# Effects of drought on leaf-litter invertebrates of an Australian Wet Tropics ecosystem: the Daintree Rainforest

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## Abstract

Climate change is impacting ecosystems worldwide, and tropical rainforests, in particular, are extremely vulnerable. Tropical rainforests are predicted to experience drought events with increasing frequency, duration and severity. Understanding how drought will impact these ecosystems is critical to management strategies. In particular, understanding how drought will impact tropical leaf-litter invertebrates will provide insight into broader impacts across the entire ecosystem. We investigated the impacts of drought on leaf-litter invertebrate abundance and diversity in the Daintree Rainforest of Far North Queensland, Australia. Additionally, we investigated the ways in which litter depth, soil moisture and substrate type impact leaf-litter invertebrate abundance. We found that neither number of functional groups nor number of orders was different in drought-treated sites compared to control sites, but that invertebrate abundance was significantly lower in drought-treated sites. We found that neither soil moisture nor litter depth had any significant effect on leaf-litter invertebrate abundance or diversity. Substrate type did not affect the number of functional groups or orders present, but we found significantly higher leaf-litter invertebrate abundance in sites with rock substrate, compared to soil substrates.

**Running Title:** Effects of drought on tropical leaf-litter invertebrates

**Keywords:** abundance, diversity, litter depth, soil moisture

## Introduction

Anthropogenic climate change is significantly altering and challenging ecosystems worldwide (Malhi *et al.* 2020). Globally, climate change is driving mass extinctions. Indeed, it is now widely accepted that we have entered a sixth major extinction event (Ceballos *et al.* 2015), the impacts of which will greatly impact on the Earth's ecosystems. While the existence and severity of climate change is now accepted across the scientific and general public, recognition of the impact a changing climate will have on tropical ecosystems was accepted much later than for ecosystems at higher latitudes. This view was exacerbated by the second Intergovernmental Panel on Climate Change (IPCC) report in 1995, which stated, 'tropical forests are likely to be more affected by changes in land use than by climate change as long as deforestation continues at its current high rate' (Corlett 2012). The view that land-use practices would have a more significant effect on tropical ecosystems than would climate change had the unfortunate consequence of a lack of research being conducted into the likely impacts of climate change on the tropics in the 1990s and 2000s (Corlett 2012). It was not until around 2007 that this view shifted and research came to focus on the potential impacts of climate change on the tropics. Today, it is widely accepted that tropical ecosystems are highly vulnerable to climate change, and that better understanding of current and potential future impacts of climate change on tropical ecosystems is needed to inform management strategies aimed at ensuring their survival.

Climate change is impacting the Australian tropics in several ways. Temperatures in the tropics are predicted to rise on average by at least 0.5–1.4°C by 2030 (Hoffmann *et al.* 2018), and periods of extreme heat and dryness are likely to be prolonged (McJannet *et al.* 2007). While flooding rains, monsoons and tropical cyclones are predicted to become more extreme, such events are also likely to become less frequent and less predictable (May & Ballinger 2007). Further changes in seasonality and water availability will be driven by reductions in mountain rainforest canopy cloud capture, due to increases in the height of the orographic cloud layer (McJannet *et al.* 2007). Combined, these factors indicate that the Australian tropics will increasingly face drought conditions, and species within the ecosystem will experience, at times, significant drought stress. A prerogative of ecological research in the Australian tropics, therefore, is to investigate the ways in which drought will impact rainforest systems, functions and species. Critically, this can be achieved through investigating the impacts of drought on tropical leaf-litter invertebrates.

