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

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# Abstract

The crucial role of tropical forests in the global carbon balance is determined by tree growth and the rapid turnover of organic material. Land-use change and forest recovery from disturbance alters species- and functional diversity, which in turn can modify decomposition processes and affect ecosystem carbon and nutrient cycling. Despite numerous studies on tropical litter decomposition, the links among plant- and invertebrate diversity and microbial function are far from clear. I investigated the influence of altered functional diversity of litter species and arthropod communities on litter decomposition and soil carbon dynamics in a semi-deciduous lowland tropical forest in Panama. I used size-based arthropod exclusions and different litter mixtures in experimental mesocosms in a 60-year-old secondary forest to assess changes in soil respiration and decomposition rates within a single experimental arena. Litter mixtures represented different combinations of tree functional groups. Arthropods >2.5 mm were excluded from half the mesocosms using wire mesh. To link functional diversity above- and belowground to soil carbon dynamics, I identified arthropods in the litter and measured litter chemistry, soil $CO_2$ efflux, and litter mass loss. I found that decomposition in mesocosms was similar to that measured with the conventional litterbag method and consequently, mesocosms are an effective method to measure litter decomposition and soil respiration in a single arena. Decomposition varied among litter types, as expected based on their physical and chemical properties, whereby pioneer species litter decomposed most rapidly and old-growth-species litter decomposed the slowest. Arthropod community composition was affected by both leaf litter treatment and sampling date. These results indicate that changes in functional diversity of litter and arthropods could have wider implications for ecosystem functioning in tropical forests.

# Introduction

The decomposition of plant material is central to ecosystem functioning. Decomposition processes underpin the cycling of carbon and nutrients (Swift et al., 1979, Cadush and Giller, 1997), which in turn influences plant growth and carbon storage (Wardle 2002, Bargett 2005). As around 90% of decomposition is carried out by soil microorganisms (Barajas-Guzman and Alvarez-Sanchez, 2003), understanding the interactions between plants and soil microbial communities will be key to determining the effect of change on ecosystem processes (Hattenschwiler et al., 2005).

Soil carbon accounts for 80% of all global terrestrial carbon (Nielsen et al., 2011, Ashford et al., 2013). Determining whether the soil acts as a sink or source for atmospheric carbon dioxide is important, especially with concerns over global climate change and increasing atmospheric carbon dioxide levels (Smith et al., 2000, Fontaine et al., 2003). Tropical forests in particular are thought to act as a major sink for carbon dioxide through increased net primary production (Lewis et al., 2009). However a recent study has shown that an increase in primary productivity could result in greater release of carbon from the soil, which could offset the projected carbon storage for tropical rainforests (Sayer et al., 2011). Reliable predictive models, which account for interactions between above- and belowground processes, are required to enable robust predictions of carbon cycling and hence future atmospheric carbon dioxide levels (Moorhead et al., 1999, Del Grosso et al., 2005, Hattenschwiler et al., 2011). Both plant functional traits and decomposer functional diversity need to be taken into consideration as input variables into such models ( Hattenschwiler et al., 2011).

A number of factors affect litter decomposition. Abiotic factors include temperature, pH, and soil moisture, and they also affect biotic factors such as microbial activity (Barajas-Guzman and Alvarez-Sanchez, 2003, Blagodatskaya and Kuzyakov, 2008). Importantly,

51 although there is a growing body of evidence for the significance of diversity for a
52 number of ecosystem processes, the relationship between plant- and decomposer
53 diversity and their influence on decomposition is still largely uncharacterised (Widmer
54 et al., 1999, Griffiths et al., 2000, Prieme et al., 2002).
55 Litter decomposition is a complex process involving interactions among plant-,
56 invertebrate-, and microbial communities. Determining taxonomic richness is of little
57 use for understanding the effects of biodiversity on decomposition (Hattenschwiler et
58 al., 2011). An alternative approach is to classify organisms by function, or specific
59 relevant traits; the results to date suggest that litter functional diversity of leaf litter is a
60 better predictor of decomposition than biodiversity *per se* (Hattenschwiler et al., 2011).
61 The rate of decomposition is governed by both the physical and chemical traits of leaf
62 litter such as shape, size and lignin, nitrogen and polyphenol concentrations, which
63 determine the quality of substrate available to decomposer organisms (Berg et al., 1993,
64 Perez-Harguindeguy et al., 2000). The importance of plant diversity in decomposition
65 processes is demonstrated by litter mixture experiments. Decomposers preferentially
66 break down high-quality litter first, resulting in the release of nutrients, particularly
67 nitrogen (Hattenschwiler et al., 2005). This enables the transfer of nutrients to facilitate
68 the decomposition of low-quality litter (Hattenschwiler et al., 2005). Consequently, a
69 number of experiments have demonstrated that litter mixtures decompose at a greater
70 rate than single-species litter (Seastedt 1984, Gartner and Cardon, 2004). Furthermore,
71 heterogeneous litter mixtures also provide a greater variety of microhabitats and this
72 diversity of resources and habitat space can increase the diversity of decomposer
73 organisms through niche partitioning (Hansen and Coleman, 1998, Hattenschwiler et al.,
74 2005)
75 The relationship between microbial functional diversity and decomposition is less clear
76 ( Scheu et al., 2002, Hattenschwiler et al., 2005). Previous work suggests that microbial
77 diversity influences decomposition by increased microbial exploitation of leaf litter

78 through functional niche complementarity (Loreau, 2001). There is evidence for
79 significant effects of decomposer community complexity on decomposition rates in the
80 tropics (Makkonen et al., 2012) and microbial succession during decomposition has also
81 been observed (Frankland, 1998). However, other studies found little evidence that
82 microbial diversity affects decomposition rates (Schimel, 1995, Wardle and Barker,
83 1997, Wardle et al., 1997).
84 Soil- and litter invertebrate communities also play an important role in litter
85 decomposition. Soil invertebrates involved in litter decomposition can be classed as
86 ecosystem engineers or litter transformers. Ecosystem engineers are typically 5-100
87 mm in length and include, for example Isoptera and Oligochaeta (Lavelle, 1996, Ruiz et
88 al., 2008). They move through the soil, changing its physical structure, mixing organic
89 matter into the mineral soil and decreasing soil density (Knoepp et al., 2000). This
90 results in the formation of a number of habitats suitable for other soil dwelling
91 organisms (Lavelle, 1996). Ecosystem engineers can also feed directly on litter due to
92 the symbiotic relationships with microorganisms in their gut. Litter transformers
93 include mesofauna (<2mm in length) such as Collembola and macrofauna (>2mm in
94 length) such as Isopoda (Verhoef and Brussaard, 1990, Ruiz et al., 2008). They feed on
95 the litter and associated microbial organisms.
96 The modification and comminution of leaf litter by soil invertebrates stimulates
97 decomposition by increasing leaching and exposing a greater leaf surface area to
98 microbial attack (Ashford et al., 2013) The activity of soil invertebrates thus indirectly
99 affects the resources available to microorganisms and plants (Giller, 1996, De Deyn et
100 al., 2004, Ashford et al., 2013) and rates of carbon cycling via decomposition can be
101 positively related to arthropod species richness ( Nielsen et al., 2011, Ashford et al.,
102 2013). Changes in land use will alter the diversity and community composition of
103 arthropod functional groups through extinction (Lavelle et al., 1997). Extinction
104 scenarios predict that larger species will be the first to go extinct (Duffy, 2003,

105 Woodward et al., 2005). If the same is true for decomposer organisms, it could affect
106 organic matter cycling because the functional diversity of decomposers has a major
107 impact on decomposition and the loss of large species can slow the cycling of carbon and
108 nutrients from litter (Handa et al., 2014).

109 Despite their importance, especially in tropical ecosystems, the contribution of soil
110 fauna to decomposition is frequently overlooked (Gonzalez and Seastedt, 2001, Wall et
111 al., 2008, Chapin et al., 2009, Brovkin et al., 2012, Makkonen et al., 2012). Soil
112 communities are extremely diverse and consist of organisms connected by complex
113 interactions (Ashford et al., 2013). Many soil invertebrates are food generalists
114 (Petersen, 2002, Maraun et al., 2003) and redundancy in soil communities is thought to
115 be high (Ponsard and Arditi, 2000). However, previous work demonstrated that
116 arthropod diversity was related to the concentrations of phosphorus, calcium and
117 sodium in the leaf litter (Ashford et al., 2013). This suggests that the diversity of
118 arthropod communities is linked to the quality or diversity of resources, supporting
119 work by Hattenschwiler and Gasser (2005) who found that the interactions between
120 macroarthropods and litter species are highly specific.
121 Despite multiple lines of evidence for links among plant-, invertebrate- and microbial
122 diversity and their influence on decomposition, few studies have experimentally tested
123 how interactions between the functional diversity leaf litter and soil invertebrates affect
124 microbial activity, especially in important and highly diverse ecosystems such as
125 tropical forests ( Hattenschwiler et al., 2005, Hattenschwiler et al., 2011, Makkonen et
126 al., 2012) . Critically, the role of larger soil animals is often overlooked, as many previous
127 decomposition experiments used mesh litterbags (Hattenschwiler et al., 2005), which
128 often exclude macro-arthropods and can create unnatural conditions by changing the
129 physical environment (Levings and Windsor, 1996, Hattenschwiler et al., 2005) .
130 My project investigated the influence of litter functional diversity and arthropod
131 communities on decomposition rates and soil respiration in a semi-deciduous lowland

tropical forest in Panama. I established a six-month litterbag and mesocosm experiment in order to determine litter decomposition and the corresponding soil respiration in different arthropod exclusion treatments and litter mixtures. By excluding arthropods greater than 2.5 mm in size, I simulated the changes in community composition due to extinction events to determine whether these changes influence decomposition, a key ecosystem process. I aimed to answer the following research questions:

**1.** Are decomposition rates measured in mesocosm experiments comparable to those measured using the conventional litterbag method?

**2.** How do decomposition rates, soil respiration and soil properties differ among litter mixtures from distinct functional groups of trees?

**3.** Is the decomposition of different litter mixtures linked to arthropod abundance and community composition?

# Methods

## *Study site*

I established my experiments in *c.* 60-year old secondary semi-deciduous lowland tropical forest on the Gigante Peninsula within the Barro Colorado Nature Monument, Panama (Appendix 1). 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 has relatively high exchangeable potassium, magnesium, calcium and total nitrogen concentrations and a relatively low concentration of phosphorus (Cavalier, 1992, Sayer et al., 2006). Soil pH is *c.* 5.5 (Cavalier, 1992, Sayer et al., 2006). Fieldwork commenced before the onset of the wet season in April, to capture the transitional phase between the dry and wet season and the resulting changes in forest arthropod community, rates of litter decomposition and soil respiration.

