Temporal variation in abundance of leaf litter beetles and ants in an Australian lowland tropical rainforest is driven by climate and litter fall

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Abstract Determining if the seasonality of leaf litter invertebrate populations in tropical rainforests is driven by climate or availability of litter, or both, is important to more accurately predict the vulnerability of litter invertebrates to climate change. Here we used two approaches to disentangle these effects. First, the influence of climatic seasonality was quantified by sampling a fixed volume of litter monthly over 4 years and counting extracted beetles and ants. Second, litter volume was experimentally manipulated (addition and exclusion) to test the influence of litter quantity independently of climatic variation. There were significant seasonal peaks for both beetle and ant abundance and these were positively correlated with rainfall, temperature and litter volume. As abundance was measured on a ‘per litter volume’ basis we conclude that there was a significant effect of climate on abundance. The litter manipulation experiment showed that beetle and ant abundance per litter volume were also influenced by litter volume, when it was low. We recognise that other factors such as litter structure or complexity may have affected temporal ant

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abundance. Beetle and ant abundance were depressed in litter exclusion plots but did not differ significantly between control and addition plots, suggesting a possible ceiling in the effect of litter volume on population sizes. We conclude that seasonality in climate and litter quantity are driving most temporal variation in insect abundance and that there may be some resilience among leaf litter insects to cope with higher temperatures. However, future responses by plants to increased climatic variability and higher CO₂ concentrations may alter litter fall dynamics and thus temporal patterns in litter insect abundances.

Keywords Leaf litter · Seasonality · Temporal variation · Beetles · Ants · Tropical forest · Climate change · Litter manipulation · Nutrient concentrations

Introduction

The majority of eukaryotic species on Earth are thought to be rainforest insects (Hamilton et al. 2010). Despite perceptions that the diversity of insects is extra-ordinarily high in rainforest canopies (Ozanne et al. 2003), the diversity of ground-based insects may, in fact, match that of canopy-based insects (Stork and Grimbacher 2006). Ground-based invertebrate assemblages play an important role in the decomposition of litter, releasing carbon dioxide to the atmosphere and recycling nutrients from plant material back into the soil (Hattenschwiler et al. 2005; Milton and Kaspari 2007). The breakdown of dead leaves is primarily driven by the interactions between microorganisms, invertebrates, and climate (Hattenschwiler et al. 2005; Kampichler and Bruckner 2009; Lavelle et al. 1993; Milton and Kaspari 2007). Given the uncertainty of climate change impacts on tropical lowland rainforests (Corlett 2011; Lyra et al. 2017), we consider it opportune to investigate the spatio-temporal dynamics of tropical litter invertebrates and ways in which climate change may affect this important fauna.

Invertebrates may have a larger influence on rates of litter decomposition in tropical wet forests than in other ecosystems (Gonzalez and Seastedt 2001). For example, Gonzalez and Seastedt (2001) found that soil faunas have a disproportionately larger effect on litter decomposition in a tropical wet forest than in a tropical dry or a subalpine forest. Nevertheless, there is conflicting evidence as to the overall magnitude of the contribution of tropical invertebrates to litter decomposition (Kampichler and Bruckner 2009; Powers et al. 2009; Wall et al. 2008). In most tropical rainforests, surprisingly few litter invertebrates directly consume litter. Exceptions include some larvae of scolytine weevils, Chrysomelidae and Oecophoridae. Rather, fungi and bacteria are responsible for most litter breakdown (Lavelle et al. 1993). Invertebrates exert an influence on decomposition via comminution and because microbivores, such as some mites and Collembola, consume microbes, sometimes along with partially decomposed litter. Other litter invertebrates may be opportunistic scavengers consuming plant, microbial and animal material.

The patchiness of litter invertebrates has been used to explore the factors regulating their distribution, diversity, and abundance (Burghouts et al. 1992; Kaspari and Yanoviak 2009; Milton and Kaspari 2007). For example, it has been shown that litter invertebrates respond to spatial variation in litter moisture (Levings and Windsor 1984), as well as litter depth and availability of nutrients (although this finding is not consistent across all invertebrate groups) (Burghouts et al. 1992; McGlynn et al. 2007, 2009; Yang et al. 2007). Differences between taxa possibly arise because the effects of litter depth and nutrient concentrations negatively interact to determine decomposition rates. For example, higher

nutrient concentrations in litter stimulate microbial activity and increase microbial populations, which in turn positively affect microbivores and subsequently predators (Kaspari and Yanoviak 2009). However, greater microbial activity accelerates decomposition, decreasing litter mass and the habitat space available for predators (Kaspari and Yanoviak 2009; Shik and Kaspari 2010). This could explain why the abundance of microbivores has been shown to be positively correlated with phosphorus (and other nutrients) concentration in the litter while the abundance of some predators was more closely correlated with litter depth in forest plots in both Panama and Peru (Kaspari and Yanoviak 2009).