Tropical insects are thought to make up the majority of eukaryotic species on the planet (Grimbacher *et al.* 2018), and their preservation is central to the sustainability of Australian ecosystems (York & Lewis, 2018). Invertebrates provide multiple ecosystem services: seed dispersal, processing of organic matter, nutrient cycling, water filtration and pollination. These services have flow-on effects for the entire ecosystem, including helping regulate photosynthesis, soil fertility, water quality and plant diversity (Crespo-Pérez *et al.* 2020). Additionally, invertebrates are central components of both brown and green food webs, and aid in promoting energy transfer across ecosystems (Crespo-Pérez *et al.* 2020). There is, therefore, an urgent need to understand how tropical leaf-litter invertebrates will respond under the drought conditions likely to be the tropics' reality in the coming decades. Importantly, understanding invertebrate response to drought will also provide invaluable insights into how the broader ecosystem will be impacted by drought. Despite their clear importance, invertebrates remain severely understudied (Eisenhauer *et al.* 2019). The consequent lack of knowledge about them further drives the need for studies of tropical invertebrates.

Our study aims to investigate how drought affects the number of functional groups, number of orders and abundance of leaf-litter invertebrates in the Australian wet tropics. Additionally, we aim to determine how environmental conditions (litter depth, soil moisture and substrate type) affect tropical invertebrate abundance and diversity. This study represents a significant contribution to ongoing endeavours to better understand invertebrate functions in tropical environments, particularly in the context of a changing climate and increasingly frequent occurrences of drought.

We hypothesised that drought will impact tropical leaf-litter invertebrates and that this will be reflected by lower numbers of functional groups and orders in drought affected sites. Additionally, we predicted that greater invertebrate abundance and higher numbers of functional groups and orders will be associated with higher soil moisture levels and greater litter depth.

# Methods

### *Study site and species*

This study was conducted in the Daintree Rainforest Observatory (DRO) in Far North Queensland (-16.103, 145.449). The DRO, located within the world heritage listed Daintree Rainforest, comprises 42 ha of tropical lowland rainforest. The Daintree is classified as a tropical ecosystem, has a mean annual temperature of 24.4°C, and receives an average 5,100 mm precipitation annually (Tng *et al*. 2016). All data presented here were collected in the week of 18–24 June 2022.

The DRO provides a unique and invaluable facility for the study of the impacts of drought: drought shelters, a series of 3,000 corrugated plastic 'rooves' covering over 4,000 $m^2$ of rainforest that redirect rainfall away from the roots of trees and the ground, stopping approximately 80–90% of rain from reaching the rainforest floor, so as to emulate severe drought conditions as might be experienced during an El Niño period (Laurance 2015). Samples were taken from under these drought shelters and from the open rainforest.

### *Field methods*

A total of 20 sites were used in this experiment: ten under the drought shelters (hereafter referred to as drought sites) and ten in the rainforest outside the drought shelters (hereafter referred as control sites). Within each treatment (control and drought sites), six of the chosen sites had a soil substrate and four had a rock substrate. Each site was randomly chosen; however, randomisation was limited by the need to have clearly rock or soil substrate, and to have at least 10 mm of leaf litter. At each site, a plot with an area of 15 x 15 cm was identified, the depth of the litter within the plot was measured using a ruler, and then all leaf litter within the plot was collected. In addition, at each site, measurements of soil moisture were taken using a soil moisture probe. Three individual measurements were taken at different points within the 15 x 15 cm square plot, and the average was recorded.

### *Laboratory methods*

Each of the 20 leaf-litter samples was poured into a Berlese funnel trap (one funnel per sample). To prevent invertebrates from climbing or flying out and prevent unwanted invertebrates from falling in, the top of each funnel was covered with a thin mesh bag. The bottom of each funnel hung into a jar containing 20 ml of ethanol. These traps were placed under three heat lamps, with the tops of the funnels 40 cm from the lamps (Figure 1). All of the traps were left under the heat lamps for at least 5.5 hours.

After the traps had been left under the heat lamps for at least 5.5 hours, the ethanol in the bottom of the jar containing invertebrates that had dropped out of the leaf litter was transferred to a petri dish for examination under a microscope. Pipettes and additional ethanol were used to rinse any remaining invertebrates from the jars. A dissecting microscope was used to identify the invertebrates taken from the traps. Invertebrates were identified to order level with the assistance of the Key to Insect Orders – Revised app (LucidMobile 2022). The remaining leaf litter in the funnel was dried in a drying oven, and the dry weight of the sample was recorded.

