

Chapter 1: Thesis Introduction

The Role of Climate in Shaping Ecosystems

Insect diversity and community structure is shaped strongly by climate variables, both means and extremes, that they are exposed to (Carroll *et al.* 2003, Beaumont *et al.* 2007, Robinson *et al.* 2012, Andrew 2013, Andrew and Terblanche 2013). Changes in climate have been observed in the past and are predicted to continue at a more rapid pace in the future (IPCC 2014), this will continue to have a strong influence on wider ecological communities (Root *et al.* 2003). The average global surface temperature of our planet has increased by up to 0.6°C over the last 100 years (IPCC 2014), this is the highest rate of increase detected over the past 1000 years (Walther *et al.* 2002). By the end of this century, temperatures are likely to increase by 2°C - 5°C in addition to changes in precipitation levels (IPCC 2014). Rainfall over the Australian continent is predicted to be variable but expected to change by -20% to +20% in the central, eastern and northern parts. Importantly, more extremes will be seen such as days of extreme rain and drought intensity (Hughes *et al.* 1996, Whetton and Power 2012).

If a species cannot adapt physiologically, morphologically or behaviourally to a rapidly changing climate (Andrew *et al.* 2013a), it's geographic range could either shrink or shift (where possible) (Stireman *et al.* 2005). Range shifts have been observed for a number of species (Hill *et al.* 2002, Thomas *et al.* 2004, Andrew and Hughes 2005a), leading to altered community structure and phenology in existing ecosystems. Range shifts are rarely synchronous for species within a community (Hodkinson 1997). This is an important consideration for specialist species, they may respond to climatic changes at a different rate to their host or prey, becoming mismatched, resulting in a loss of food resource (Hughes 2003, Westoby and Burgman 2006).

It is likely that extreme weather events associated with climate change will affect species composition and the functional attributes of entire ecosystems. The ability of ecosystems to resist

and recover from major disturbance events is dependent upon the frequency and duration of the extreme weather event and the evolutionary history of the species (Parmesan *et al.* 2000).

Ecosystems with low species diversity may be the most sensitive to climatic extremes (Ayres and Lombardero 2000, Dornelas *et al.* 2011). It is also becoming clear that trait diversity can play a major role in a community's resilience to climatic shifts (Bêche and Statzner 2009, Eronen *et al.* 2010, Angert *et al.* 2011, Pavoine and Bonsall 2011).

When studying the effects of climate change on physically small insect communities, it is important to consider the range of thermal microhabitats they occur in (Willmer 1982). Microhabitats can sometimes reduce temperature variability, insects in these habitats may not experience the extreme temperatures measured in ambient air (Woods *et al.* 2014), hence standard weather station data is not ideal for determining how insects are adapted and limited by temperature (Baudier *et al.* 2015). The surface temperature of a leaf can also be quite different to ambient temperature depending on the plant, Woods *et al.* (2014) found that apple leaves were warmer than ambient air when exposed to solar radiation, but cooler than air during the night.

Some organisms are dependent on signals from changes in precipitation and temperature to initiate certain stages in their development cycles (Yukawa 2000, Stireman *et al.* 2005). Climate warming is expected to increase winter survival and accelerate development and reproduction (Ayres and Lombardero 2000). Warming could therefore favour invasive species over indigenous ones (Chown *et al.* 2007), and generalist species over specialists (Bale *et al.* 2002). Invasive species may have shorter generation times and higher abundances, making them more likely to evolve adaptations to the new environmental conditions (Dukes and Mooney 1999). Generalist species may be able to simply move to a different host if they become displaced with their existing host under climate change (Laštůvka 2009).

Changes in temperature and rainfall can also affect life cycle events such as reproduction and migration in many species (Ayres and Lombardero 2000, Hughes 2003). If the cycles become

mismatched between host and herbivore due to different responses the insect could be at greater risk of extinction due to lower food quality or even a complete loss of food source. This risk is even greater at range edges where the climate is generally less favourable for an insect (Parmesan *et al.* 2000), as the plant growth stages may only be available for a short period of time during an insect's development (Bale *et al.* 2002).

Rapid climate change has occurred in the past (pre-human dominated world), and research exists that considers how insect communities respond to this, generally mobile species shifted their ranges and immobile species adapted (Coope 2004). This led to asynchronous taxonomic composition between communities, however many of these shifted over time to resemble the pre-change communities (Parmesan *et al.* 2000, Coope 2004). The problem in the current human dominated landscape is the combined effects of rapid climate change and anthropogenic disturbance and fragmentation of the environment. As spatial distance increases, any two observations of ecological communities are likely to become less similar (Nekola and White 1999). This is partly due to environmental gradients, but when there are major dispersal barriers such as fragmentation of habitats, the similarity decreases far more abruptly (Soininen *et al.* 2007). The confinement of ecosystems into small, isolated fragments greatly limits the options of response to rapid changes in extreme climates and disturbance frequency/intensity. Smaller isolated populations result in lower genetic variation which limits the potential for immobile species to adapt (Parmesan *et al.* 2000).