Temporal, as well as spatial, variability may also influence litter invertebrate assemblages. For example, seasonal variation in abundance of several groups of ground-based invertebrates has been documented (Basu 1997; Frith and Frith 1990; Levings and Windsor 1985; Pearson and Derr 1986). Climate is likely to be an important driver of temporal variation among invertebrates (Wolda 1988). However, many other physical and biological variables also vary temporally. For example, litter fall in tropical rainforests is usually seasonal (Brasell et al. 1980; Burghouts et al. 1992; Chave et al. 2010; Proctor et al. 1983; Roderstein et al. 2005; Stocker et al. 1995), and the nutritional quality of litter (e.g. concentration of carbon, nitrogen and phosphorus) may also vary temporally (Anu and Sabu 2007; Brasell et al. 1980; Proctor et al. 1983; Wood et al. 2005). Thus, disentangling the effect of seasonality of climate from seasonality of resource quantity and quality requires careful experimentation (Didham and Springate 2003; Grimbacher and Stork 2009). To the best of our knowledge, no one has quantified temporal variation of litter invertebrates due to climatic variability under an experimental design that simultaneously accounts for temporal variation in quantity and quality of litter fall. Previous studies therefore could not discriminate variation due to climate from that due to litter fall.

In a previous study Grimbacher and Stork (2009) showed that the abundance of adult beetles sampled near the ground and in the canopy were poorly correlated with precipitation, temperature, and solar radiation, and that peak abundances for the most abundant species did not coincide with any climatic maxima or minima, instead occurring late in the dry season. Guided by this, we set out to determine whether variation in the abundance of litter-dwelling beetles and ants is driven by seasonality of climate or seasonality of resources, or both. To do this we took two approaches. In the first the influence of climatic seasonality was quantified by measuring ant and beetle abundance in a standard volume of litter across seasons. In the second approach litter fall was manipulated to explore the influence of litter quantity. We used the results to postulate the ways in which climate change may influence leaf litter insects. We chose ants and beetles as they are often among the most abundant groups of macroinvertebrates in leaf litter and because they usually have different roles in leaf litter: most litter beetles are solitary and eat litter, fungi and other insects whereas ants use litter as nesting sites, are predatory and live in colonies.

Methods

Study site

This study was conducted at the Daintree Rainforest Observatory (www.jcu.edu.au/daintree), a Long-Term Ecological Research site near Cape Tribulation (16°17'S, 145°29'E) Queensland, Australia (Stork 2007). The focal site of this research the canopy crane, was approximately 40 m asl and > 300 m from the forest edge in complex mesophyll vine forest,

Type 1a (Tracey 1982). This patch of rainforest is contiguous with lowland and upland rainforests of the Daintree National Park and the Wet Tropics World Heritage Area (0 to > 1300 m asl). The area within the circumference of the crane jib covers approximately 1 ha of rainforest containing 745 individual trees (> 10 cm dbh) from 82 species and 34 families based on a recent (2010) survey at the crane site that updates data reported in Laidlaw et al. (2007). The soil at the site is an acidic, dystrophic, brown Dermosol (Isbell 2002) with many (20–50%) cobbles and stones throughout the profile. The soil is developed in colluvium from the metamorphic and granitic mountains to the west. The litter exclusion experiment was conducted about 1 km south-east of the crane and, although the area has not been mapped in detail, it is floristically similar, is at the same elevation, and has similar topography and soils to the crane site.

Beetles and ants were chosen as study taxa, building on previous long-term studies on these taxa at this location (Bluethgen et al. 2004; Grimbacher and Stork 2009; Stork and Grimbacher 2006; Wardhaugh et al. 2012a, b, 2013a, b, 2015), since both taxa are ecologically diverse.

Study 1—correlation between insect abundance and litter volume and climatic variables

To investigate temporal patterns in insect abundance in litter we sampled beetles and ants within a standardised volume of litter each month over 4 years (January 2006–December 2009). Sampling was not possible in April 2006, resulting in 47 samples in total. Sampling involved a volume of five litres of sifted litter, collected from the ground. Throughout this study we make the assumption that equal volume standardises mass (Parsons et al. 2009). Sampling was based on randomly selected handfuls of litter collected from the ground. This included litter near woody debris (but avoided collecting larger twigs as these might include twig-nesting ants and other invertebrates), adjacent to the base of trees, but all other ground features (i.e. boulders, etc.) were excluded. Leaf litter availability changes during the year and since our aim was to standardise litter volume we sampled each month across many locations in an area of approximately 1 ha. All litter was placed into a sifter (1 cm mesh size) to separate fine litter (and invertebrates) from coarse leaf and small woody material. Sampling continued until 5 litres of fine litter was collected. This material was then divided into equal subsamples and placed in a Tullgren funnel (internal diameter ~400 mm) for 12 h. All beetles and ants were separated, counted and stored in ethanol. We recognize that many of the ants in the leaf litter layer are twig nesting, even in some very small twigs, and hence will have most likely have under-sampled these.

Over the 4 year sampling period daily rainfall, maximum, minimum and average daily temperature, and relative humidity were recorded using an automatic weather station (Weathermaster 2000 model, Envirodata) located on site, 20 m from the edge of the forest. We chose two climate variables to examine for correlations with insect abundance: daily average temperature and daily total rainfall. We chose daily average temperature because all measures of temperature were significantly and strongly positively correlated when assessed by simple rank correlation. Rainfall, on the other hand, was not strongly correlated with any temperature variable and thus represents an explanatory variable that may reveal pattern independent of temperature.

To examine seasonality in leaf litter, 25 litter traps (each 0.5 m²) were randomly positioned across a 1-ha plot approximately 1 m above ground level. Trap monitoring began in January 2007, and all material falling into them was removed, sorted into constituent

components of leaf litter, flowers/fruits and larger woody debris at approximately two-week intervals. Here we concentrate solely on litter. One trap was not monitored with the same intensity due to restricted access by flooding and was thus removed prior to analyses. Other traps lacked records at individual times. Where missing values like this occurred we inserted zero, since we had no reason to suspect that the value was indeed “missing”. Because the amount of material collected at any point in time represents the accumulation since the previous collection, we divided the collected mass by the number of days in the sampling period to generate an estimate of daily production over that period. We centered each litter production value within the sampling period before analysing trends over time (see Edwards et al. (2017) for further details on leaf litter collection).