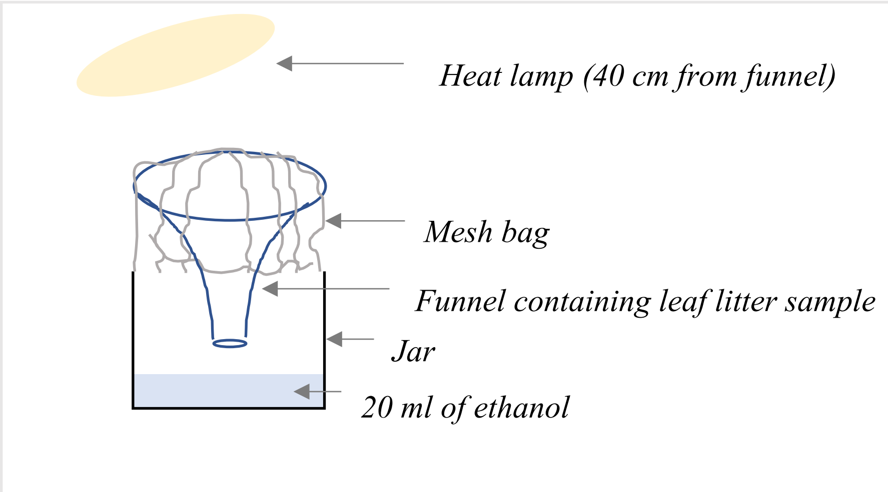


***Figure 1:*** *Diagram showing set-up of the Berlese funnel trap, used to extricate invertebrates from the leaf litter collected from sample sites.*

### *Data analysis*

The number of individuals and number of orders taken from each site were recorded. Identified invertebrates were classified into key functional groups in order to determine the number of functional groups present in each plot. These functional groups were identified according to Santos *et al.* (2021). Each measure (number of functional groups, number of orders and number of individuals) was converted from a raw total into a measure per 100 g of dried litter. This was calculated by dividing each measure by the dry litter weight of the sample, and then multiplying the result by 100.

Analysis of variance (ANOVA) tests were conducted to test for s significant difference between numbers of invertebrate functional groups and orders in control and drought plots. ANOVA was also used to test for significant differences in total invertebrate abundance and numbers of functional groups and orders between the two substrate types (rock and soil). Linear models were used to test for relationships between soil moisture and invertebrate abundance and diversity on the one hand and litter depth and invertebrate abundance and diversity on the other. For all tests, a significance threshold of $p = 0.05$ was used to determine statistical significance.

## Results

### *Assigning functional groups*

Across all 20 sites we captured 60 individual invertebrates from 12 orders. These orders were classified into four key functional groups (Table 1). Where two functions are joined (for example, 'Predators/Saprophages'), the identified orders perform both of these functions in the ecosystem.

**Table 1:** Functional groups and orders of invertebrates captured in the Daintree Rainforest

| Functional group | Included orders |
|---|---|
| Predators | *Hymenoptera, Neuroptera, Himenptera, Aranae* |
| Predators/Saprophages | *Acari, Coleoptera* |
| Saprophages/Microphages | *Amphidoda, Zoraptera, Collembola* |
| Saprophages | *Protura, Isoproda, Diploptera* |

*Invertebrate abundance and numbers of functional groups and orders*

There was no statistically significant difference in the number of orders per 100 g of leaf litter between control and drought sites [F(1,18) = 2.89, p= 0.106] (Figure 2a). Similarly, there was no significant difference in number of functional groups between control and drought sites [F(1,18) = 1.87, p=0.489] (Figure 2b). We found that invertebrate total abundance was significantly different between drought and control sites [F(1,18) = 6.43, p=0.0264], with invertebrate abundance being higher in the control sites (Figure 2c).

