYER, E. J., TANNER, E. V. J. & LACEY, A. L. 2006. Effects of litter manipulation on early-stage decomposition and meso-arthropod abundance in a tropical moist forest. *Forest Ecology and Management,* 229**,** 285-293.

SAYER, E. J., WRIGHT, S. J., TANNER, E. V., YAYITT, J. B., HARMS, K. E., POWERS, J. S., KASPARI, M., GARCIA, M. N. AND TUNER, B. L. 2012. Variable responses of lowland tropical forest nutrient status to fertilisation and litter manipulation. *Ecosystems*, 15, 387-400.

SEASTEDT, T. R. 1984. The role of microarthropods in decomposition and mineralization process. *Annual Review of Entomology,* 29**,** 25-46.

SETALA, H. & MCLEAN, M. A. 2004. Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. *Oecologia,* 139**,** 98-107.

SWIFT, M. J., HEAL, O. W. & ANDERSON, J. M. 1979. Decomposition in Terrestrial Ecosystems. Berkeley: University of California Press. 509 pp.

TANNER, E. V. J. 1981. The decomposition of leaf litter in Jamaican montane rain forests. *Journal of Ecology,* 69**,** 263-275.

R CORE TEAM 2015. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

SWAINE, M.D. & WHITMORE, T. C. 1988. On the definition of ecological species groups in tropical forests. *Vegetatio,.* 75, 81-86.

WALTER, D. E. & IKONEN, E. E. 1989. Life history and behavior of mites in the genus *Lasioseius* (Acari: Mesostigmata: Ascidae) from grassland soils in Colorado, with taxonomic notes and description of a new species. *Canadian Journal of Zoology,* 67, 2797-2813.

WARDLE, D. A. 2002. Communities and ecosystems: linking the aboveground and belowground components. Princeton, NJ: Princeton University Press 392 pp.

WARDLE, D. A., BONER, K. I. & NICHOLSON, K. S. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos,* 79, 247-58

WESTBROOK, J. W., KITAJEMA, K., BURLEIGH, J. G., KRESS, W. J., ERICKSON, D. L & WRIGHT, S. J. 2011. What makes a leaf tough? Patterns of correlated evolution between leaf toughness traits and demographic rates among 197 shade-tolerant woody species in a Neotropical forest. *American Naturalist*, 177, 800-811.

511 WIEDER, R. K. & LANG, G. E. 1982. A Critique of the Analytical Methods Used in Examining
512 Decomposition Data Obtained from Litter Bags. *Ecology,* 63**,** 1636-1642.
513 WEIDER, R. K. & WRIGHT, S. J. 1995. Tropical forest litter dynamics and dry season irrigation on
514 Barro Colorado Island, Panama. *Ecology*, 76, 1971-1979.
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TABLES

TABLE 1. The four leaf litter mixtures used in a six-month decomposition experiment in lowland tropical forest in Panama; the mixtures contained an equal mass of litter from each of the constituent species.

Litter Mixture	**Constituent Litter (Tree Species)**
Pioneer	*Ochroma pyramidale* (Cav. ex. Lam.) Urb *Cecropia peltata* L. *Luehea seemannii* Triana & Planch
Old growth	*Dipteryx panamensis* Pittier Record & Mell *Tetragastris panamensis* Engl. *Prioria copaifera* Griseb.
Pioneer and old growth	*Dipteryx panamensis* *Tetragastris panamensis* *Prioria copaifera* *Ochroma pyramidale* *Cecropia peltata* *Luehea seemannii*
Control	Mixed leaf litter from the study site

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TABLE 2: Litter properties for a) individual species and b) litter mixtures used in a decomposition study in lowland tropical forest in Panama; in a) mean values of specific leaf surface area (SLA; *n* = 9 fresh leaves per species), carbon to nitrogen ratios (C:N; *n* = 3 litter samples), and leaf toughness (*n* = 6 fresh leaves) are shown for individual species, where FG is functional group, OG is old-growth and PI is pioneer species; and in b) values shown are from one composite sample per mixture for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and C:N:P ratios, and means ± standard errors are shown for *n* = 5 litterbags per mixture for decay rates (*k*).

a) Species	FG	SLA ($mm^2 g^{-1}$)	C:N	Toughness (g)
Dipteryx panamensis	OG	185.8	36.4 ±0.9	57.85
Tetragastris panamensis	OG	72.1	57.1 ± 4.3	202.67
Prioria copaifera	OG	95.9	46.7 ± 1.0	122.29
Cecropia peltata	PI	72.4	44.6 ± 0.4	21.50
Luehea seemannii	PI	145.3	44.1 ± 2.7	55.00
Ochroma pyramidale	PI	86.3	76.5 ± 5.2	15.67