Linking temporal patterns in insect abundance with litter- and climate-related variables requires understanding of long-term seasonal changes. Generalised additive models (GAMs) are excellent choices in these situations because they are formula-free and do not impose a constant periodicity or amplitude (Wood 2006, 2011). Thus, under GAM, peaks and troughs in the data that are associated with seasons are allowed to vary in timing and magnitude as might be expected due to between-year seasonal variability. For this reason, GAMs can potentially characterise patterns of seasonality in biological and climatological responses more sensitively than simple wave functions. Thus, we chose to fit GAMs to characterise trends in our abundance data, estimates of leaf litter fall (see Edwards et al. (2017) for full description) and climate data. We then used the temporal predictions from the GAM models to examine all pair-wise possible correlations between these measures across time using simple Spearman’s rank correlation.

By assessing change via GAM we could not necessarily rule out changes in leaf litter quality, rather than quantity as a possible driving mechanism for changes in invertebrate abundances. Although we did not expect to find seasonality in nutrient concentrations of litter (Anu and Sabu 2007; Brasell et al. 1980; Proctor et al. 1983; Wood et al. 2005) we sought to confirm this by comparing nitrogen and carbon contents of litter between ‘wet’ and ‘dry’ seasons. The three full years of monitoring represents 25 traps, each sampled approximately every 2 weeks over 3 years (a total of 1800 samples). Unfortunately, budgetary constraints did not allow for individual chemical analyses on each sample. Therefore, we chose samples from ten randomly selected times during 3 years (i.e. 30 dates). Litter samples for those dates were combined and ground to a fine powder by passing them through a 0.5 mm screen of an electrical miller (IKA MF10 basic). Carbon and nitrogen concentrations were analysed using an elemental analyser (Costech). We classed samples as either wet (December–April) or dry (May–November) season based on date of collection and used Multiple Response Permutation Procedure (MRPP) (Oksanen et al. 2017; R Core Team 2017) based on 9999 permutations to compare nutrient profiles between seasons. We report the A and p values. The A statistic is the chance-corrected within-group agreement. When $A=1$, all attributes within a group are identical, when $A=0$, within-group heterogeneity equals that expected by chance, and when $A<0$, within-group heterogeneity is greater than expected by chance (Oksanen et al. 2017). The p value indicates the likelihood that the observed difference is due to chance (the fraction of permuted δ s that are less than the observed δ) (Oksanen et al. 2010).

Study 2—effects of litter manipulation on ant and beetle abundances

In order to further assess the influence of litter quantity on insect abundance we implemented a litter manipulation experiment with control, litter exclusion and litter addition treatments. This experiment was carried out from September 2008 to early February 2009

so that it coincided with the season of peak abundance for ants and beetles. For each treatment we used six replicate 3 m×3 m plots, established approximately 1 km from the Canopy Crane to avoid potential damage in the long-term monitoring plot itself. Plots were set as groups of three (one plot for each treatment) at each of six sites (“blocks”), over a total area of approximately 30 m×30 m, to account for possibility of high spatial variation in litter quantity caused by the identity of overstory tree species (Donoso et al. 2010; Townsend et al. 2008). For litter exclusion plots, naturally falling litter was excluded via black nylon bird netting (mesh size 2 cm×2 cm) suspended 50–100 cm above the ground. For litter addition plots we added coarse litter collected nearby and sifted to remove invertebrates and the fine litter, using the protocol described in *Study 1*. This is an advance over previous similar experiments that have typically ignored sifting for invertebrates (Sayer et al. 2010). 60 L of coarse litter was added to each litter addition plot every month for the 5 months over which the experiment ran. Control plots were marked out but otherwise unaltered. At the conclusion of the experiment, litter from each plot was collected and bagged and the mass of coarse and fine litter were measured. All insects were extracted from the fine litter using Tullgren funnels (as described in *Study 1*—above). We used standard blocking to remove variance attributable to location, after which we compared abundances of ants and beetles between treatments.

All analyses were conducted in R (R Development Core Team 2015). GAMs were fitted using R package *mgcv* (Wood 2017) and MRPP was performed using the *Vegan* package (Oksanen et al. 2017). Figures describing simultaneous pairwise differences in the manipulation experiment were produced in *SPlus* (Jones et al. 2014).

Results

Study 1—correlation between invertebrate abundance and litter/climatic variables

In this study 7909 beetles and 7772 ants were captured. Both seasonal and yearly variation in beetle and ant abundance was observed (Supplementary information). Neither the abundances of ants nor beetles were normally distributed (Shapiro–Wilk normality test: $W=0.87$, $p<0.001$ and $W=9.2$, $p=0.002$, respectively). We therefore used $\ln$ transformation to normalise the data prior to GAM model fitting (Shapiro–Wilk test on $\ln$ transformed values; ants, $W=0.98$, $p=0.64$; beetles, $W=0.96$, $p=0.15$) (Fig. 1).

There was distinct seasonal variation in ant and beetle abundances and in the litter and climatic variables presented in Table 1. All measures show consistent peaks during the warmer (Wet Season) months of November to May (Fig. 2). In all cases the smoothing function was a significant improvement in explaining patterns of change over time, and the significance of all smoothing terms was <0.01 (Table 1). Predicted estimates from GAM models all showed very similar periodicity in peaks and troughs, with a high degree of concordance between all measures (Fig. 2). Overall seasonality of climatic variables was in the range of values recorded in previous years (Grimbacher and Stork 2009; Hopkins et al. 1996).