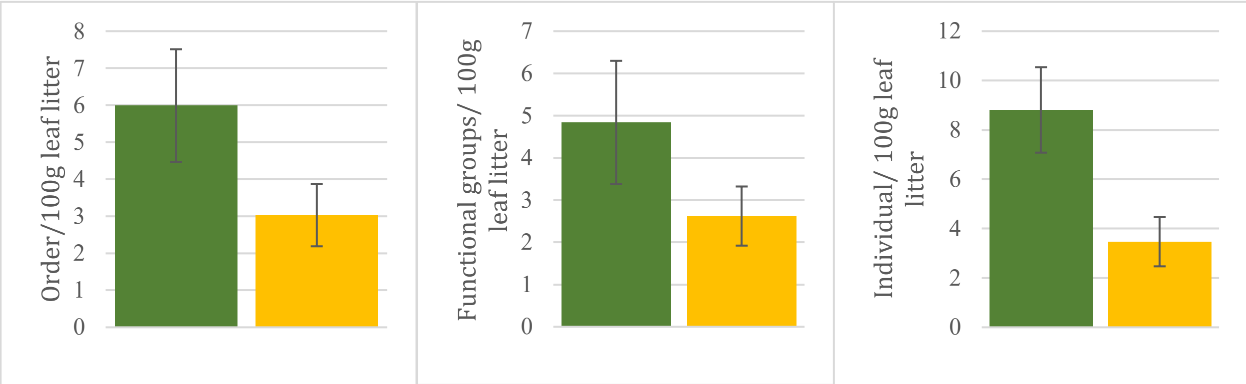


***Figure 2: a)** orders per 100g of leaf litter across control and treatment (drought) sites **b)** functional groups per 100g of leaf litter across control and treatment (drought) sites and **c)** total invertebrate abundance per 100g of leaf litter across control and treatment (drought) sites. For all plots, error bars show standard error, green shows control sites and yellow shows drought sites.*

*Impact of soil moisture on invertebrate abundance and numbers of functional groups and orders*

There were very weak linear trends of higher levels of soil moisture corresponding to increases in number of functional groups ($R^2$= 0.05632, p=0.1615) (Figure 3a), number of orders ($R^2$= 0.02289, p=0.2449) (Figure 3b) and abundance ($R^2$= 0.03772, p=0.2044) (Figure 3c); however, none of these trends was statistically significant.

*Impact of litter depth on invertebrate abundance and numbers of functional groups and orders*

We found potential weak linear trends of greater litter depth corresponding to decreases in the number of functional groups ($R^2$ = -0.04227, p = 0.6377) (Figure 4a), number of orders ($R^2$ = -0.02322, p = 0.4605) (Figure 4b) and total invertebrate abundance ($R^2$ = -0.02322, p = 0.4605) (Figure 4c). However, none of these trends was statistically significant.