	N	P	K	Ca	Mg	C:N:P	*k*
b) Mixture	(%)	(mg/g)					
Pioneer	0.97	0.75	4.20	25.76	4.40	63.3	1.51 ± 0.23
Control	1.23	0.41	3.30	12.64	3.16	88.2	1.21 ± 0.26
Mixed	1.06	0.60	4.38	20.62	3.12	85.8	0.86 ± 0.10
Old growth	1.14	0.44	4.56	15.5	1.84	108.3	0.72 ± 0.16

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TABLE 3: Arthropod community metrics in different litter mixtures in a decomposition study in a lowland tropical forest in Panama, showing arthropod abundance, total number of taxa, Shannon's Diversity (H) and Simpson's Evenness (D) indices in litter samples collected from mesocosms after three and six months of decomposition; values are means of *n* = 5 per mixture at three months and *n* = 5 for old-growth, *n* = 3 for controls, and *n* = 4 for pioneer and mixed litter at six months; the litter mixtures are described in Table 1.

Litter mixture	**Abundance**		**No. of taxa**		**Shannon's H**		**Simpson's D**	
Month	*3*	*6*	*3*	*6*	*3*	*6*	*3*	*6*
Control	96.20	81.67	17.00	14.00	1.95	1.93	0.79	0.80
Pioneer	139.40	110.16	16.20	15.50	1.94	1.81	0.79	0.72
Mixed	58.80	105.25	17.20	14.25	1.97	1.78	0.80	0.75
Old growth	167.30	179.50	17.00	15.80	1.84	1.74	0.78	0.74

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FIGURE LEGENDS:

FIGURE 1: Schematic diagram of mesocosms used to measure litter decomposition and arthropod communities in litter mixtures during a 6-month experiment in a lowland tropical forest in Panama.

FIGURE 2: Boxplots of mass loss during decomposition in mesocosms (grey) and litterbags (white) for different litter mixtures in a lowland tropical forest in Panama during (A) the dry season (months 0-3), (B) the wet season (months 3-6) and (C) the whole 6-month study period.

FIGURE 3: Mean mass loss from litterbags and mesocosms during six months of decomposition in a lowland tropical forest in Panama; where green squares indicate old growth, pink circles indicate mixed litter, orange triangles indicate control litter and blue stars indicate pioneer litter; means and standard deviations are shown for $n = 5$.

FIGURE 4: Non-metric-mutidimensional scaling (NMDS) ordinations of arthropod community composition in a decomposition experiment in lowland tropical forest in Panama showing differences in arthropod communities based on Jaccard similarity for (A) forest floor and control mesocosms at three months; (B) in mesocosms with different litter mixtures at three months and (C) at six months, and (D) the comparison between arthropod communities in mesocosms at three and six months; where purple is forest floor (FF), blue is control litter (CNT), green is old-growth litter (OG), pink is pioneer litter (PI), and yellow is mixed litter (PIOG); ellipses in (A), (C) and (B) indicate separation of

communities in ordination space based on the standard error of the weighted average of scores.