## *Litter mixtures*

To investigate differences in litter decomposition for different functional groups of trees, I used litter treatments representing pioneer species, old-growth species and a mixed litter treatment containing an equal mass of litter from both functional groups. I also included a single-species treatment with litter of *Cecropia peltata* L., a common pioneer tree in the study area (Table 1). As a control, I used natural mixed litter from the study site, where tree species composition includes both pioneer and old-growth forest species (D. Dent, pers. comm).

## *Soil Respiration and Litter Decomposition Rates*

To measure leaf litter decomposition and the corresponding soil respiration in different litter mixtures and arthropod treatments, I installed 20 mesocosms in each of five replicate blocks, giving a total of 100 mesocosms. I applied two size-based arthropod exclusion treatments and five different litter mixtures (Table 1) to the mesocosms in a factorial design, giving a total of 10 treatment combinations. Within each replicate block, there were two sets of mesocosms for each treatment to allow destructive sampling of one set after three months; the remaining set was harvested after six months.

The mesocosms consisted of plastic tubes (20cm in diameter and 12 cm in height) with four 5-cm diameter holes drilled into the side at equal intervals to allow access by arthropods (Fig. 1).

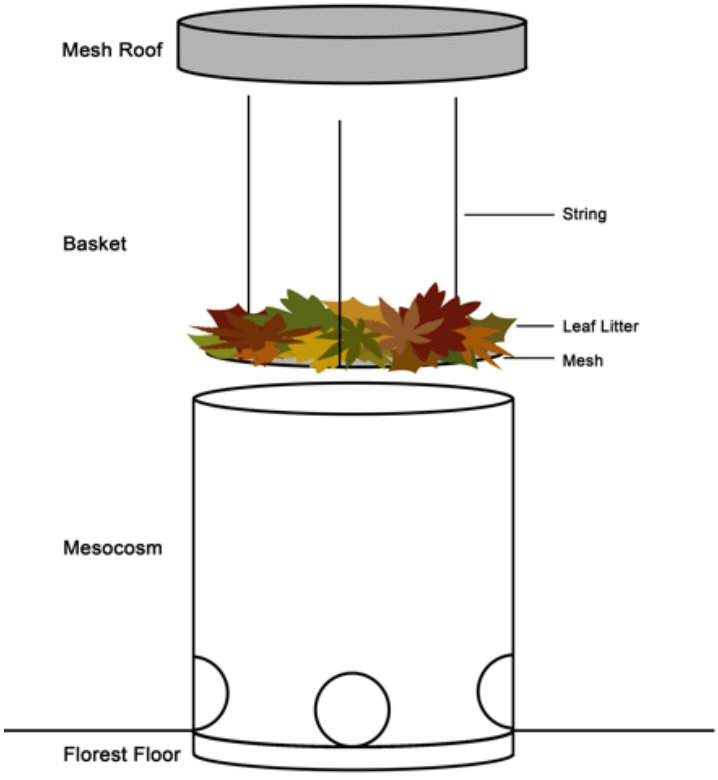



**Figure 1:** Schematic diagram of the mesocosms used to measure litter decomposition and associated soil respiration and arthropod communities in a 6-month experiment in a lowland tropical forest in Panama.

In half of the mesocosms ('exclusion treatment'), the holes were covered with 2.5-mm galvanised steel mesh to exclude arthropods greater than 2.5 mm in size. In the other half ('inclusion treatment'), the holes were left open to allow arthropods of all sizes to enter the mesocosm. The mesocosms were inserted approximately 2 cm into the soil so that the access holes for arthropods were at ground level. Leaf litter from inside the mesocosms was removed and the soil cleared of debris.

To determine respiration from the mineral soil, I installed two soil additional mesocosms without access holes (henceforth 'soil collars') in each block. Leaf litter and debris was removed from inside the collars.

To enable measurements of litter mass loss in the field, I placed a pre-weighed 19-cm diameter mesh disc on the soil surface within each mesocosm. Three pieces of string were attached to the mesh disc to enable easy removal and prevent leaf litter disturbance; this is henceforth referred to as 'basket' (Fig. 1). I placed 16.1g of leaf litter from one of the five treatments (Table 1) loosely on top of the basket to ensure a continuous litter layer between the litter inside the mesocosm and the surrounding area. The mass of litter was chosen to represent the litterfall in the study area in February 2015, estimated from existing litter traps. Control litter was collected from litter traps at the experimental site; leaf litter for the other four treatments was collected in the same forest type on Barro Colorado Island, *c*. 2-km from the study site. Immediately after collection, the litter was dried to constant weight at 35ºC.

**Table 1:** The five leaf litter treatments used in a six-month decomposition experiment in lowland tropical forest in Panama; the litter 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. |
| Control | Mixed leaf litter from the study site |
| Pioneer and old growth | *Dipteryx panamensis* |
| | *Tetragastris panamensis* |
| | *Prioria copaifera* |
| | *Ochroma pyramidale* |
| | *Cecropia peltata* |
| | *Luehea seemannii* |
| Single species | *Cecropia peltata* |

To exclude natural litterfall, a 5-mm mesh roof was placed over each mesocosm and soil collar. After two months, the roofs on the exclusion treatments were replaced with 2.5-mm mesh because I observed that macroarthropods were entering the mesocosms from above.

Mesocosms were installed in April 2015 and left undisturbed for 16 days after installation. I applied the leaf litter treatments on the 6$^{th}$ of April 2015 and took initial soil temperature and soil water content measurements for each mesocosm. Soil temperature, soil water content, litter decomposition and soil $CO_2$ efflux measurements were then taken fortnightly for the first three months and monthly for the remaining three months. Mean soil moisture content was determined from three measurements taken within a 1-m radius around each mesocosm using a Thetaprobe (Delta-T Devices, Cambridge, UK). Soil temperature was measured at 0-10 cm depth within a 1-m radius of each mesocosm using a soil temperature probe (Fisher Scientific, Leicestershire, UK).

I measured litter mass loss in the field by carefully removing the basket with the leaf litter and placing it on a portable balance (Ohaus, New Jersey, USA) to measure fresh weight. To estimate the dry weight of the litter, I installed two additional baskets in each experimental block every month. The additional baskets contained either *Cecropia* or control litter; they were placed on bare soil and covered with a 5-mm mesh roof. I collected the additional samples on the same day as the monthly mass loss measurements, measured fresh weight in the field and then determined the litter water content after drying the samples to constant weight at 40ºC.

For measurements of soil $CO_2$ efflux, I sealed the holes in the side of the mesocosms with wide elasticated bands and a plastic ring. I tested the system for leaks and found no significant difference between the $CO_2$ efflux of mesocosms and soil collars. Soil $CO_2$ measurements were made using an infra-red gas analyser with a 20-cm diameter soil survey chamber (Li-8100, LiCor Biosciences, Nebraska, USA). The volume of each mesocosm was determined from three height measurements on the insides of the mesocosms and measurements were taken during 240 minutes, with a dead-band of 30 seconds after chamber closure

### *Litter Decomposition Rates Using Litter Bags*

To compare decomposition rates in the mesocosms with the conventional litterbag method, I installed four litterbags for each litter treatment within each block. Litterbags were constructed of 2.5-mm nylon mesh and measured 17.7-cm × 17.7-cm, to give the same total area as the mesocosms (314.16 $cm^2$), and each received 16.1 g of leaf litter. I placed the bags on bare soil in the same experimental blocks as the mesocosms and secured them with nails. During mesocosm measurements, I carefully removed any leaf litter than had fallen onto the litterbags. In a few cases, I observed holes in the bags, possibly due to animal activity; and these were sewn up as soon as they were detected. I

collected two bags per litter treatment and block after three and six months, weighed their fresh weight and then stored them in the fridge until they could be processed. The leaf litter was carefully separated from the bag and washed for 75 seconds under a continuous stream of water. The litterbags and corresponding litter samples were oven-dried to constant weight at 40ºC and then weighed separately.

I calculated the decay rate $k$ for all litter treatments in litterbags and mesocosms from total mass loss at 6 months according to Olson (1963; Equation 1):

$$\ln (X/X_o) = - kt \quad \text{(Eq 1)}$$

Where $t$ is time, $X$ is litter dry mass at collection and $X_o$ is the litter dry mass at time zero

### *Arthropod diversity and abundance*

To determine the abundance and diversity of litter arthropods at the study site, I collected four litter samples from each block seven days after installation by placing a 20-cm diameter tube on the forest floor and cutting around it before collecting the litter inside the tube and placing it into plastic bags. I collected additional samples in the same manner after three months to compare with arthropod communities in the mesocosms.

To determine arthropod communities within the mesocosms, I harvested the litter from one set of 10 mesocosms (one per treatment) per block after three months and the second set at the end of the study after six months. I carefully removed the baskets and litter from each mesocosm and placed them in plastic bags. 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 the samples from drying out. Arthropods were extracted during 48 hours and stored in 95% ethanol. Subsamples of litter were taken

and examined by microscope to monitor the efficacy of the extraction, as previous studies have found that some arthropods are killed in the funnels (Ashford et al., 2013). After 48 hours, all litter samples were oven-dried to constant weight at 40ºC and the litter and baskets were weighed separately.

I identified arthropods at least to order following Gibb and Oseto (2006) and measured them to the nearest 0.02 mm using a dissecting microscope with an optical micrometer. I calculated Simpson's diversity and Shannon's evenness for each sample according to Hill (1973). Due to time constraints, the single-species *Cecropia* litter treatment was not included for arthropod identification and was therefore excluded from all comparisons of arthropod communities.

### *Soil Analysis*

Once the baskets and litter had been collected during the three- and six-month harvests, I took soil cores at 0-5 cm and 5-10 cm depth from inside the mesocosms and all samples were immediately returned to the lab. I measured the soil pH of all samples in a 1:3 mixture of sieved fresh soil and deionised water using a STARTER 2100 Bench pH meter (OHAUS, New Jersey, USA). I measured total soil carbon and nitrogen content on subsamples collected at six months using a vario ELIII Element analyser (Elementar, Hessia, Germany).