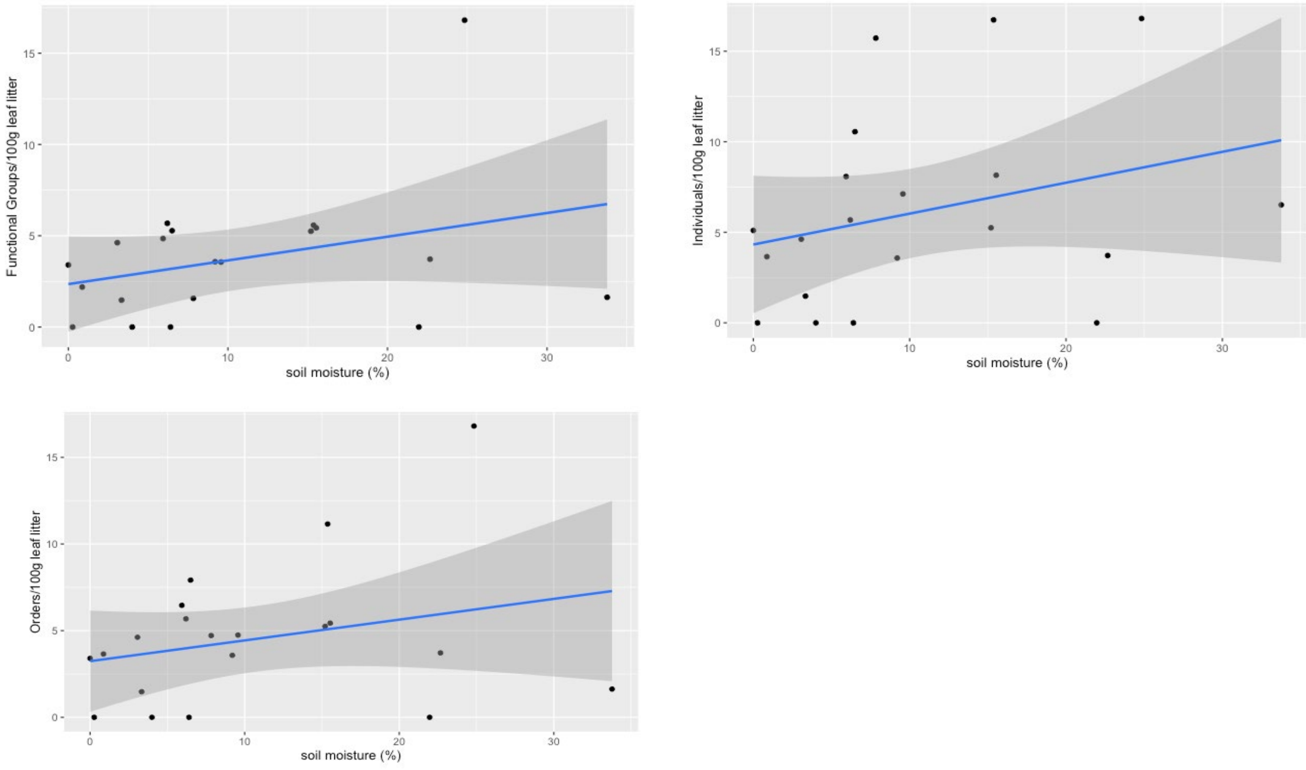


***Figure 3:*** *Relationships between soil moisture (%) and* ***a)*** *number of functional groups per 100 g of leaf litter,* ***b)*** *total individuals per 100 g of leaf litter and* ***c)*** *number of orders per 100 g of leaf litter.*