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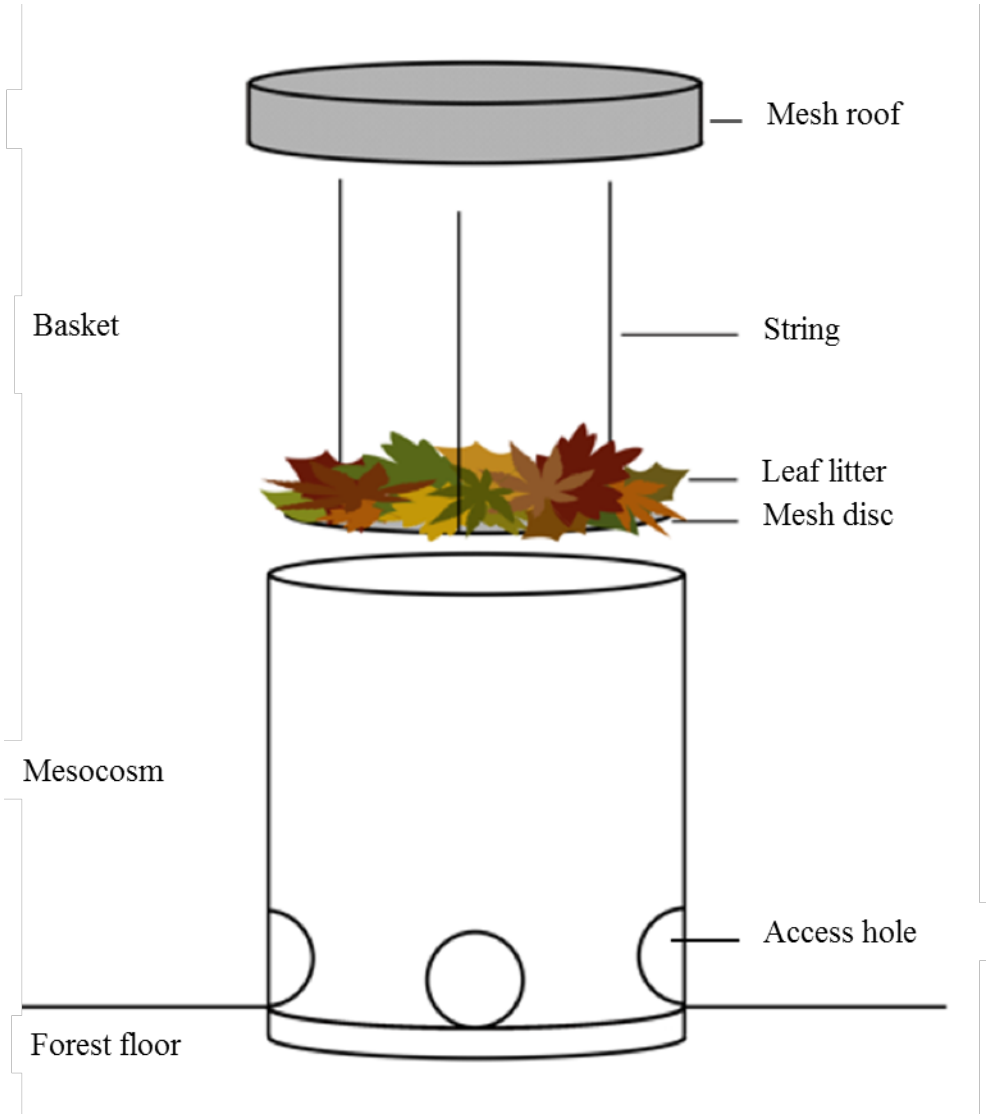
Mesh roof
Basket
String
Leaf litter
Mesh disc
Mesocosm
Access hole
Forest floor