GAM predictions of ant and beetle abundances were significantly positively correlated ($R_s=0.78$, $p<0.01$) and both were also significantly positively correlated with all environmental variables (Table 2). Ant abundance was most strongly associated with average daily temperature ($R_s=0.86$, $p<0.01$), while beetle abundance was most

Fig. 1 Frequency distribution of number of ants and number of beetles (top panels) and log number of ants and beetles (bottom panels) per 5-L fine litter sample recorded in 47 trapping occasions at the Daintree Rainforest Observatory across 2006–2009. Neither untransformed numbers of ants nor numbers of beetles were normal (Shapiro–Wilk normality test: $W=0.87$, $p<0.001$ and $W=9.2$, $p=0.002$, respectively). Log transformation normalised these distributions (ants, $W=0.98$, $p=0.64$; beetles, $W=0.96$, $p=0.15$)

Table 1 Summary of the significance of the smoothing terms for all response variables

Response	edf	F	P
Log(ant)	9	3.14	0.006
Log(beetle)	9	6.69	<0.001
Leaf litter	17	64.08	<0.001
Average temperature	9	340	<0.001
Log(rainfall)	9	39.03	<0.001

Ant and beetle abundances are ln transformed, as is rainfall. Smoothing terms for invertebrate abundances, temperature and rainfall are derived from data January 2006–December 2009. Predictions of leaf litter estimates are taken from GAMM described in Edwards et al. (2017), which covers the period January 2007–December 2013

strongly associated with leaf litter volume ($R_s=0.6$, $p<0.01$). Nevertheless, these correlations, while identified as strongest, cannot be considered in isolation, since all environmental variables were themselves positively correlated (Table 2), as illustrated in Fig. 2.

Seasonal changes in abundances were not likely due to differences in litter quality over time. There was no significant difference between litter samples from the wet and

Fig. 2 Predictions from GAM models for temporal patterns of ant and beetle abundance (/5-L fine litter), litter fall (mg/trap/day), average daily temperature (°C) and daily rainfall (mm). Where GAM fitting required log transformation, predictions are back-transformed. Solid line is GAM model prediction and grey polygon is 95% confidence interval

dry season samples in terms of carbon and nitrogen concentrations (MRPP, $A = -0.008$, $p(\delta) = 0.51$).

Study 2—effects of litter manipulation on ant and beetle abundances

A total of 3337 beetles and 4289 ants were captured in this experiment. There was no significant effect of location (“block”) for either ants ($F_{5,10} = 0.42$, $p = 0.82$) or beetles

Table 2 Strength and magnitude of the Spearman's rank correlation (R_s) between GAM predictions of ant and beetle abundance (per volume of leaf litter), leaf litter fall, average daily temperature and daily rainfall between January 2006 and December 2009 at the Daintree Rainforest Observatory

	Log(beetle)	Leaf litter	Average temperature	Log(rainfall)
Log(ant)	$R_s=0.78$ $p<0.01$	$R_s=0.83$ $p<0.01$	$R_s=0.86$ $p<0.01$	$R_s=0.56$ $p<0.01$
Log(beetle)		$R_s=0.60$ $p<0.01$	$R_s=0.55$ $p<0.01$	$R_s=0.42$ $p<0.01$
Leaf litter			$R_s=0.86$ $p<0.01$	$R_s=0.45$ $p<0.01$
Average temperature				$R_s=0.73$ $p<0.01$

Correlations between Leaf litter and all others is based on the period January 2007–December 2009

($F_{5,10}=0.39$, $p=0.84$). For both ants and beetles there was a significant effect of litter manipulation (ants, $F_{2,10}=8.85$, $p=0.006$; beetles, $F_{2,10}=6.65$, $p=0.015$). In both cases the significance of the manipulation effect came about due to significantly higher numbers of individuals in addition versus exclusion, and control versus exclusion treatments (Fig. 3). Estimated mean (SE) abundances were 280.2 (40.8), 395.6 (85.0) and 39.0 (13.2) per 5-L litter sample for ants in addition, control and exclusion treatments, respectively. A very similar pattern occurred for beetles (248.8 (39.7), 268.6 (64.9) and 38.7 (7.3) per 5-L litter sample in addition, control and exclusion treatments, respectively). As can be seen in the mean estimates, there were slightly higher mean abundances in control than addition plots, but these were not significant (estimated pairwise difference between addition and control plots (and 95% CI); ants – 115 (– 353 to 122), beetles – 19.8 (– 211 to 172). The manipulation treatment meant that all treatments differed in total litter material available ($F_{2,10}=82.8$, $p<0.001$), with addition having significantly more than control, which

Fig. 3 Estimated pairwise difference between treatment means (and 95% CI of difference) for ant abundance (upper panel) and beetle abundance (lower panel) per 5 L fine litter, among litter manipulation treatments. Y axis labelling denotes the pairwise contrast for differences between treatment means. The test is conducted on all pairwise comparisons across the three treatments, resulting in three possible pairwise tests. For example, addition-control is a comparison between these two treatment groups; and represents the estimated mean of addition treatment minus estimated mean for control. In this instance the estimated difference is negative (i.e. the control was higher than the addition value), but confidence intervals of the difference indicate this difference was not significant at $p=0.05$

had significantly more than exclusion (Fig. 4—bottom panel). This was also the case for coarse material ($F_{2,10} = 163.92$, $p < 0.001$) (Fig. 4—middle panel). It was not the case for the amount of fine litter material ($F_{2,10} = 2.58$, $p = 0.12$) (Fig. 4—top panel). This was not unexpected, however, because sifting litter to remove invertebrates prior to the addition treatment also removed fine particulate matter.