### *Statistical Analysis*

All statistical analyses were performed in R version 3.2.2 (Team, 2015) using the lme4 package (Bates et al., 2015) for linear mixed effects models and the vegan package (Oksanen et al., 2007) for multivariate analyses; non-normally distributed data were

log-transformed prior to analysis and appropriate error distributions were selected for Generalised Linear Models.

**Litter decomposition, soil respiration and soil properties**

Preliminary analyses showed that arthropod exclusion had no effect on decomposition rates, soil respiration or other measured soil parameters and all analyses of mesocosm data were therefore based on the means per litter treatment and block for each time point.

To assess treatment effects on litter decay rate ($k$) and mass loss during decomposition, I used Generalised Linear Models (GLMs). As the number of blocks (five) was less than the recommended number of levels required for a linear mixed effects models, block was included as a fixed effect to account for non-independence of measurements among blocks (Gelman and Hill, 2007). Preliminary analyses showed that decomposition rates also varied among replicate blocks and consequently, 'block' was retained as a term in all analyses (Appendix 2 - model outputs). The maximal models included litter treatment, experiment type, and the interaction between treatment and type, including block as a fixed effect. The models were simplified by sequentially dropping terms until a minimal adequate model was identified following procedures recommended by Crawley (2007).

To identify patterns in decomposition during the dry season and the wet season, I performed separate analyses for mass loss during the first three months and the final three months.

To establish treatment effects on soil respiration, I used linear mixed effects models (lmer function in the lme4 package (Bates et al., 2015) with litter treatment, arthropod exclusion and their interaction as fixed effects and block and time as random effects.

I used GLMs to assess the effect of litter treatment on soil pH and the soil C:N ratio within the mesocosms at the end of the experiment.

**Arthropod diversity, abundance and community composition**

I used GLMs to model Shannon's diversity (*H*), Simpson's evenness (*D*) or total abundance as a function of litter treatment, arthropod exclusion treatment, block, time and the interaction between litter and exclusion treatments.

To explore the efficacy of the arthropod exclusion treatments, I compared both mean arthropod body length and maximum arthropod body length in inclusion and exclusions mesocosms across litter treatments using GLMs.

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 were assessed by permutational multivariate analysis of variance (PerMANOVA; *adonis* function) after testing for homogeneity of dispersions among treatments (*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 treatments, including mesocosm type (nested within litter treatment), collection time, and their interaction.

# Results

## *Litter decomposition*

### Effects of experiment type on litter decomposition

Litter decay rate ($k$) was best explained by experiment type, litter treatment, block and the interaction between experiment type and litter treatment (minimum adequate model; Appendix 2.1 - 2.3). Across all litter treatments, the litter decay rate ($k$) was similar in litterbags and mesocosms but the pattern of mass loss over time differed between the types of experiment. In the dry season (months 0-3), mass loss from litter in bags was significantly higher compared to litter in mesocosms ($t$ = -7.958, $p$ < 0.001; Appendix 2.2), whereas in the wet season (months 3-6), mass loss was greater in mesocosms ($t$ = 2.133, $p$ = 0.041; Fig. 2; Appendix 2.3).

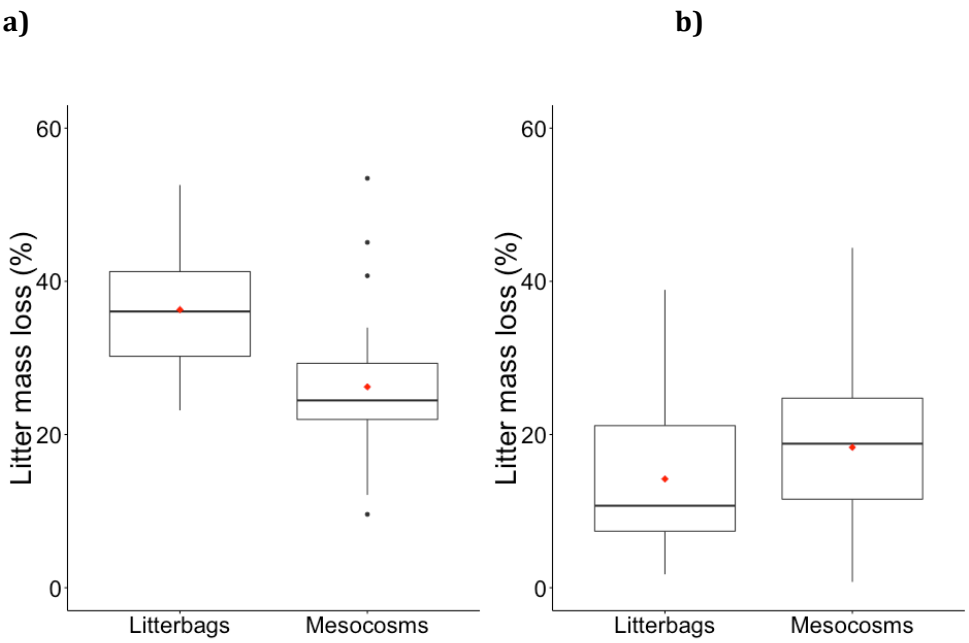



**Figure 2:** Relative mass loss from litter in litterbags and mesocosms in a decomposition experiment in a lowland tropical forest in Panama during **a)** the dry season (months 0-3) and **b)** the wet season (months 3-6). Red diamonds indicate the mean for $n$ = 24 for litterbags and $n$ = 22 for mesocosms.

328 **Effects of litter treatment on litter decomposition**

329 Regardless of the type of experiment, the decay rate $k$ differed significantly among
330 treatments, whereby $k$ for *Cecropia* litter > pioneer litter > control litter > mixed litter >
331 old-growth litter (Table 2). The greatest proportion of mass loss occurred in the first
332 three months, even though this was during the dry season (Fig. 3). The mass loss of
333 *Cecropia* litter was greater than all other litter treatments both during the dry season
334 (months 0-3: $t$ = 7.685, $p$ < 0.001; Fig. 3, Fig. 4) and during the wet season (months 3-6: $t$
335 = 3.208, $p$ = 0.003; Fig. 3, Fig. 4). Mass loss of the old growth litter mixture was
336 significantly lower than any of the other treatments during the dry season (0-3 months:
337 $t$ = -4.450, $p$ < 0.001), whereas mass loss of the pioneer litter mixture was marginally
338 greater than the mixed litter and old-growth litter treatments during the wet season (3-
339 6 months pioneer litter: $t$ = 1.834, $p$ = 0.076; Fig. 3, Fig. 4).

**Table 2:** Properties of leaf litter species and mixtures used in a decomposition study in lowland tropical forest in Panama; mean leaf surface area are given for *n* = 9 per species, carbon to nitrogen ratios (C:N) are given for *n* = 3 analytical replicates per species and litter decay rate (*k*) are given for *n* = 5 samples.

| Species/Mixture | Functional Group | Specific leaf area ($mm^2$) | C:N | Decay rate k |
|---|---|---|---|---|
| *Dipteryx panamensis* | OG | 43.58 ± 16.61 | 36.41 ± 0.90 | |
| *Tetragastris panamensis* | OG | 33.14 ± 5.65 | 57.05 ± 4.34 | |
| *Prioria copaifera* | OG | 42.87 ± 10.21 | 46.67 ± 1.04 | |
| *Cecropia peltata* | PI | 826.32 ± 242.54 | 44.58 ± 0.41 | 3.37 ± 0.60 |
| *Luehea seemannii* | PI | 83.94 ± 37.53 | 44.13 ± 2.70 | |
| *Ochroma pyramidale* | PI | 301.57 ± 186.03 | 76.50 ± 5.23 | |
| Control | | 42.69 ± 34.08 | 40.36 ± 1.53 | 1.21 ± 0.26 |
| Old growth (OG) | | 39.86 ± 10.82 | 46.71 ± 2.09 | 0.72 ± 0.16 |
| Pioneer (PI) | | 413.94 ± 155.37 | 55.07 ± 2.78 | 1.51 ± 0.23 |
| Mixed | | 226.90 ± 166.19 | 50.89 ± 2.44 | 0.86 ± 0.10 |

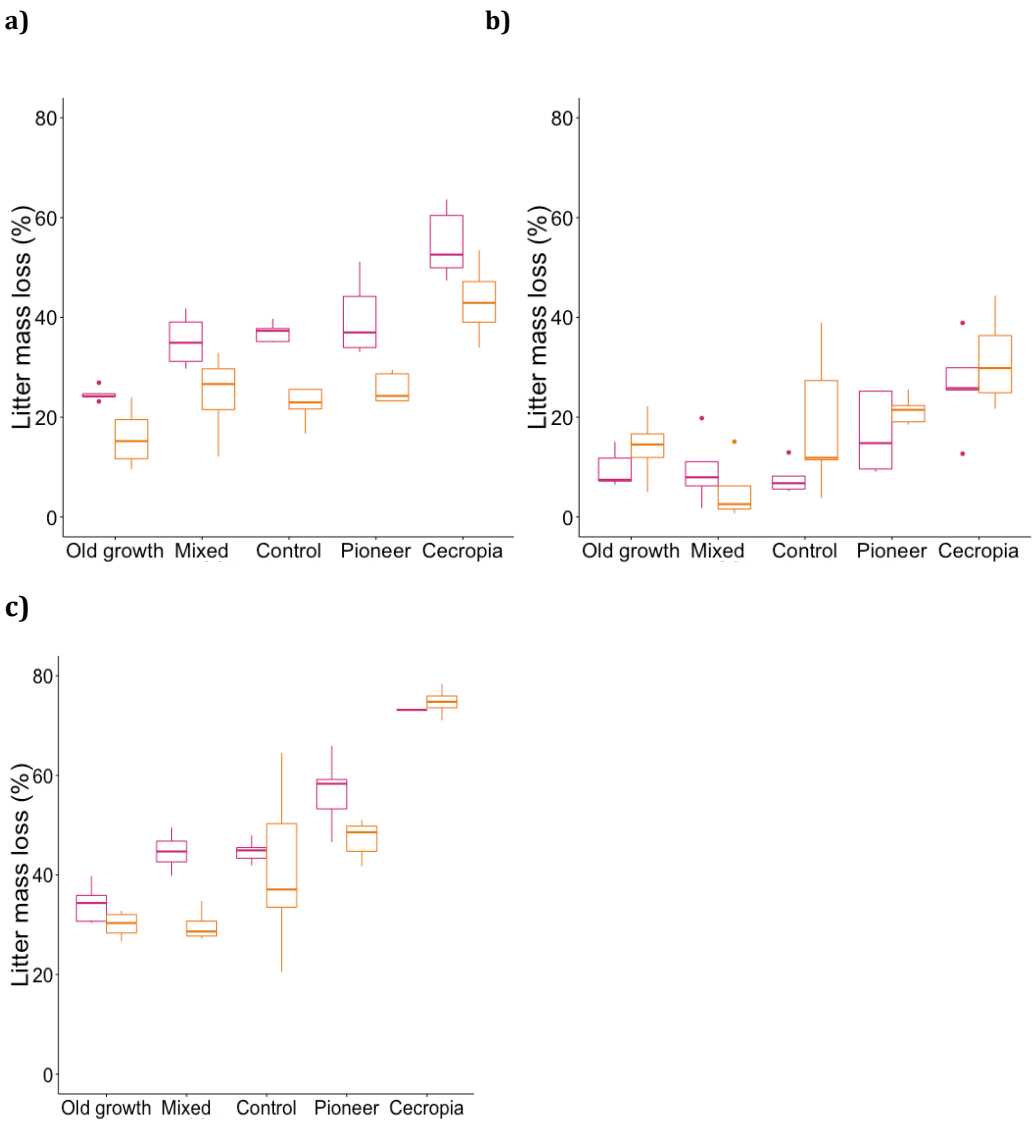



**Figure 3:** Boxplots of mass loss during litter decomposition in mesocosms (orange) and litterbags (pink) for different leaf litter mixtures in a lowland tropical forest in Panama during **a)** the dry season (months 0-3), **b)** the wet season (months 3-6) and **c)** the whole 6-month study period.