FIGURE 1

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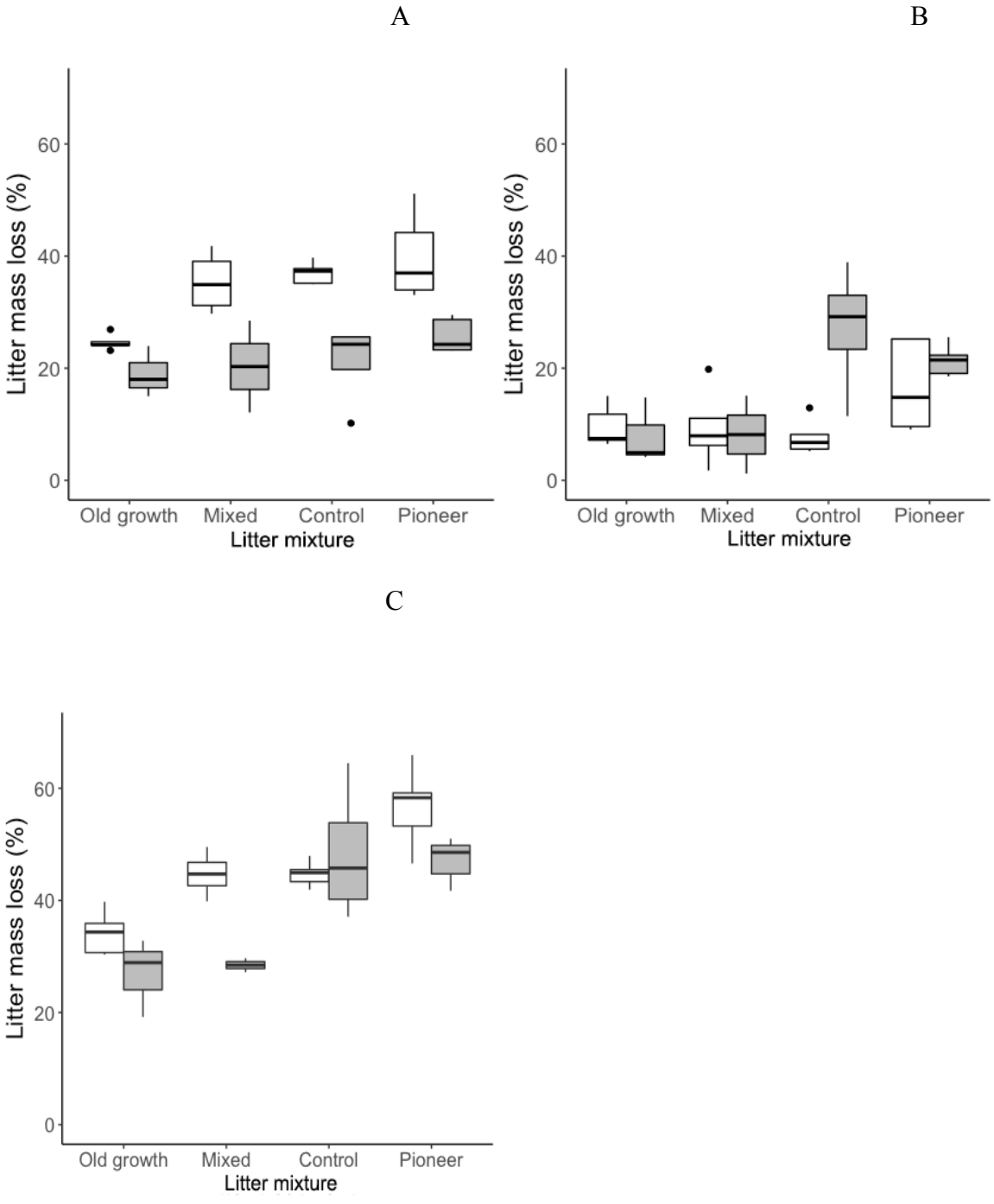

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FIGURE 2

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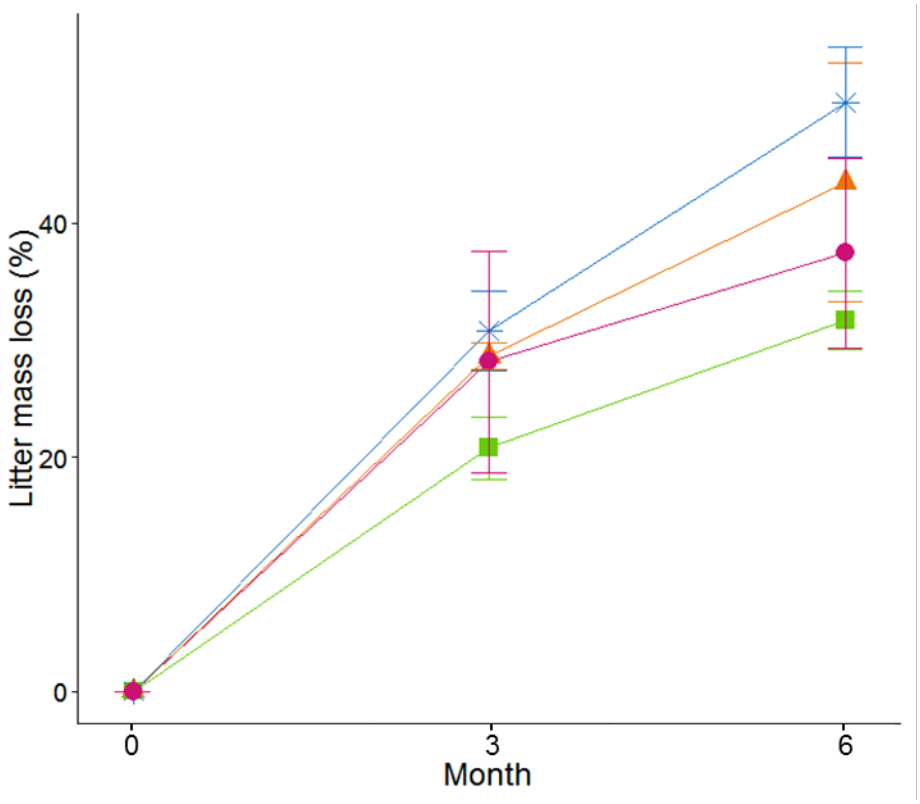