Discussion

We set out to determine what drives temporal variation in the abundance of litter-dwelling beetles and ants. We attempted a first order separation of the effects of seasonality of climate from seasonality of litter biomass by standardising litter volume (proxy for mass) while sampling through time and measuring climatic conditions on site. Subsequently we deconstructed the observed changes in insect density against both the variation in climatic variables and changes in litter inputs. The alternative approach of manipulating climate is very difficult to achieve in the field except for dry season watering experiments (Levings and Windsor 1984) or shading to reduce temperature (Lessard et al. 2011). The observed seasonality of climate and litter fall at our study site justified our experimental approach.

We found that the abundance of litter-dwelling beetles and ants was significantly seasonal, peaking early in the wet season, resulting in significant correlations with temperature and rainfall (Table 2; Fig. 2). This concurs with many previous studies that have attributed (either formally or informally) seasonality of tropical invertebrates to the seasonality of climate (Frith and Frith 1990; Grimbacher and Stork 2009; Levings and Windsor 1985; Novotný and Basset 1998; Sakchoowong et al. 2015; Wolda 1988). Some insects use climatic variables as cues to emerge from diapause and these may act differently to other variables that may affect growth, reproduction, and population size (Didham and Springate

Fig. 4 Estimated pairwise difference between treatment means (and 95% CI of difference) for fine litter mass (upper panel), coarse litter mass (middle panel) and total litter mass (lower panel) among litter manipulation treatments. Y axis labelling denotes the pairwise contrast for differences between treatment means as described in Fig. 3

2003; Tauber and Tauber 1976; Wolda 1988). Further, this study looked at Ordinal-level responses, whereas many individual species may have their own species-specific cues or tolerances and display their own seasonal changes in abundance, which were not detected here. In a previous study at the same location as this study, peak abundances of most common beetle species (species with > 20 individuals captured in Malaise-flight interception traps positioned in the canopy and on the ground) was late in the dry season (Grimbacher and Stork 2009). So while many canopy beetle species peak in abundance in the late dry season when it is peak flowering for several of the dominant species, for leaf litter beetles and ants it seems that peak abundances are one or 2 months later when precipitation and temperature are higher.

Ant and beetle abundances were strongly correlated with litter fall in non-manipulated forest (Fig. 2). However, since we had standardised the volume of litter sampled we can conclude that seasonality in beetle abundance is driven, at least in part, by climate rather than by litter quantity. Seasonal variation in litter fall is presumably also driven by climate. It is perhaps surprising that given the differences in biology of ants and beetles that groups responded in a similar way to leaf litter fall. We can rule out the influence of potential seasonal changes in litter quality as measured by carbon and nitrogen content, since we found that temporal variation in litter quality was aseasonal, a result consistent with other studies showing that seasonal variation in litter quality was absent or relatively minor (Anu and Sabu 2007; Brasell et al. 1980; Proctor et al. 1983; Wood et al. 2005). However, at least for ants, other factors such as leaf complexity and structure may be important and we did not test for this. Further ants in some ecosystems are ecosystem engineers and may greatly affect physical, chemical and biological properties of soil and leaf litter (Frouz and Jilkova 2008).

Does increased litter fall influence the abundance of beetles and ants in litter?

In our experiment manipulating litter fall, mass of all litter and coarse litter, but not fine litter, differed significantly between treatments (Fig. 4). This result was as expected, since we had added coarse litter, and confirmed that our experimental approach manipulating coarse litter was successful. Furthermore, because all three litter treatments were conducted concurrently, we can rule out the influence of climate on differences between insect abundances in the different treatments of this experiment. We found that variations in coarse litter inputs influenced beetle and ant populations, although threshold responses were apparent. That is, beetle and ant abundance was diminished by reducing coarse litter inputs, but additional litter did not increase insect abundance per volume of fine litter beyond the controls. Based on the observation that at the end of the experiment only the exclusion plots had patches of exposed soil, we speculate that in the field this insect population density response threshold corresponds to the mass of litter that is necessary to cover the ground. Several other studies have demonstrated that particular invertebrate groups inhabiting litter respond to variations in the mass of litter (Burghouts et al. 1992; Kaspari and Yanoviak 2009; Yang et al. 2007). Proposed reasons for this relationship are that increased litter mass provides greater density and diversity of resources (Armbrecht et al. 2004; Hansen 2000), as well as more habitat space per se (Kaspari and Yanoviak 2009; Shik and Kaspari 2010). Our results concur with other litter manipulation experiments; most studies found that litter invertebrates respond negatively to litter removal but not always positively to litter addition (reviewed by Sayer (2006); but see also Sayer et al. (2010)).

Implications for the effects of climate change

A review on the impacts of warming on lowland tropical forests showed a range of contrasting views (Corlett 2011), reflecting a high level of uncertainty. In our study we have shown that it is extremely difficult to fully disentangle the influence of temporal variation in climate from temporal variation in resource quality and quantity, even with careful manipulation. Our results suggest that climate is likely to influence temporal variation in leaf litter insects in this lowland rainforest, but in a complex way. Given the threshold effect of litter mass found in *Study 2*, the fact that litter normally covers the ground year-round, and the aseasonality of nutrient quality, we conclude that climate is likely to be responsible for most of the current temporal variation in population densities (per volume of litter) of litter-dwelling beetles and ants in the lowland rainforest of Cape Tribulation. However, population per unit area of land is driven by litter quantity as well as climate.