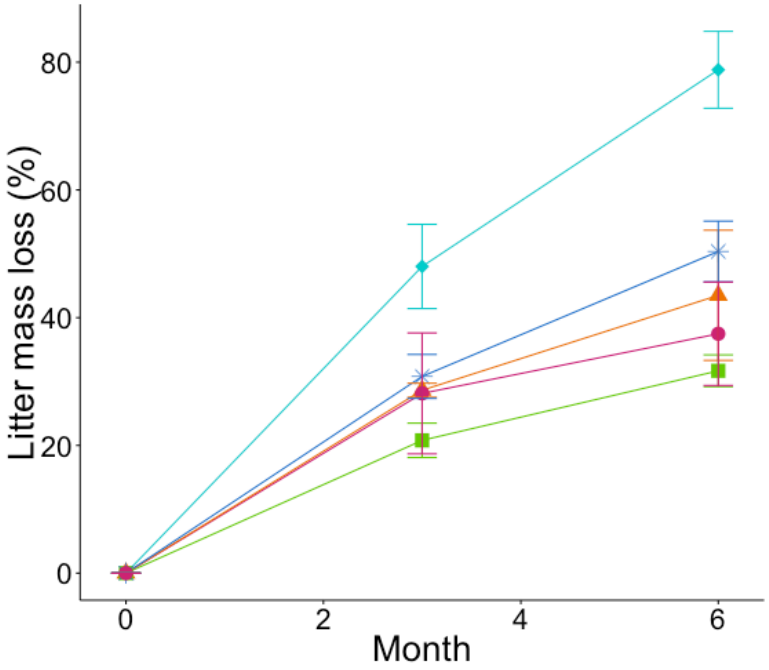
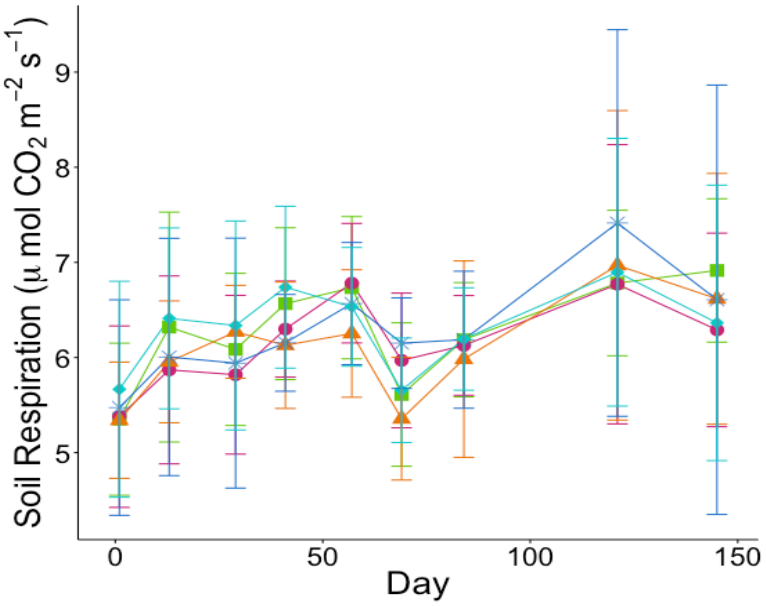



**Figure 4:** Mean mass loss from litterbags and mesocosms during six months of decomposition in a lowland tropical forest in Panama; where green squares indicate old growth, pink circles indicate mixed litter, orange triangles indicate control litter, blue stars indicate pioneer litter and turquoise diamonds indicate *Cecropia* litter; means and standard deviations are shown for $n = 5$.

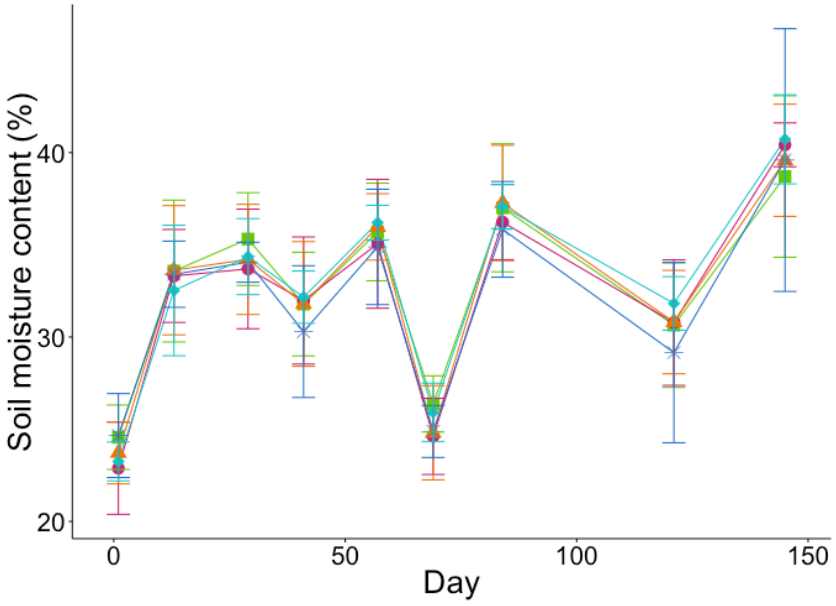
## ***Soil Respiration***

Soil respiration did not differ among litter treatments (Appendix 2.4). However, there was a clear seasonal pattern in soil respiration, which tracked changes in soil water content. Soil respiration in the dry season (6.271 µmol $CO_2$ $m^{-2}$ $s^{-1}$) was *c.* 13% lower than in the wet season (7.168 µmol $CO_2$ $m^{-2}$ $s^{-1}$; Fig. 5).

**a)**


Soil Respiration (μ mol $CO_2$ $m^{-2}$ $s^{-1}$)
9
8
7
6
5
0
50
100
150
Day

**b)**


Soil moisture content (%)
40
30
20
0
50
100
150
Day

**c)**

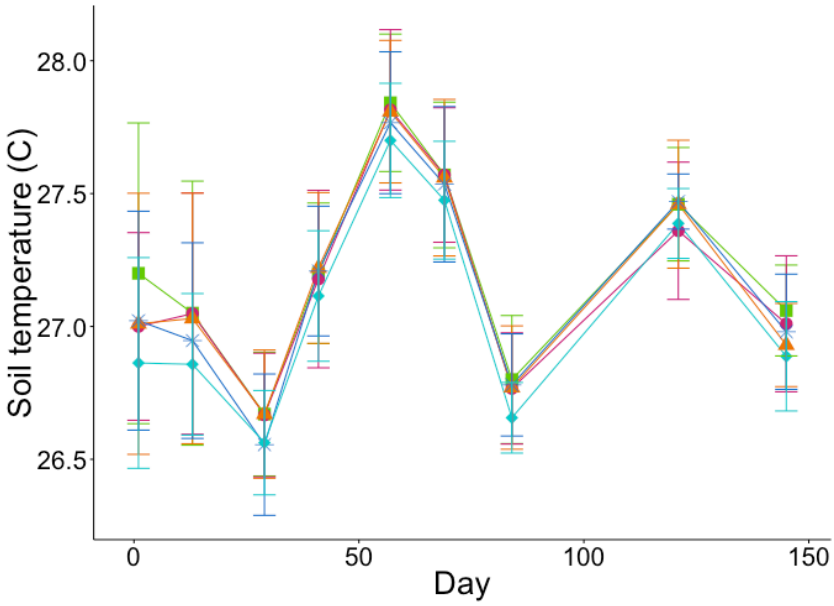



**Figure 5**: **a)** Soil $CO_2$ efflux, **b)** soil water content, and **c)** soil temperature during six months in a lowland tropical forest in Panama; where green squares indicate old growth, pink circles indicate mixed litter, orange triangles indicate control litter, blue stars indicate pioneer litter and turquoise diamonds indicate *Cecropia* litter; means and standard deviations are shown for $n$ = 5 for old growth, pioneer, mixed litter and control, and $n$ = 4 for *Cecropia*.

## ***Soil and litter properties***

I found no clear pattern in litter C:N ratios among species or mixtures of different functional groups (Table 2) and there were no differences in soil C:N ratio among mesocosms with different litter treatments after six months (Appendix 2.5). Soil pH at 0-5 cm was significantly higher in mesocosms with *Cecropia* and pioneer litter compared to the other litter treatments after six months of decomposition (Cecropia: t = 2.573, $p$ = 0.0212; pioneer: $t$ = 2.795, $p$ = 0.0136; Fig. 6; Appendix 2.6).