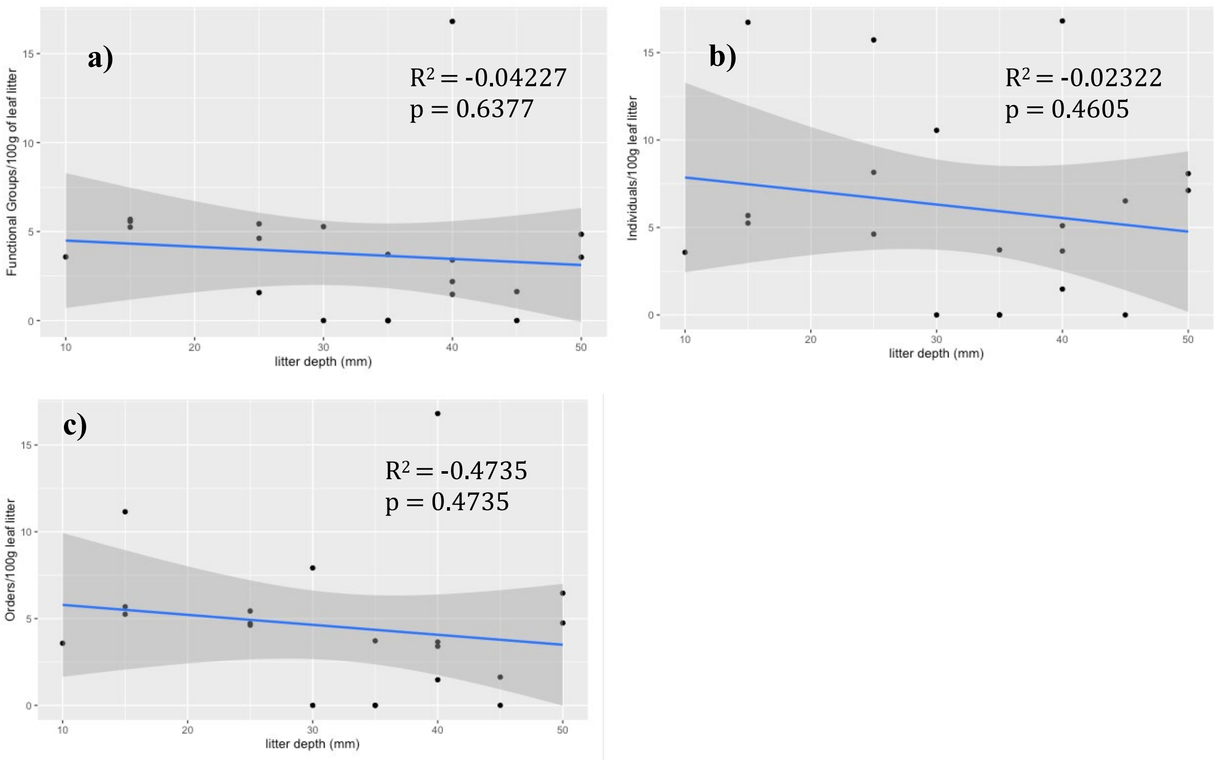


**Figure 4:** *Relationships between litter depth (mm) and* ***a)*** *number of functional groups per 100g of leaf litter,* ***b)*** *total individuals per 100g of leaf litter, and* ***c)*** *number of orders per 100g of leaf litter.*

*Impact of substrate on invertebrate abundance and numbers of functional groups and orders*

There was no significant difference in the number of invertebrate functional groups or between sites with rock versus soil substrate ([F(1,18) = 4.18, p = 0.0557] and [F(1,18) = 3.52, p = 0.0767] respectively) (Figure 5b & 5c). There was a significant difference in invertebrate abundance across sites with rock versus soil substrate ([F(1,18) = 4.90, p = 0.040]) (Figure 5a), with higher concentrations of individuals being found in sites with a rock substrate.

Segregating data by treatment, we found no significant difference in numbers of functional groups and orders between the two substrates in either control or drought plots ($F_{1,8}$ = 1.86, p = 0.210) for number of functional groups in the control site, ($F_{1,8}$ = 2.48, p = 0.154) for number of functional groups in the drought plots, ($F_{1,8}$ = 1.75, p= 0.222) for number of orders in the control plots and ($F_{1,8}$ = 4.52, p = 0.066) for number of orders in the drought plots). We found no difference in total invertebrate abundance across sites with rock and soil substrates in the control plot ($F_{1,8}$ = 2.73, p=0.137), but found significantly higher concentrations of individuals in rock substrate sites in the drought plot ($F_{1,8}$ = 5.92, p = 0.0410).