Because many factors influence spatio-temporal variation in populations of litter-dwelling insects, predicting how climate change will affect these insects is difficult. The positive relationships with temperature suggest a degree of resilience among ants and beetles to cope with higher temperatures in the future. This is a surprising result given that this is a lowland tropical insect assemblage, and such fauna are supposedly at the limit of their maximum thermal tolerances (Colwell et al. 2008). If, as our study suggests, ant abundance responds to increased temperatures in a positive manner, this may lead to increased ant densities and alter interactions with other decomposer invertebrates. Ants can strongly influence other invertebrates, for example by promoting the abundance of honeydew producing scale insects (Abbott and Green 2007) or by consuming non-ant prey (Floren et al. 2002), although there remains much to discover regarding exactly how ants influence the diversity and abundance of other invertebrates (Klimes et al. 2011).

Future effects on litter-dwelling insects caused by climate change may not all be positive. Various climate change scenarios for the Australian Wet Tropics predict increased seasonality of rainfall with more severe dry seasons (Zvereva and Kozlov 2006). During a strong El Nino drought (2002–2003) prior to the commencement of this study, when rainfall was almost 40–50% below the annual mean, the forest displayed massive leaf loss (Stork and Liddell pers. obs.). Edwards et al. (2017) suggest that peaks in leaf litter fall associated with high temperatures and high rainfall (i.e. late dry and early wet seasons) may be explained by trees shedding older leaves to escape severe water stress and avoid cavitation risk at the end of the dry season. Plants may respond to the increased aridity and extension of the dry season predicted under future climates (Pachauri et al. 2015) by shedding more leaves, or shedding leaves earlier (as peak periods of water stress and cavitation risk shift to earlier times within the year), or both. This would result in little litter covering the ground during late spring–summer. Our study suggests that this could negatively affect litter insect abundance. In particular, ants are likely to be particularly susceptible, as tropical ants have lower warming tolerances in general than their temperate counterparts (Diamond et al. 2012) and a reduction in litter cover will increase the temperature in the litter/soil microhabitat, an effect which is known to place soil-dwelling insect populations at higher risk of thermal stress (Andrew et al. 2013). In addition, climate change is likely to increase decomposition rates and more rapid turnover of litter could have a depressing effect on invertebrate abundances especially in low litter environments.

Our results predict that climate change may elicit positive or negative responses by insects inhabiting litter and that these responses may be mediated by the way in which

plants respond to climate change. If in the future, changes in the climate alter litter fall or decomposition patterns, resulting in periods with very little litter on the forest floor, we can expect to see significant reductions in the abundances of litter dwelling insects. The responses of particular feeding guilds or species may also differ in response to climate change, even if overall abundances are unaffected (Delsinne et al. 2013). This of course could have ramifications for the functioning of leaf litter insect communities and ecosystem services they provide. Our still limited understanding of how the decomposer invertebrate community functions means that many of the consequences of climate change are yet to be predicted.

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References

- Abbott KL, Green PT (2007) Collapse of an ant-scale mutualism in a rainforest on Christmas Island. *Oikos* 116:1238–1246
- Andrew NR, Hart RA, Jung M-P, Hemmings Z, Terblanche JS (2013) Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, *Iridomyrmex purpureus* (Formicidae), with potential climate change. *J Insect Physiol* 59:870–880
- Anu A, Sabu TK (2007) Seasonal variation in the litter chemical quality of a wet evergreen forest in the Western Ghats. *Curr Sci* 93:391–394
- Armbrrecht I, Perfecto I, Vandermeer J (2004) Enigmatic biodiversity correlations: ant diversity responds to diverse resources. *Science* 304:284–286
- Basu P (1997) Seasonal and spatial patterns in ground foraging ants in a rain forest in the western Ghats, India. *Biotropica* 29:489–500
- Bluethgen N, Stork NE, Fiedler K (2004) Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. *Oikos* 106:344–358
- Brasell HM, Unwin GL, Stocker GC (1980) Quantity, temporal distribution and mineral-element content of litterfall in two forest types at two sites in tropical Australia. *J Ecol* 68:123–139
- Burghouts T, Ernsting G, Korthals G, De Vries T (1992) Litterfall, leaf litter decomposition and litter invertebrates in primary and selectively logged dipterocarp forests in Sabah, Malaysia. In: Marshall AG, Swaine MD (eds) *Tropical rainforest: disturbance and recovery*. Philosophical Transactions of the Royal Society of London, London, pp 407–416
- Chave J, Navarrete D, Almeida S, Alvarez E, Aragao L, Bonal D, Chatelet P, Silva-Espejo JE, Goret JY, von Hildebrand P, Jimenez E, Patino S, Penuela MC, Phillips OL, Stevenson P, Malhi Y (2010) Regional and seasonal patterns of litterfall in tropical South America. *Biogeosciences* 7:43–55
- Colwell RK, Brehm G, Cardelus CL, Gilman AC, Longino JT (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258–261
- Corlett RT (2011) Impacts of warming on tropical lowland rainforests. *Trends Ecol Evol* 26:606–613
- Delsinne T, Arias-Penna T, Leponce M (2013) Effect of rainfall exclusion on ant assemblages in montane rainforests of Ecuador. *Basic Appl Ecol* 14(4):357–365
- Diamond SE, Sorger DM, Hulcr J, Pelini SL, Toro ID, Hirsch C, Oberg E, Dunn RR (2012) Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Glob Change Biol* 18:448–456
- Didham RK, Springate N (2003) Determinants of temporal variation in canopy arthropod community structure. In: Basset Y, Novotny V, Miller SE, Kitching RL (eds) *Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy*. Cambridge University Press, Cambridge, pp 28–39
- Donoso DA, Johnston MK, Kaspari M (2010) Trees as templates for tropical litter arthropod diversity. *Oecologia* 164:201–211