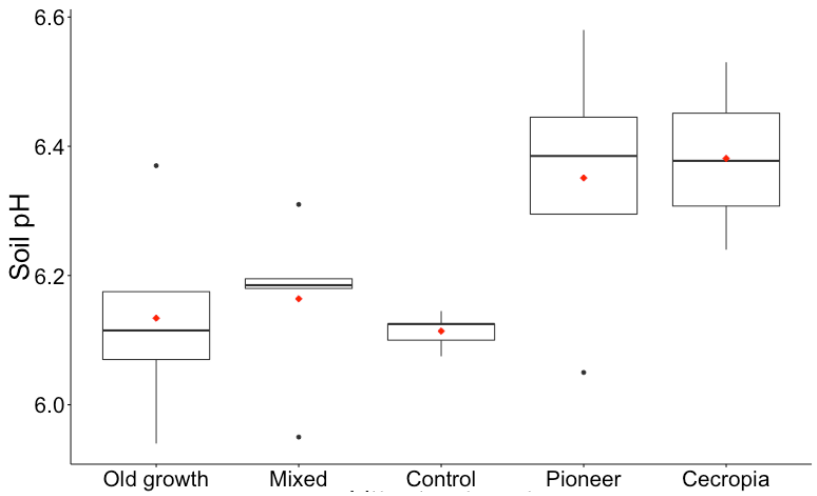



**Figure 6:** Soil pH in mesocosms with different litter treatments after six months of decomposition in a lowland tropical forest in Panama. The red diamonds represent mean soil pH for $n$ = 5 for old growth, pioneer, mixed litter and control, and $n$ = 4 for *Cecropia*.

## ***Arthropod abundance, diversity and evenness***

The diversity, evenness and abundance of arthropods was influenced by litter treatment, block, collection time, arthropod exclusion treatment and the interaction between litter treatment and arthropod exclusion treatment (minimal adequate model, Appendix 2.7 - 2.9). 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 marginally greater at six months than at three months ($S$: $t$ = 1.843, $p$ = 0.0715; $D$: $t$ = 1.898, $p$ = 0.0637).

Litter treatment alone had no significant effect on the evenness or diversity of arthropods but the abundance of arthropods was significantly greater in the old growth litter compared to the other litter treatments ($t$ = 2.255, $p$ = 0.0287; Fig. 7).

Across all litter treatments there was no significant difference in arthropod mean or maximum body length between inclusion and exclusion mesocosms at either three or six months.

**Table 3:** Mean abundance, number of taxa, Shannon's Diversity and Simpson's Evenness for arthropods in different litter treatments in a decomposition study in a lowland tropical forest in Panama; means at three months are for *n* = 5 per treatment and at six months for *n* = 5 for old growth litter, *n* = 4 for pioneer and mixed litter and *n* = 3 for controls.

| Leaf litter treatment | Mean abundance | | Total no. of taxa | | Shannon Index | | Simpsons Index | |
|---|---|---|---|---|---|---|---|---|
| Month | 3 | 6 | 3 | 6 | 3 | 6 | 3 | 6 |
| Control | 53.70 | 56.00 | 24.00 | 21.00 | 1.55 | 1.74 | 0.76 | 0.75 |
| *Cecropia* | 61.33 | NA | 24.00 | NA | 1.69 | NA | 0.79 | NA |
| Pioneer | 62.67 | 48.50 | 24.00 | 24.00 | 1.63 | 1.82 | 0.71 | 0.76 |
| Mixed | 58.80 | 59.50 | 22.00 | 27.00 | 1.57 | 2.06 | 0.77 | 0.83 |
| Old growth | 63.44 | 64.71 | 25.00 | 32.00 | 1.71 | 1.66 | 0.73 | 0.72 |

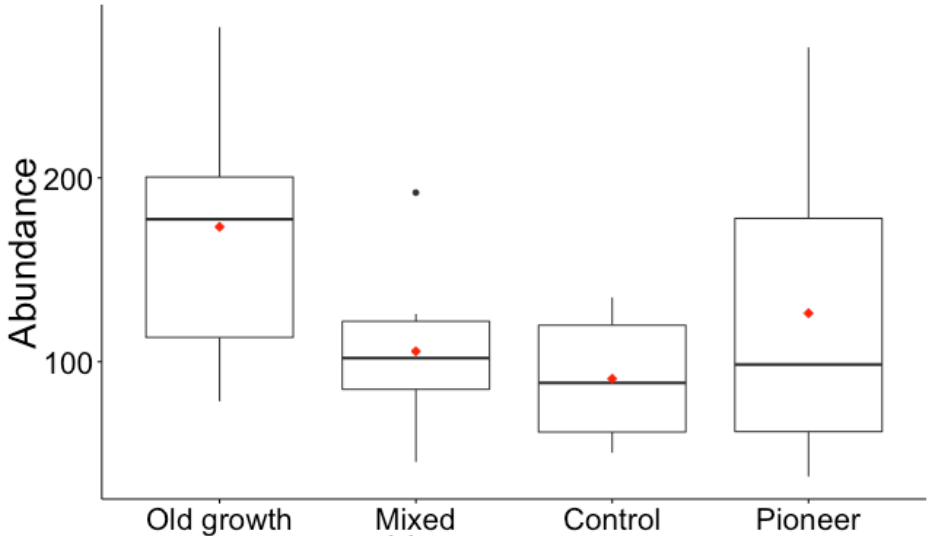



**Figure 7:** The total abundance of arthropods in different litter mixtures during a six-month decomposition experiment in a lowland tropical forest in Panama; data from collections at three and six months are pooled; red diamonds represent means for *n* = 10 for old growth litter, *n* = 9 for pioneer and mixed litter and *n* = 8 for control litter.

366 The comparison of arthropods in control mesocosms and forest floor litter samples after
367 three months showed a minor effect of mesocosm installation on community
368 composition (PERMANOVA, main treatment effect: $F_{1,24} = 1.77$, $p = 0.061$; Fig. 8).

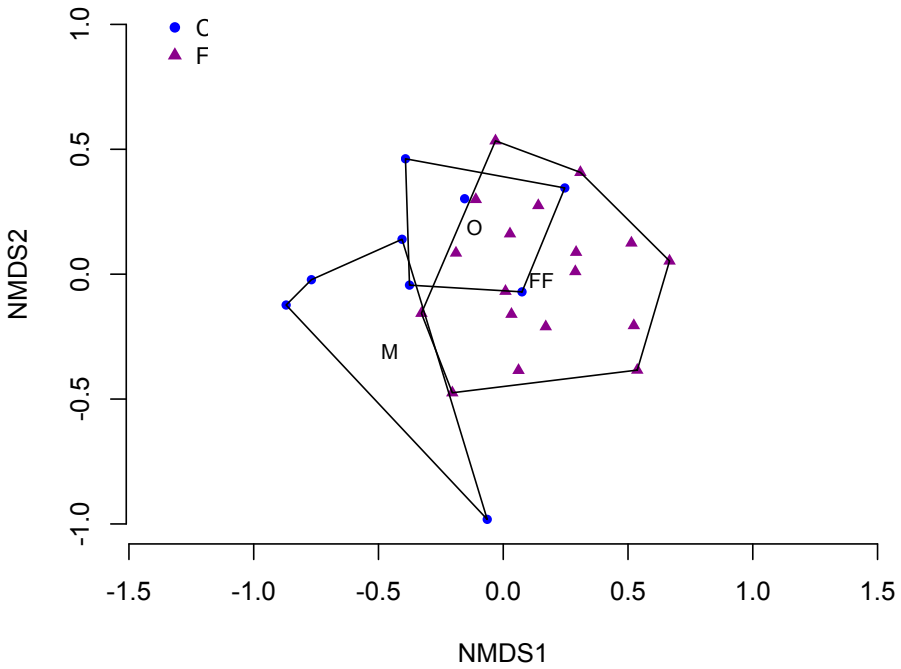
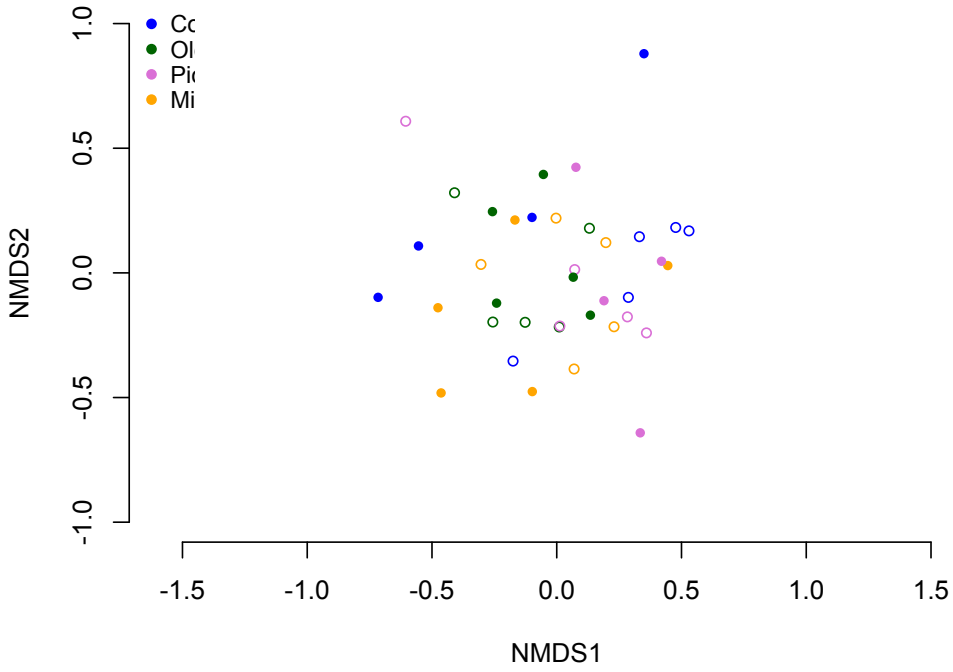


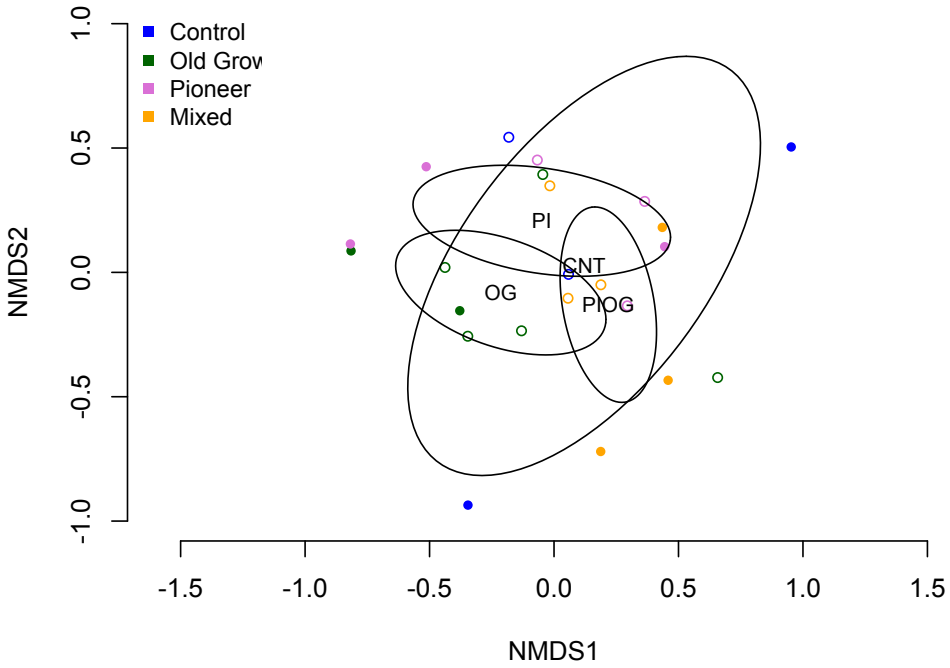

**Figure 8:** Arthropod community composition of forest floor litter and control mesocosms after three months of decomposition in a lowland tropical forest in Panama; blue circles represent control litter and purple triangles represent forest floor (FF) litter; 'O' indicates inclusion (open) mesocosms and 'M' indicates exclusion (mesh) mesocosms.