Insects are the most diverse group of organisms on earth (Coope 2004). Their short lifespans, large population sizes and sensitivity to environmental change (Speight *et al.* 1999) make them useful as indicators for conservation (Kremen *et al.* 1993). There have been a number of studies that assess the importance of climate in shaping insect and associated communities (Hill and Hodkinson 1992, Drake 1994, Hill *et al.* 1999, Bale *et al.* 2002, Andrew and Hughes 2004, Crozier 2004, Andrew and Hughes 2005a, Andrew and Hughes 2005b, Grimbacher *et al.* 2006, Andrew and Hughes 2007, Musolin 2007), although there is still a lack of knowledge in Australia on the actual mechanisms

behind this (Hughes 2003), this is especially the case for the insect order Thysanoptera. Part of the reason for this knowledge gap, is that climate affects insect communities in very different ways. For example, even if an insect itself is resilient to a certain level of change, it could be indirectly affected via changes in host plant quality (Phelps and Gregg 1991, Drake 1994). The effect of weather events could also have different consequences depending on the current life stage of the insect. For example, unfavourable temperature or precipitation is likely to have less of an affect if the insect is in diapause (Kingsolver 1989, Bale and Hayward 2010) and freeze tolerance or avoidance behaviour can vary between egg, Larvae, pupae and adult stages (Sinclair *et al.* 2003).

Australia encompasses a range of climatic conditions that can influence insect assemblages. In north eastern NSW we can characterise four major climate zones (Bureau of Meteorology 2014). Arid zones are furthest west, they are characterised by high mean maximum temperatures (24°C), low mean minimum temperatures (11°C) and low mean annual rainfall (380mm). Vegetation in arid zones is typically sparse, shorter and with harder, less nutritious foliage. Semi-arid zones are east of the arid zones; they have high mean maximum temperatures (24°C), low mean minimum temperatures (8°C) and low mean annual rainfall (650mm). Semi-arid vegetation is much taller and slightly more dense. Temperate zones are east of semi-arid zones, they have lower mean maximum (19°C) and minimum (7°C) temperatures, moderate mean annual rainfall (1000mm) and much more dense vegetation. Sub-tropical zones are on the east coast, they have high mean maximum (23°C) and minimum (15°C) temperatures. Mean annual rainfall is very high (1600mm) in sub-tropical zones and vegetation is very dense and tall with typically softer foliage.

Thysanoptera

Thysanoptera (thrips), are an insect order comprised of approximately 5500 species (Mound 2011) that is greatly underrepresented in terms of research. The unusual biology of thrips in terms of feeding styles, social behaviours, morphological variation and haplodiploidy (Crespi 1992, Mound *et al.* 1998, Crespi and Abbot 1999, Mound and Morris 2000, Gilbert *et al.* 2012) makes them useful for

investigating interesting biological questions. Community structure of thrips has generally been influenced mainly by environmental variables such as rainfall and the temperatures experienced by the populations during development (Davidson and Andrewartha 1948, Kirk 1984a, Morsello *et al.* 2010, Krumov and Karadjova 2012), although there are very few studies that assess this.

Figure 1 shows the results of a Scopus search done in January 2013 for papers that mention Thysanoptera in Australia and the world. Numbers of papers that mention some of the more highly represented insect orders identified in Andrew *et al.* (2013b) are included as a comparison. There are just over 100 papers published in Australia that mention Thysanoptera, and under 1500 worldwide. Of all the Thysanoptera papers, 30 mention climate change and none of those are from Australia. There are a number of papers that assess the effects of temperature (McDonald *et al.* 1998, Chaisuekul and Riley 2005, Rhainds *et al.* 2007, Morsello *et al.* 2008, Mo *et al.* 2009, Varikou *et al.* 2009, Shibao *et al.* 2010, Pakyari *et al.* 2011) and carbon dioxide (Hughes and Bazzaz 1997, Seki and Murai 2012) on Thysanoptera development, however these focus on one or a few species of pest thrips in agricultural or quarantine environments rather than natural communities.