- Edwards W, Liddell MJ, Franks P, Nichols C, Laurance SGW (2017) Seasonal patterns in rainforest litterfall: detecting endogenous and environmental influences from long-term sampling. *Austral Ecol* 43:225–235
- Floren A, Biun A, Linsenmair KE (2002) Arboreal ants as key predators in tropical lowland rainforest trees. *Oecologia* 131:137–144
- Frith D, Frith C (1990) Seasonality of litter invertebrate populations in an Australian upland tropical rainforest. *Biotropica* 22:181–190
- Frouz J, Jilkova V (2008) The effect of ants on soil properties and processes (Hymenoptera: Formicidae). *Myrmecol News* 11:191–199
- Gonzalez G, Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* 82:955–964
- Grimbacher PS, Stork NE (2009) Seasonality of a diverse beetle assemblage inhabiting lowland tropical rainforest in Australia. *Biotropica* 41:328–337
- Hamilton AJ, Basset Y, Benke KK, Grimbacher PS, Miller SE, Novotny V, Samuelson A, Stork NE, Weiblen GD, Yen JDL (2010) Quantifying uncertainty in estimation of global arthropod species richness. *Am Nat* 176:90–95
- Hansen RA (2000) Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology* 81:1120–1132
- Hattenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annu Rev Ecol Evol S* 36:191–218
- Hopkins MS, Head J, Ash JE, Hewett RK, Graham AW (1996) Evidence of a Holocene and continuing recent expansion of lowland rain forest in humid, tropical North Queensland. *J Biogeogr* 23:737–745
- Isbell RF (2002) The Australian soil classification. CSIRO Publishing, Collingwood
- Jones R, Gilliver R, Robson S, Edwards W (2014) S-plus for the analysis of biological data. James Cook University, Townsville
- Kampichler C, Bruckner A (2009) The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. *Biol Rev* 84:375–389
- Kaspari M, Yanoviak SP (2009) Biogeochemistry and the structure of tropical brown food webs. *Ecology* 90:3342–3351
- Klimes P, Janda M, Ibalim S, Kua J, Novotny V (2011) Experimental suppression of ants foraging on rainforest vegetation in New Guinea: testing methods for a whole-forest manipulation of insect communities. *Ecol Entomol* 36:94–103
- Laidlaw M, Kitching RL, Goodall K, Small A, Stork NE (2007) Temporal and spatial variation in an Australian tropical rainforest. *Austral Ecol* 32:10–20
- Lavelle P, Blanchart E, Martin A, Martin S, Spain A, Toutain F, Barois I, Schaefer R (1993) A hierarchical model for decomposition in terrestrial ecosystems—application to soils of the humid tropics. *Biotropica* 25:130–150
- Lessard JP, Sackett TE, Reynolds WN, Fowler DA, Sanders NJ (2011) Determinants of the detrital arthropod community structure: the effects of temperature and resources along an environmental gradient. *Oikos* 120:333–343
- Levings SC, Windsor DM (1984) Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. *Biotropica* 16:125–131
- Levings SC, Windsor DM (1985) Litter arthropod populations in a tropical deciduous forest—relationships between years and arthropod groups. *J Anim Ecol* 54:61–69
- Lyra A, Imbach P, Rodriguez D, Chou SC, Georgiou S, Garofolo L (2017) Projections of climate change impacts on central America tropical rainforest. *Clim Change* 141:93–105
- McGlynn TP, Salinas DJ, Dunn RR, Wood TE, Lawrence D, Clark DA (2007) Phosphorus limits tropical rain forest litter fauna. *Biotropica* 39:50–53
- McGlynn TP, Fawcett RM, Clark DA (2009) Litter biomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest. *Biotropica* 41:234–240
- Milton Y, Kaspari M (2007) Bottom-up and top-down regulation of decomposition in a tropical forest. *Oecologia* 153:163–172
- Novotný V, Basset Y (1998) Seasonality of sap-sucking insects (Auchenorrhyncha, Hemiptera) feeding on *Ficus* (Moraceae) in a lowland rain forest in New Guinea. *Oecologia* 115:514–522
- Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara RB, Simpson G, Solymos P, Stevens MHH, Wagner H (2010) Vegan: community ecology package. R package version 1.17-4
- Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens HH, Szoecs E, Wagner H (2017) Vegan: community ecology package. R package version 2.4-4. <https://cran.r-project.org>, <https://github.com/vegandevs/vegan>