Arthropod community composition did not differ among treatments after three months of decomposition (Fig. 9a) but there was a significant effect of litter treatment after six months (PERMANOVA, main treatment effect: $F_{3,15} = 1.7$, $p = 0.01$). Ordination plots showed a clear separation of the arthropod communities in litter of pioneer tree species compared to old-growth species (Fig. 9b). There was no effect of inclusion or exclusion mesocosms at either time-point. Comparison of the arthropod communities in decomposing litter at three and six months showed that community composition diverged over time (PERMANOVA, main time effect: $F_{1,45} = 10.9$, $p = 0.001$; Fig. 9c).

**a)**


Co
Ol
Pi
Mi
NMDS2
NMDS1
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5

**b)**


Control
Old Grov
Pioneer
Mixed
PI
CNT
OG
PIOG
NMDS2
NMDS1
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5

**c)**

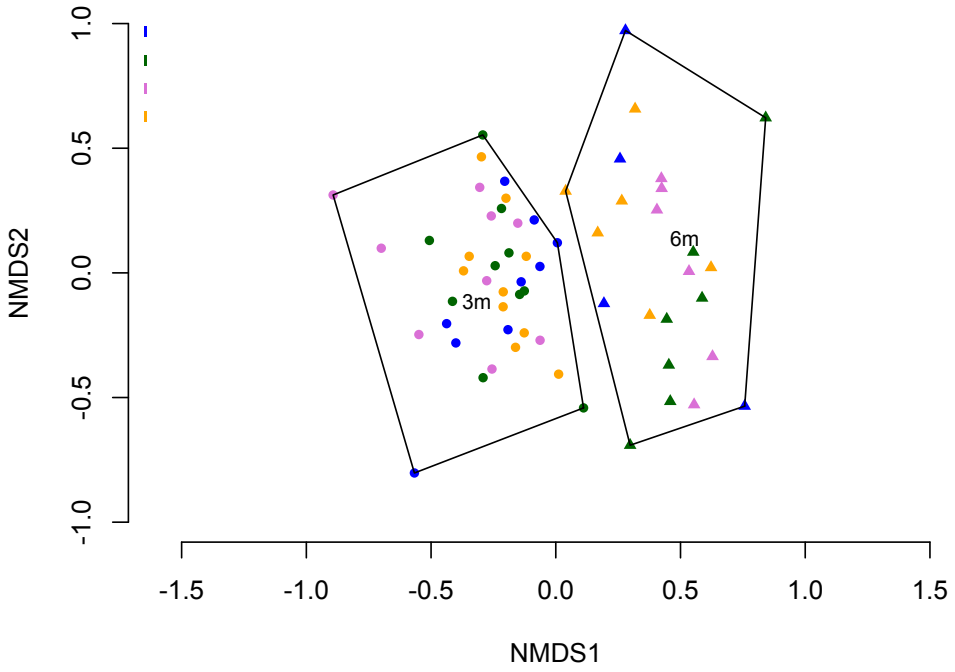



**Figure 9:** Arthropod community composition in different litter mixtures in a decomposition experiment in a lowland tropical forest in Panama at **a)** three months, **b)** six months and **c)** both three and six months; blue circles indicate control litter (CNT), green circles indicate old-growth litter (OG), pink circles indicate pioneer litter (PI), and yellow circles indicate mixed litter (PIOG); ellipses in b) indicate separation of litter mixtures in ordination space based on the standard error of the weighted average of scores.

# Discussion

I tested a novel method to measure litter decomposition in the field using mesh baskets in mesocosms. Unlike the conventional litterbag method, this approach allowed me to take soil respiration measurements over the decaying litter and investigate the short-term influence of different litter mixtures on soil properties and litter arthropod communities.

## *Comparison of litterbags and mesocosms for measuring litter decomposition*

My method comparison showed that the litter decay rate did not differ between litterbags and mesocosm over the six-month study period (Fig. 3). However, mass loss from litterbags was highest in the first three months, whereas mass loss from mesocosms was greater during months three to six (Fig. 2). This slight discrepancy can be explained by the different microenvironments in litterbags and mesocosms. Climatic conditions affect litter decomposition directly through changes in temperature and moisture, and indirectly by limiting the decomposer community and causing changes in litter quality (Berg et al., 1993, Couteaux et al., 1995, Aerts, 1997, Wardle et al., 2004a, Wardle et al., 2004b,) and one critique of the litterbag method is that they retain more water than the surrounding forest floor (Tanner, 1981, Sayer et al., 2006). As the first three months of my experiment took place during the dry season, the litterbags would have stayed moister for longer after rainfall and thus presented a more favourable environment for decomposers compared to the forest floor, where there are strong fluctuations in temperature and humidity (Gessner et al., 2010). The microenvironment in the mesocosms is more representative of natural litter on the forest floor and hence had a lower water content during the dry season. The wet season started approximately

400 half-way through the experiment and here, the mesocosms may have represented the
401 more favourable environment as the litter is less compressed.

402 Regardless of season, the initial stages of decomposition are generally rapid as the
403 readily available carbon and nitrogen is quickly used by microorganisms and arthropods
404 (Maraun and Scheu, 1996b, Maraun and Scheu, 1996a). Once most of the labile carbon
405 has been depleted, decay rates tend to slow (Wieder and Lang, 1982, Olson, 1963). The
406 litter in bags will have reached this point more rapidly because of the faster
407 decomposition in the first three months, and so decomposition rates slowed during the
408 remaining three months. Nonetheless, the two methods produced highly comparable
409 decomposition rates after six months (Fig. 3), validating the use of mesocosms for future
410 litter decomposition studies.
411 I aimed to link soil respiration rates to litter decomposition by weighing the litter in the
412 mesh baskets after the measurements of soil $CO_2$ efflux. Unfortunately, some of the mesh
413 baskets were made of non-galvanised mesh, which began to oxidise over the course of
414 the experiment. As a result, the litter weights I estimated *in situ* were inaccurate and had
415 to be excluded from my analyses. As I only had data on litter decomposition from the
416 collections at three and six months, I was unable to make a direct comparison of litter
417 decomposition and respiration rates. A number of samples were also excluded due to
418 termite activity and large amounts of soil adhering to the litter in the mesh baskets,
419 which could not be removed without losing litter material. However, as there was no
420 difference in litter decay between inclusion and exclusion mesocosms, I had sufficient
421 reliable data for each litter treatment for my analyses of decomposition.

## *Influence of litter type on decomposition rates*

Litter decomposition differed among litter types, (Fig. 3) and the decay rates were as expected based on the theoretical chemical and physical properties of litter from pioneer *vs*. old-growth species. Litter of the pioneer species *Cecropia* decomposed most rapidly in this study. *Cecropia* has low dry mass per leaf area, a high nutrient concentration and low fibre and lignin contents (Arnone et al., 1995, Hirschel et al., 1997). Thus, it is considered a high-quality resource, which decomposers preferentially break down (Hirschel et al., 1997). The pioneer mixture, which also contained *Cecropia* leaves decomposed the second fastest.

On the other hand, the old-growth litter mixture decomposed slowly over the experimental period (Fig. 3). 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 (Hattenschwiler et al., 2011).

It is worthy of note that the mixed litter decomposed at a similar rate to the control litter collected from litter traps (Fig. 3). The forest at the study site was a *c.* 60-year old secondary forest with pioneer and old-growth tree species. Hence, the mixed litter was broadly representative of the chemical and physical diversity of the litter at the study site, even though it only contained litter of six common species.

Litter chemical and physical traits are usually better predictors of decomposition of litter mixtures than species richness (Ball et al., 2008, Meier and Bowman, 2008). Although the C:N ratios of my litter mixtures did not correspond to decay rates (Table 2), other chemical properties I did not measure may have been more important. Litter traits such as lignin and polyphenol concentrations and the ratio of lignin to nitrogen limit substrate availability for soil organisms and therefore affect decomposition (Berg et al., 1993, Perez-Harguindeguy et al., 2000). Furthermore non-lignin carbon

compounds have a greater effect on litter decomposition rates compared to litter nutrients (Hattenschwiler et al., 2011) and lignin to nitrogen ratios have been found to account for little variation in the rate of decomposition (Makkonen et al., 2012). Additionally, physical leaf attributes that contribute to its water holding capacity, such as shape, size, surface structure and colour, all affect decomposition (Hattenschwiler et al., 2005).

### *Effects of spatial heterogeneity on litter decomposition*

Litter decomposition also varies as a result of spatial heterogeneity. In my study, the litter in blocks C and E decomposed more slowly compared to the other blocks. This could be the result of heterogeneity in environmental variables such as canopy openness. Block C had lower tree cover and was consequently drier than the other block, providing a less favourable environment for decomposition by microorganisms and arthropods.

### *Soil Respiration*

Soil respiration was not affected by litter treatment or arthropod exclusion. Previous work in old-growth forest near the study site noted that *c*. 20-40% of soil respiration is derived from roots (Sayer and Tanner, 2010) and root-rhizosphere respiration is likely to be higher in younger secondary forest (Hanson et al., 2000). This would possibly override any difference due to variation in decomposition rates among leaf litter treatments. Furthermore, leaf litter was not continually added to the mesocosms and as a result, the impact of litter treatment was probably marginal compared to the other factors that influence soil respiration. In my study, soil respiration was largely related

tso soil moisture content (Fig. 5), which also influences litter decomposition, so there was an overriding effect of soil moisture on soil respiration, regardless of litter type.