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FIGURE 3

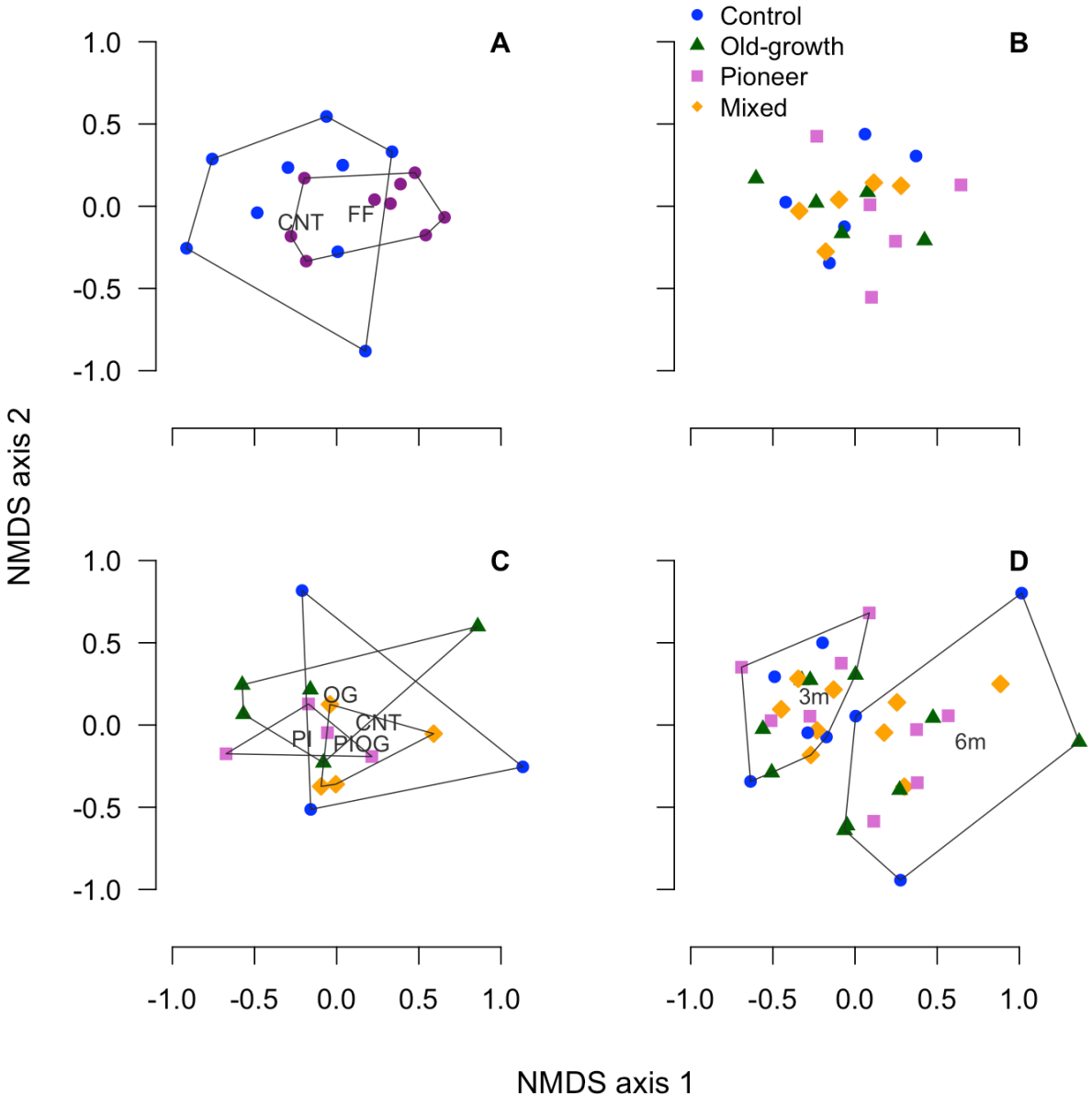
A
B
C
D
Control
Old-growth
Pioneer
Mixed
CNT
FF
OG
CNT
PI
PIOG
3m
6m
NMDS axis 1
NMDS axis 2
1.0
0.5
0.0
-0.5
-1.0

FIGURE 4

SUPPORTING INFORMATION

Mean abundance of identified arthropod taxa in different litter mixtures after three months (dry season; DS) and six months (wet season; WS) showing all individuals by class, subclass or order; where identification was possible to a lower taxonomic level than order, the number of individuals is listed separately; means are given for $n = 3$ to $n = 5$ mesocosms per mixture.