- Ozanne CMP, Anhuf D, Boulter SL, Keller M, Kitching RL, Körner C, Meinzer FC, Mitchell AW, Nakashizuka T, Silva Dias PL, Stork NE, Wright SJ, Yoshimura M (2003) Biodiversity meets the atmosphere: a global view of forest canopies. *Science* (Washington, DC) 301:183–186
- Pachauri RK, Meyer L, Plattner G-K, Stocker T (2015) IPCC, 2014: climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC
- Parsons SA, Shoo LP, Williams SE (2009) Volume measurements for quicker determination of forest litter standing crop. *J Trop Ecol* 25:665–669
- Pearson DL, Derr JA (1986) Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. *Biotropica* 18:244–256
- Powers JS, Montgomery RA, Adair EC, Brearley FQ, DeWalt SJ, Castanho CT, Chave J, Deinert E, Ganzhorn JU, Gilbert ME, Gonzalez-Iturbe JA, Bunyavejchewin S, Grau HR, Harms KE, Hiremath A, Iriarte-Vivar S, Manzano E, de Oliveira AA, Poorter L, Ramanamanjato JB, Salk C, Varela A, Weiblen GD, Lerdau MT (2009) Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. *J Ecol* 97:801–811
- Proctor J, Anderson JM, Fogden SCL, Vallack HW (1983) Ecological studies in 4 contrasting lowland rain forests in Gunung-Mulu-National-Park, Sarawak. 2. Litterfall, litter standing crop and preliminary-observations on herbivory. *J Ecol* 71:261–283
- R Core Team (2017) R package stats: a language and environment for statistical computing. Vienna. <https://www.R-project.org/>
- R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Roderstein M, Hertel D, Leuschner C (2005) Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *J Trop Ecol* 21:483–492
- Sakchoowong W, Hasin S, Pachey N, Amornsak W, Bunyavejchewin S, Kongnoo P, Basset Y (2015) Influence of leaf litter composition on ant assemblages in a lowland tropical rainforest in Thailand. *Asian Myrmecol* 7:57–71
- Sayer EJ (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biol Rev* 81:1–31
- Sayer EJ, Sutcliffe LME, Ross RIC, Tanner EVJ (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
- Shik JZ, Kaspari M (2010) More food, less habitat: how necromass and leaf litter decomposition combine to regulate a litter ant community. *Ecol Entomol* 35:158–165
- Stocker GC, Thompson WA, Irvine AK, Fitzsimon JD, Thomas PR (1995) Annual patterns of litterfall in a lowland and tableland rainforest in tropical Australia. *Biotropica* 27:412–420
- Stork NE, Grimbacher PS (2006) Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proc R Soc B Biol Sci* 273:1969–1975
- Tauber MJ, Tauber CA (1976) Insect seasonality: diapause maintenance, termination, and postdiapause development. *Annu Rev Entomol* 21:81–107
- Townsend AR, Asner GP, Cleveland CC (2008) The biogeochemical heterogeneity of tropical forests. *Trends Ecol Evol* 23:424–431
- Tracey J (1982) Vegetation of the humid tropical region of North Queensland. CSIRO, Melbourne
- Wall DH, Bradford MA, St John MG, Trofymow JA, Behan-Pelletier V, Bignell DDE, Dangerfield JM, Parton WJ, Rusek J, Voigt W, Wolters V, Gardel HZ, Ayuke FO, Bashford R, Beljakova OI, Bohlen PJ, Brauman A, Flemming S, Henschel JR, Johnson DL, Jones TH, Kovarova M, Kranabetter JM, Kutny L, Lin KC, Maryati M, Masse D, Pokarzhevskii A, Rahman H, Sabara MG, Salamon JA, Swift MJ, Varela A, Vasconcelos HL, White D, Zou XM (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Glob Change Biol* 14:2661–2677
- Wardhaugh CW, Stork NE, Edwards W (2012a) Feeding guild structure of beetles on Australian tropical rainforest trees reflects microhabitat resource availability. *J Anim Ecol* 81:1086–1094
- Wardhaugh CW, Stork NE, Edwards W, Grimbacher PS (2012b) The overlooked biodiversity of flower-visiting invertebrates. *PLoS ONE* 7:e45796
- Wardhaugh CW, Edwards W, Stork NE (2013a) Body size variation among invertebrates inhabiting different canopy microhabitat: flower visitors are smaller. *Ecol Entomol* 38:101–111
- Wardhaugh CW, Stork NE, Edwards W (2013b) Specialization of rainforest canopy beetles to host trees and microhabitats: not all specialists are leaf-feeding herbivores. *Biol J Lin Soc* 109:215–228
- Wardhaugh CW, Edwards W, Stork NE (2015) The specialization and structure of antagonistic and mutualistic networks of beetles on rainforest canopy trees. *Biol J Lin Soc* 114:287–295
- Wolda H (1988) Insect seasonality: why? *Annu Rev Ecol Syst* 19:1–18

- Wood S (2006) Generalized additive models: an introduction with R. Chapman & Hall, Boca Raton
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc Ser B* 73:3–36
- Wood SN (2017) mgcv: mixed GAM computation vehicle with automatic smoothness. R package version 1.8-22. <https://cran.r-project.org/web/packages/mgcv>
- Wood TE, Lawrence D, Clark DA (2005) Variation in leaf litter nutrients of a Costa Rican rain forest is related to precipitation. *Biogeochemistry* 73:417–437
- Yang XD, Warren M, Zou XM (2007) Fertilization responses of soil litter fauna and litter quantity, quality, and turnover in low and high elevation forests of Puerto Rico. *Appl Soil Ecol* 37:63–71
- Zvereva EL, Kozlov MV (2006) Consequences of simultaneous elevation of carbon dioxide and temperature for plant–herbivore interactions: a metaanalysis. *Glob Change Biol* 12:27–41