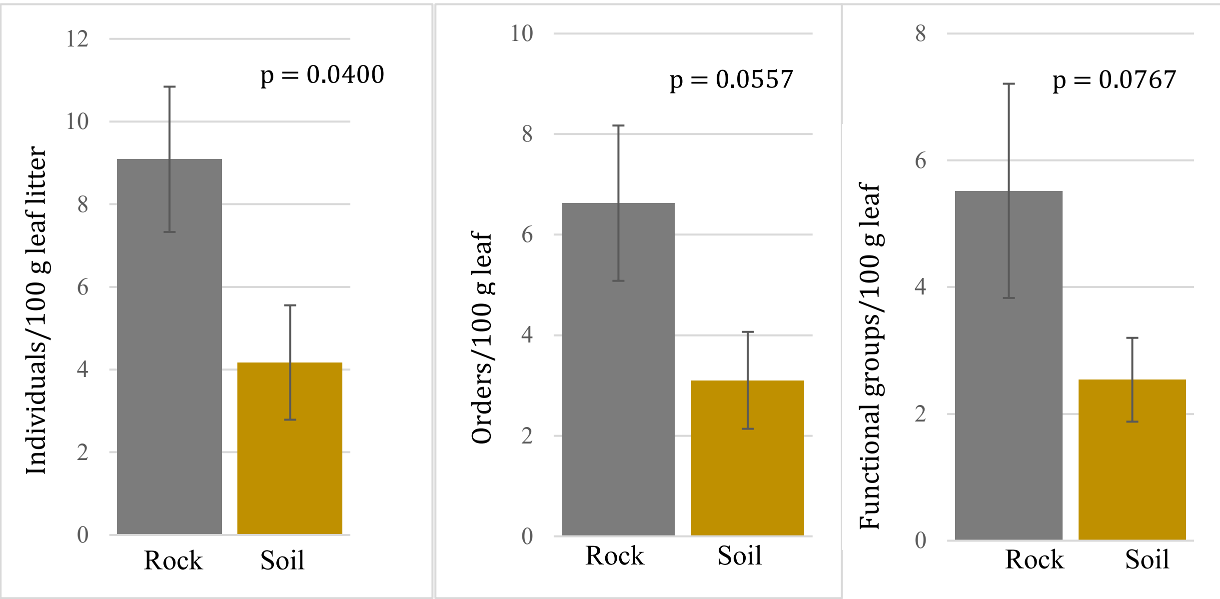


**Figure 5:** ***a)*** *total individuals per 100 g of leaf litter across sites with rock vs soil substrate* ***b)*** *number of orders per 100 g of leaf litter across sites with rock vs soil substrates* ***c)*** *number of functional groups per 100 g of leaf litter across sites with rock vs soil substrates. For all plots, error bars show standard error. Grey shows sites with rock substrate, yellow shows sites with soil substrate.*

## Discussion

The aim of this study was to investigate how invertebrate abundance and diversity responded to drought in a tropical rainforest. Additionally, we sought to investigate how environmental factors (litter depth, soil moisture and substrate) impacted total invertebrate abundance and numbers of functional groups and orders. We found that neither number of functional groups nor number of orders was significantly different across the control and drought sites, but that total abundance of invertebrates did significantly differ. We found that neither litter depth nor soil moisture had an impact on number of functional groups, number of orders or total invertebrate abundance. Finally, we found that only invertebrate abundance differed significantly across the two substrate types (rock and soil).

The finding of no statistically significant differences between drought and control plots for abundance and numbers of orders and functional groups was inconsistent with our hypothesis. The finding that invertebrate abundance did significantly differ across control and drought sites was consistent with our hypothesis. These results may indicate that invertebrates across all functional and taxonomic groups are impacted by drought pressures to the same degree, explaining why diversity was not significantly different across treatments, but abundance was. Previous, similar, studies also report decreases in tropical invertebrate abundance under drought conditions. Notably, França *et al.* (2020) report a decrease in tropical dung beetle abundance under El Niño years compared to neutral or La Niña years. There are several potential drivers behind the reduction in invertebrate abundance in the drought sites in this study. Periods of prolonged drought reduce microorganism activity, resulting in a decrease in soil nutrient cycling (Yavitt *et al.* 2004). This may have significant flow-on impacts for all invertebrate functional groups and orders, and explain the reduced invertebrate abundance seen in the drought sites. Three of the twelve orders sampled here are classified as microphages/saprophages, and these orders/functional groups may be experiencing a reduction in available food sources in drought sites. A reduction in these orders may in turn result in a trophic cascade, impacting the predator and predator/saprophages functional groups.