### *Soil chemistry*

I observed no effect of litter treatment on the soil C:N ratio after six months (Table 2). Other studies that have noted effects of litter treatments on soil chemical properties applied the treatments either continually and/or for a longer time period (Mcclaugherty et al., 1985, Hobbie, 2000, Sayer et al., 2006). It is therefore likely, that the single litter application and short duration of my study was not sufficient to affect soil surface properties. Nonetheless, soil pH was higher in *Cecropia* and the pioneer litter treatments after six months (Fig. 6). A study in temperate forest demonstrated that tree species can influence soil pH via organic acids (Finzi et al., 1998) and it is possible that the rapid decomposition of pioneer species produced a greater immediate effect on soil surface pH.

### *Arthropod abundance, biodiversity and dominance*

The exclusion treatment was not as effective as hoped, as I found no differences in mean or maximum body size, arthropod abundance, diversity or community composition between the inclusion and exclusion mesocosms. It is possible that the exclusion mesocosms excluded larger arthropods, but as these arthropods are relatively rare in the community, compared to smaller arthropods such as Isoptera and Acari, no overall difference in community composition was observed as a result of the exclusion treatments (Peterson and Luxton, 1982). However, arthropod community composition at three months differed markedly between forest floor samples and the control litter in

492 the mesocosms (Fig. 8), which indicates that the mesocosms probably exclude a number
493 of arthropods, irrespective of whether they have access holes. Alternatively, the
494 disturbance to the litter in the mesocosms and the lack of fresh litter inputs over time
495 could also have altered arthropod community composition.

496 Surprisingly, I found few effects of litter mixtures on arthropod abundance, diversity,
497 evenness or community composition. Nonetheless, the abundance of arthropods was
498 greater in old growth litter at both three and six months, which may be a result of
499 greater litter mass and habitat structure in the old-growth litter relative to rapidly
500 decomposing litter mixtures (Sayer et al., 2010). Previous studies show that there is a
501 degree of redundancy in taxonomic richness as decomposition rates saturate at low
502 species richness (Setala and McLean, 2004, Hedde et al., 2010). Consequently, arthropod
503 functional diversity is a better predictor of soil process rates than arthropod species
504 diversity (Coulis et al., 2015). Although I was unable to investigate this within the scope
505 of the present study, I aim to use the data I have collected to compare functional
506 diversity of arthropod samples across litter and exclusion treatments in future.

507 After six months there was a visible separation of arthropod communities in litter from
508 pioneer species compared to old-growth litter (Fig. 9). This is likely explained by the
509 differences in chemical and physical properties of these litter mixtures, as discussed
510 above, which influences decomposer communities and may have a more pronounced
511 effect at the later stages of litter decay because of the differences in decomposition rates.

512 The shift in arthropod community composition over time (Fig. 9) is likely an effect of
513 seasonality. The majority of litter falls during the dry season, when soil moisture content
514 drops below a critical level. The litter accumulates until the start of the wet season,
515 when the increase in soil moisture content accelerates litter decomposition (Levings and
516 Windsor, 1996). Differences in litter decomposition over time will affect resource
517 availability, which in turn influences arthropod community composition (Levings and

Windsor, 1996). Such changes in community structure have been observed in microbial communities with changes in resource availability as a result of litter decomposition (Kjøller and Struwe, 2002).

Environmental conditions also affect arthropod populations, as many species are sensitive to dry conditions (Levings and Windsor, 1996). A study on nearby Barro Colorado Island found that population levels of nine major arthropod groups, including Araneae and Formicidae, increased in the wet season, compared to increases in only two groups in the dry season (Levings and Windsor, 1996). In my study, the taxa present only at the three month collection were all either predators or parasitoids (*Dermaptera*, *Phoridae*, *Geophilamorpha*, *Chalicoidae* and *Scolopendromorpha*; Appendix 3), whereas those present only in the six month collection feed on plant material (Petersen and Luxton, 1982). This could be because decomposer activity is lower in the dry season due to the low moisture levels, whereas conditions are more favourable for litter decomposers during the wet season. Further work is needed to determine the effect of arthropod functional groups on litter decomposition and to investigate the influence of experimental type on arthropod biomass.

# Conclusions

I show that the decomposition rates of different litter mixtures in mesocosms and litterbags are highly comparable. Thus, mesocosm experiments represent an effective method to measure both litter decomposition and soil respiration in a single system. My study highlighted differences in decomposition rates among mixtures of leaf litter from different tree functional groups and changes in the associated litter arthropod communities. My results indicate that shifts in species composition due to changes in climate and land use could have wider implications for litter decomposition, which in turn may alter carbon and nutrient cycling in tropical forests.

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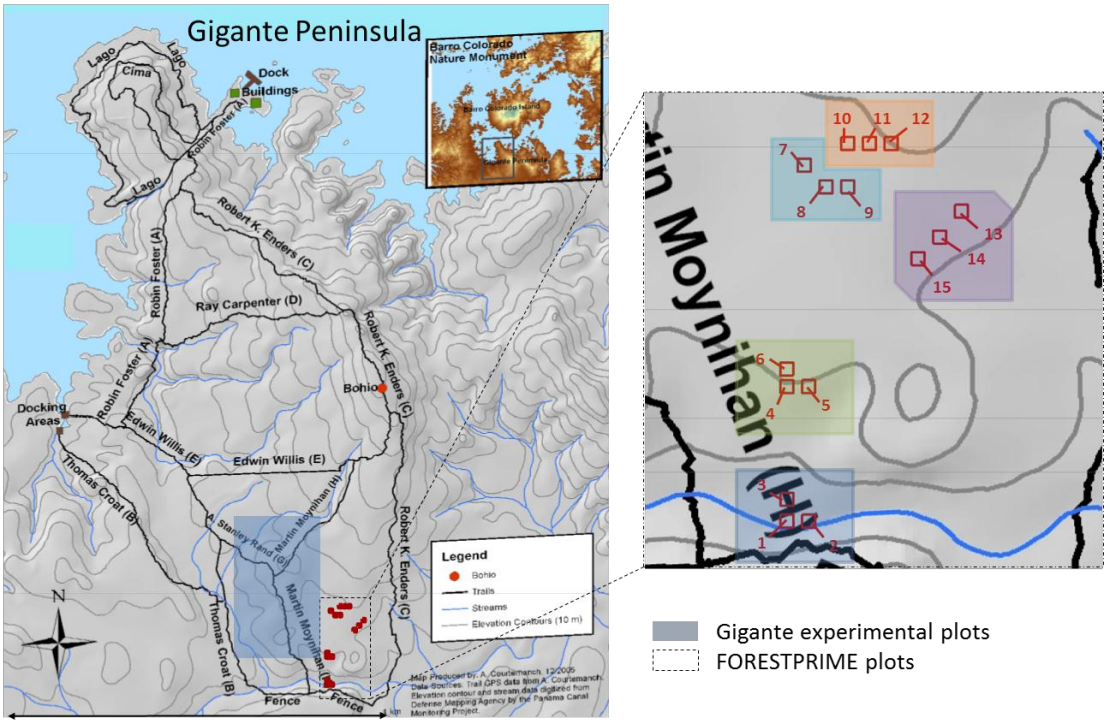
# Appendix

**Appendix 1:** Map of Barro Colorado National Monument including Gigante Peninsula and the location of the study site.



**Appendix 2: Model outputs**

**2.1** The minimum adequate Generalised Linear Model for litter decay (k): the full model included litter treatment, experimental type, experimental block and the interaction between litter treatment and experimental type.

```
Call:
glm(formula = Litter.decay.rate.k ~ Type + Treatment + Type *
    Treatment + Block, data = mb6)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-0.70696  -0.10729   0.01011   0.14704   0.48413

Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)            0.31343    0.14410   2.175   0.0365 *
TypeMESO              -0.06357    0.17207  -0.369   0.7140
TreatmentCP            1.06248    0.17207   6.175 4.55e-07 ***
TreatmentOG           -0.36300    0.17207  -2.110   0.0421 *
TreatmentPI            0.33509    0.17207   1.947   0.0595 .
TreatmentPIOG         -0.08947    0.17207  -0.520   0.6064
BlockB                -0.20196    0.12167  -1.660   0.1059
BlockC                -0.29003    0.12167  -2.384   0.0227 *
BlockD                -0.04445    0.12167  -0.365   0.7170
BlockE                -0.11655    0.12582  -0.926   0.3606
TypeMESO:TreatmentCP  -0.05618    0.25165  -0.223   0.8246
TypeMESO:TreatmentOG  -0.37158    0.24334  -1.527   0.1357
TypeMESO:TreatmentPI  -0.20876    0.24334  -0.858   0.3968
TypeMESO:TreatmentPIOG -0.59109    0.24334  -2.429   0.0204 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.0740179)

    Null deviance: 19.5571  on 48  degrees of freedom
Residual deviance:  2.5906  on 35  degrees of freedom
AIC: 25

Number of Fisher Scoring iterations: 2
```

**2.2** The minimum adequate Generalised Linear Model for the proportion of litter lost over the first three months: the full model included litter treatment, experimental type, experimental block and the interaction between litter treatment and experimental type. The data were not normally distributed and under-dispersed and so quasibinomial error distributions were used.

```
Call:
glm(formula = Proportion.litter.lost.03m ~ Type + Treatment +
    Block, family = quasibinomial, data = loss364)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-0.23426  -0.06125  -0.01741   0.07686   0.18849

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)   -0.40350    0.10871  -3.712 0.000693 ***
TypeMESO      -0.58192    0.07312  -7.958 1.90e-09 ***
TreatmentCP    0.83282    0.10836   7.685 4.23e-09 ***
TreatmentOG   -0.53718    0.12071  -4.450 7.95e-05 ***
TreatmentPI    0.14629    0.10849   1.348 0.185962
TreatmentPIOG -0.02490    0.11703  -0.213 0.832737
BlockB        -0.25254    0.11192  -2.256 0.030210 *
BlockC        -0.38423    0.11688  -3.287 0.002262 **
BlockD        -0.09252    0.10752  -0.861 0.395169
BlockE        -0.19860    0.11253  -1.765 0.086081 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 0.0123591)

    Null deviance: 3.20814  on 45  degrees of freedom
Residual deviance: 0.45173  on 36  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 4
```