		Control		**Pioneer**		**Mixed**		**Old growth**	
Class/subclass/order	Lowest identified taxonomic level	DS	WS	DS	WS	DS	WS	DS	WS
Acari		14.50	25.00	33.33	55.50	28.00	34.89	47.22	79.10
Acari	Oribatidae	30.20	3.50	40.44	2.50	35.70	2.78	29.22	0.00
Annelida		0.00	0.00	0.11	0.25	0.10	0.00	0.22	0.57
Araneae		4.80	6.25	4.78	4.75	7.00	16.33	6.22	20.86
Blattodea	Cockroaches	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14
Blattodea	Isoptera	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.00
Coleoptera		0.60	1.00	0.33	0.50	0.70	0.11	0.67	4.00
Coleoptera	Apenes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	Cucujiformia	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.14
Coleoptera	Hypothenemus	0.10	0.25	0.22	0.25	0.20	0.00	0.44	0.00
Collembola		1.10	0.25	2.56	0.00	1.80	0.00	3.00	0.00
Collembola	Entomobryomorpha	10.40	13.25	20.11	8.50	14.00	14.33	21.22	17.14
Collembola	Poduromorpha	3.60	1.00	4.22	11.00	2.40	3.33	1.89	6.00
Collembola	Symphypleona	0.00	1.75	0.00	2.25	0.00	2.22	0.00	2.10
Dermaptera	Dermaptera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dictyoptera		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Diplopoda		1.20	0.00	5.11	0.25	3.30	0.44	2.78	0.00
Diplura		0.40	0.00	0.11	3.25	0.00	0.56	0.00	4.86
Diptera		1.40	3.75	1.78	5.75	3.80	2.11	2.89	8.43
Diptera	Phoridae	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda		0.60	0.00	1.11	0.75	0.40	0.78	0.33	1.00
Geophilomorpha		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Glomerida		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Haripacticoda		0.00	0.00	0.00	0.00	0.00	0.78	0.00	0.00
Hemiptera		0.40	0.25	0.44	0.00	0.70	0.11	0.89	0.29
Hemiptera	Cicadellidae	0.30	0.75	0.11	0.25	0.20	0.00	0.00	0.43
Hemiptera	Delphacidae	0.00	0.00	0.44	0.00	0.10	0.00	0.00	0.14
Hemiptera	Psyllidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hymenoptera		0.60	0.25	0.79	0.75	0.60	0.00	1.78	0.71
Hymenoptera	Chalicoidae	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00
Hymenoptera	Formicidae	23.90	27.50	15.78	0.50	14.50	9.44	59.00	36.29
Isopoda		0.80	1.00	1.22	0.75	0.40	1.56	0.22	0.57
Larvae		1.60	1.25	0.89	0.25	0.60	0.78	3.22	4.57
Lepidoptera		0.10	0.00	0.11	0.25	0.30	0.11	0.33	0.43
Lepidoptera	Gelechiidea	0.00	0.50	0.00	0.75	0.50	0.11	0.11	0.57
Lepidoptera	Limacodidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Megaloptera		0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00
Megaloptera	Corydalidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mesostigmata		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Opiliones		0.00	0.50	0.00	0.25	0.00	0.00	0.00	0.14
Orthoptera		0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.14
Orthoptera	Gryllidae	0.10	0.00	0.00	0.00	0.00	0.22	0.00	0.14
Polydesmida		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polyxenida		1.00	0.00	1.56	0.50	0.70	1.11	0.00	1.29

Pseudoscorpionidae		1.70	1.75	2.00	1.25	1.30	1.56	1.00	0.43
Psocoptera		0.80	1.75	0.22	1.00	0.70	0.33	1.11	2.43
Scolopendromorpha	Zorotypus	0.10	0.00	0.00	0.00	0.00	0.00	0.11	0.00
Thysanoptera		0.70	0.25	0.33	0.00	0.00	0.00	0.33	0.00
Trichoptera		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polyxenida		0.00	0.25	0.00	0.00	0.00	0.00	0.11	0.00
Unknown sp. 14		0.10	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Unknown sp. 15		0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00
Zoraptera	Zorotypidae	0.10	0.50	0.00	1.00	0.00	0.11	0.00	0.14