Drought also leads to tree mortality and a reduction in the amount of leaf litter produced (Davidson *et al.* 2008). Again, this will likely result, directly or indirectly, in a significant decrease of a critical food source for saphrophagous and microphagous invertebrates. Additionally, tropical invertebrates commonly use leaf litter as shelter and as a critical habitat. This may also explain why we found lower abundance in drought sites; however, there are some counter-indications against this explanation. Here, we hypothesised that there would be more invertebrates in areas with greater litter depth, reflecting the importance of leaf litter as a critical food source for saprophages, yet we found no such trend. We found no statistically significant relationship between litter depth and invertebrate abundance. This result is supported by Roeder *et al.* (2021), who found that litter depth was rarely an accurate predictor of invertebrate abundance in North American forests. This indicates that while invertebrates (and saprophages specifically) rely on litter for nutrition, greater litter depths do not result in greater diversity or abundance. Further study into litter depth and invertebrate abundance and diversity would shed valuable light on how invertebrates are using litter.

We found that soil moisture had no significant impact on invertebrate abundance, number of functional groups or number of orders. This finding appears to be inconsistent with McGee *et al.* (2020), who report that variation in invertebrate community composition in tropical secondary forests at the class, order and family level is best explained by soil moisture. One possible explanation for our result may be that it rained a few hours before the soil moisture measurements were taken, and this may have resulted in a skewing of invertebrate distribution in relation to soil moisture. A clear avenue for a future study, therefore, would be to investigate the relationship been invertebrates and soil moisture before, during and after rainfall. A comprehensive study in this fashion would provide valuable information on how soil moisture impacts invertebrates overall, and thus what drought means for these animals.

Finally, we found that while substrate type did not have a significant effect on number of functional groups or orders, it did significantly impact invertebrate abundance, with more individuals being found on sites with a rock substrate. The reasons for this finding are unclear, and thus future research on the impact of substrate types on invertebrate abundance is needed.

*Limitations*

There are three limitations associated with this study that should be mentioned, and potentially improved upon in further studies. First, this study only used data from ten drought sites and ten control sites. Second, only four rock substrate sites were used for each treatment type. This is a small sample size. A larger data set would likely paint a more comprehensive picture of the effects of drought on invertebrates. Unfortunately, some invertebrates could not be satisfactorily identified to the order level and had to be excluded from the study. Third, as mentioned above, sampling over a greater range of weather conditions would provide a more holistic understanding of invertebrate abundance, diversity and relationship with environmental factors.

## Conclusions

Despite this study's limitations, its findings provide several key insights into tropical invertebrates. Invertebrates play a critical role in the ecosystem, and are identified as essential to ensuring the sustainability of Australian forests (York & Lewis 2018). Thus, the lower invertebrate abundance found in the drought plot indicates a worrying trend that will potentially impact the decomposition processes, predator–prey interactions and overall ecosystem health of this tropical ecosystem. Of the four functional groups identified in this study, three are at least partly associated with the decomposition of litter material. This means that a large proportion of the invertebrates found play a significant role in nutrient cycling and the decomposition process, which in turn leads to regrowth that feeds primary producers (David & Handa 2010). If numbers of such invertebrates are reduced at forest scale due to decreases in precipitation, numerous large-scale flow-on effects can be expected. Excessive leaf litter accumulation increases the risk, and the severity, of fires (Laurance & Curran 2008). Declines in saprophagous invertebrates may put areas of the rainforest, particularly edges, at elevated risk of experiencing bushfires.

This study also highlights some important avenues for future research. Firstly, here we were only able to identify invertebrates to the order level, but there is an ongoing need for studies that can help in identifying invertebrates to the family, genus or even species level. Being able to more accurately describe invertebrates' taxonomy will aid in more correctly assigning them to functional groups, and in understanding the likely impacts of drought conditions on invertebrates at more specific levels. Secondly, patterns of latitudinal abundance suggest that the effects of drought are likely highly related to patterns of rising temperatures (David & Handa 2010). A clear avenue for future research would be to conduct a study similar to this one that would examine the impacts of rising temperatures on invertebrate abundance and diversity. The results of such a study would supplement this study's findings, and help paint a more complete picture of the impacts of climate change on tropical invertebrates.

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