**2.3** The minimum adequate Generalised Linear Model for the proportion of litter lost over the last three months: the full model included litter treatment, experimental type, experimental block and the interaction between litter treatment and experimental type. The data were not normally distributed and under-dispersed and so quasibinomial error distributions were used.

```
Call:
glm(formula = Proportion.litter.lost.36m ~ Type + Treatment +
    Type * Treatment + Block, family = quasibinomial, data = loss364)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-0.40048  -0.11550  -0.04351   0.09148   0.44287

Coefficients:
                    Estimate Std. Error t value Pr(>|t|)
(Intercept)          -2.41592    0.43005  -5.618 3.29e-06 ***
TypeMESO              1.00863    0.47289   2.133  0.04070 *
TreatmentCP           1.46254    0.45589   3.208  0.00303 **
TreatmentOG           0.23670    0.52652   0.450  0.65606
TreatmentPI           0.87927    0.47942   1.834  0.07596 .
TreatmentPIOG         0.22120    0.56100   0.394  0.69598
BlockB               -0.06328    0.29172  -0.217  0.82964
BlockC               -0.01736    0.30316  -0.057  0.95468
BlockD               -0.03457    0.28674  -0.121  0.90479
BlockE               -0.21462    0.31445  -0.683  0.49982
TypeMESO:TreatmentCP -0.80676    0.58720  -1.374  0.17902
TypeMESO:TreatmentOG -0.56534    0.68102  -0.830  0.41261
TypeMESO:TreatmentPI -0.70935    0.60491  -1.173  0.24959
TypeMESO:TreatmentPIOG -1.64404    0.81404  -2.020  0.05187 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 0.05424002)

    Null deviance: 3.9174  on 45  degrees of freedom
Residual deviance: 1.7336  on 32  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 5
```

**2.4** The minimum adequate Linear Mixed-Effects Model for soil: the full model included litter treatment, experimental block and time.

```
Data: mbtr
Models:
modmbtr5: Soil.Resp ~ 1 + (1 | Block) + (1 | days)
modmbtr3: Soil.Resp ~ Treatment + (1 | Block) + (1 | days)
         Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
modmbtr5  4 505.62 519.12 -248.81   497.62
modmbtr3  8 511.13 538.13 -247.56   495.13 2.4945      4     0.6456
>     summary(modmbtr5)
Linear mixed model fit by REML ['lmerMod']
Formula: Soil.Resp ~ 1 + (1 | Block) + (1 | days)
   Data: mbtr

REML criterion at convergence: 498

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.7835 -0.5589  0.0415  0.4859  3.5743

Random effects:
 Groups   Name        Variance Std.Dev.
 days     (Intercept) 0.1929   0.4392
 Block    (Intercept) 0.4436   0.6660
 Residual             0.4958   0.7041
Number of obs: 216, groups:  days, 9; Block, 5

Fixed effects:
            Estimate Std. Error t value
(Intercept)   6.2056     0.3354    18.5
```

**2.5** The minimum adequate Generalised Linear Model for soil C:N ratio after six months: the full model included litter treatment and experimental block.

```
Call:
glm(formula = Soil.C.N ~ Treatment + Block, data = ph)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-0.68978  -0.44671  -0.00194   0.31387   1.17277

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)   13.74599    0.39233  35.037 2.96e-14 ***
TreatmentOG    0.23992    0.43989   0.545  0.59471
TreatmentPIOG -0.11784    0.40880  -0.288  0.77769
TreatmentPI   -0.16803    0.40880  -0.411  0.68775
TreatmentCP   -0.03066    0.48732  -0.063  0.95079
BlockB         0.54635    0.43989   1.242  0.23617
BlockC         1.26572    0.40880   3.096  0.00851 **
BlockD        -0.54003    0.44176  -1.222  0.24324
BlockE        -0.34764    0.44176  -0.787  0.44543
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.4177971)

    Null deviance: 15.3904  on 21  degrees of freedom
Residual deviance:  5.4314  on 13  degrees of freedom
  (2 observations deleted due to missingness)
AIC: 51.659

Number of Fisher Scoring iterations: 2
```

**2.6** The minimum adequate Generalised Linear Model for soil pH after six months: the full model included litter treatment and experimental block.

```
Call:
glm(formula = pH.0.5 ~ Treatment + Block, data = ph)

Deviance Residuals:
      Min         1Q     Median         3Q        Max
-0.187688  -0.075750   0.002313   0.084891   0.223312

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)   6.12669    0.08072  75.903   <2e-16 ***
TreatmentCP   0.23456    0.09117   2.573   0.0212 *
TreatmentOG   0.02000    0.08479   0.236   0.8167
TreatmentPI   0.23700    0.08479   2.795   0.0136 *
TreatmentPIOG 0.05000    0.08479   0.590   0.5642
BlockB        0.05700    0.08479   0.672   0.5116
BlockC        0.04200    0.08479   0.495   0.6275
BlockD       -0.01900    0.08479  -0.224   0.8257
BlockE       -0.14344    0.09117  -1.573   0.1365
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.0179734)

    Null deviance: 0.67245  on 23  degrees of freedom
Residual deviance: 0.26960  on 15  degrees of freedom
AIC: -19.624

Number of Fisher Scoring iterations: 2
```

**2.7** The minimum adequate Generalised Linear Model for differences in Shannon's Diversity; the full model included litter treatment, experimental block, time and the interaction between litter treatment and time.

```
Call:
glm(formula = Shannon ~ Set * Treatment + Treatment + Set + Block +
    Time, family = quasipoisson, data = shansimset)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-0.44075  -0.13047   0.00052   0.11552   0.34655

Coefficients:
                  Estimate Std. Error t value Pr(>|t|)
(Intercept)        0.43131    0.09186   4.695 2.26e-05 ***
SetO               0.11584    0.08514   1.361   0.1800
TreatmentOG        0.05803    0.08621   0.673   0.5041
TreatmentPI        0.15190    0.08643   1.757   0.0852 .
TreatmentPIOG     -0.05560    0.08589  -0.647   0.5205
BlockB            -0.08064    0.05858  -1.377   0.1750
BlockC            -0.08919    0.06188  -1.441   0.1559
BlockD            -0.04006    0.05997  -0.668   0.5074
BlockE            -0.04587    0.06321  -0.726   0.4715
Time               0.02428    0.01317   1.843   0.0715 .
SetO:TreatmentOG  -0.11108    0.11380  -0.976   0.3339
SetO:TreatmentPI  -0.15104    0.11501  -1.313   0.1953
SetO:TreatmentPIOG 0.08261    0.11323   0.730   0.4692
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasipoisson family taken to be 0.03848236)

    Null deviance: 2.5756  on 60  degrees of freedom
Residual deviance: 1.8724  on 48  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 4
```

**2.8** The minimum adequate Generalised Linear Model for differences in Simpson's Evenness; the full model included litter treatment, experimental block, time and the interaction between litter treatment and time.

```
Call:
glm(formula = Simpson ~ Set * Treatment + Treatment + Set + Block +
    Time, data = shansimset)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-0.17496  -0.04575   0.01072   0.05129   0.12341

Coefficients:
                   Estimate Std. Error t value Pr(>|t|)
(Intercept)        0.708916   0.047223  15.012   <2e-16 ***
SetO               0.002896   0.043722   0.066   0.9475
TreatmentOG       -0.019412   0.043722  -0.444   0.6591
TreatmentPI        0.029478   0.044916   0.656   0.5148
TreatmentPIOG     -0.056598   0.042759  -1.324   0.1919
BlockB            -0.045429   0.030944  -1.468   0.1486
BlockC            -0.041054   0.032324  -1.270   0.2102
BlockD            -0.009319   0.031971  -0.291   0.7719
BlockE            -0.018420   0.033200  -0.555   0.5816
Time               0.013178   0.006941   1.898   0.0637 .
SetO:TreatmentOG   0.022655   0.058594   0.387   0.7007
SetO:TreatmentPI   0.002505   0.060337   0.042   0.9671
SetO:TreatmentPIOG 0.086787   0.058271   1.489   0.1429
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.006039518)

    Null deviance: 0.38384  on 60  degrees of freedom
Residual deviance: 0.28990  on 48  degrees of freedom
AIC: -125.18

Number of Fisher Scoring iterations: 2
```

**2.9** The minimum adequate Generalised Linear Model for differences in arthropod abundance; the full model included litter treatment, experimental block, time and the interaction between litter treatment and time. The data were not normally distributed and under-dispersed and so quasipoisson error distributions were used.

```
Call:
glm(formula = SUM ~ Set * Treatment + Treatment + Set + Block +
    Time, family = quasipoisson, data = shansimset)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-13.837   -5.243   -1.428    3.733   14.992

Coefficients:
                   Estimate Std. Error t value Pr(>|t|)
(Intercept)         4.29583    0.45180   9.508 1.28e-12 ***
SetO                0.36189    0.43715   0.828   0.4119
TreatmentOG         0.90892    0.40308   2.255   0.0287 *
TreatmentPI         0.52601    0.43252   1.216   0.2299
TreatmentPIOG       0.28379    0.44092   0.644   0.5229
BlockB              0.25600    0.25035   1.023   0.3116
BlockC              0.11998    0.26794   0.448   0.6563
BlockD              0.04128    0.26961   0.153   0.8790
BlockE             -0.15347    0.29891  -0.513   0.6100
Time               -0.01633    0.05736  -0.285   0.7771
SetO:TreatmentOG   -0.41602    0.51335  -0.810   0.4217
SetO:TreatmentPI   -0.47467    0.56008  -0.847   0.4009
SetO:TreatmentPIOG -0.17749    0.56018  -0.317   0.7527
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasipoisson family taken to be 51.97413)

    Null deviance: 3313.3  on 60  degrees of freedom
Residual deviance: 2571.8  on 48  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 5
```

**Appendix 3:** 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 treatment.

| | | **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 |
| Annalida | | 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 |

## Declaration

This project was planned in collaboration with Emma Sayer and Laetitia Brechet. Emma Sayer undertook the multivariate analysis. Fieldwork and laboratory work was undertaken with help from Laetitia Brechet, Biancolini Castro and Wessley Ferguson. All other work is entirely my own work, undertaken with support from my supervisors, and does not include any plagiarised material.

**Full name:** Benita Laird-Hopkins

**Signature:**

**Date:** 29th January 2015