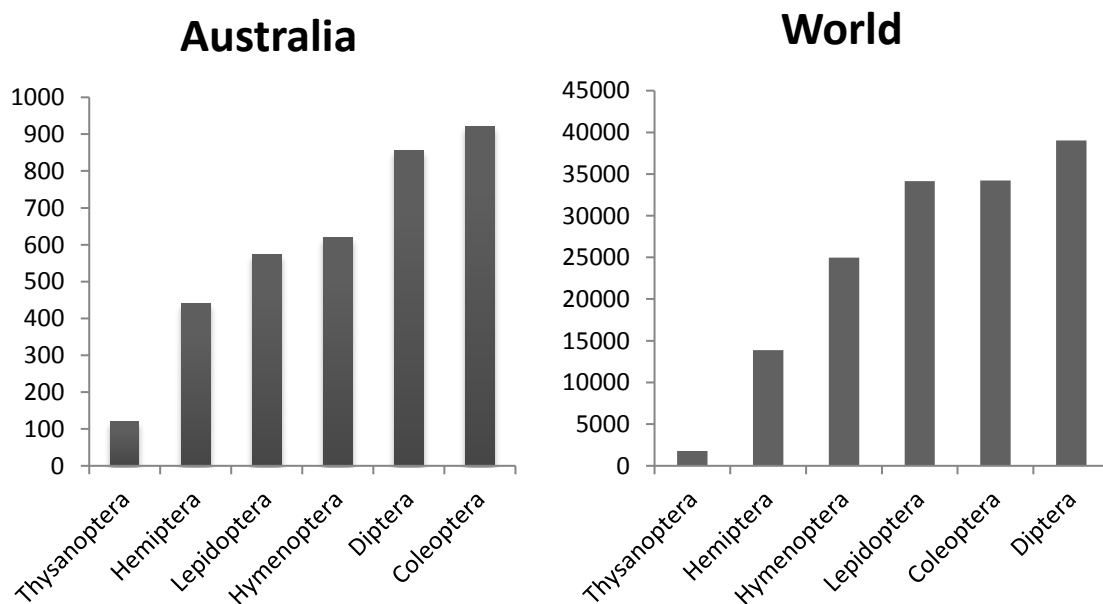


Figure 1: Number of peer reviewed papers published up until January 2013 of Thysanoptera as identified by SCOPUS, popular insect orders also shown for comparison.

Thysanoptera species vary considerably in terms of feeding and social behaviour. Some of the most behaviourally diverse thrips are associated with *Acacia*. These include gall-inducers (Crespi *et al.* 1997), domicile-builders (Morris *et al.* 2002), kleptoparasites (Mound and Morris 1999) and opportunistic invaders (Crespi *et al.* 2004). Eusociality is prevalent in thrips (mainly *Acacia* thrips) (Crespi 1992), presenting itself as species with an emphasis on parental care (Kiestler and Strates 1984) and also as species that produce specialised, non-reproductive morphs (Crespi and Yanega 1995) with specific functions in the colony such as soldiers with no wings and enlarged forelegs (Perry *et al.* 2003). These morphs can be so different in appearance that taxonomists have previously classified them into different families (Mound and Morris 2004). There is also behavioural diversity in domicile creating thrips, such as species of *Dunatothrips* forming colonies with multiple foundresses (pleometrosis), and *Lichanothrips* species establishing colonies with male and female (Morris *et al.* 2002).

Interestingly, thrips diversity has previously not been found to correlate with floristic diversity (Mound 2004). The assumption that related insect taxa are associated with related plant taxa is often not the case with Thysanoptera (Mound 2004). Mechanisms of host association can be based on plant nutrition (ie nitrogen content (Atakan 2006) and nitrogen content of soil (Stavisky *et al.* 2002, Chow *et al.* 2012)), plant secondary metabolites and plant architecture (Brodbeck *et al.* 2002). Individual plants within the same patch may even harbour very different numbers of a thrips species, possibly due to small physiological differences in each plant (Mound 2004).

The flowering cycle of a host plant also determines Thysanoptera diversity. Flowers are very important in the life cycle of some thrips (Mound 2004), for example *Chirothrips* are dependent on grass flowers for breeding (Mound and Palmer 1972) and *Thrips fuscipennis* is dependent on rose pollen for feeding (Kirk 1984b). While thrips may consume and destroy a lot of pollen (Kirk 1987), there are cases where plants benefit from Thysanoptera pollination (Williams *et al.* 2001).

Pest thrips

A number of Thysanoptera are regarded as economically significant pests. *Frankliniella occidentalis* (western flower thrips) is one of the major worldwide pests, it is highly polyphagous being found attacking chrysanthemums, tomatoes, cotton, pepper (Kirk and Terry 2003). *F. occidentalis* is also one of only ten thrips species (Mound 2002) capable of tospovirus transmission (Latham and Jones 1997). *Frankliniella schultzei* and *Thrips tabaci* are other highly polyphagous (to the point of sometimes preying on mites (Milne and Walter 1997)) pest thrips, also capable of transmitting tospovirus (Best 1968). These pest species are generally polyphagous, but that doesn't mean all populations of that species can actually breed on the host plants. Polyphagous thrips also tend to have distinct preferences when there is a choice of potential hosts, for example individuals of *Thrips tabaci* are not likely to move to suitable surrounding hosts when a locally preferred host is in abundance (Mound 2004).

Grass thrips

Of the 5500 species of Thysanoptera, approximately 3000 are phytophagous and 300 are known to be fully dependent on Poaceae (Mound 2011). Phlaeothripidae is one of the two major families of grass dwelling thrips. Phlaeothripidae contains genera that feed and breed in inflorescences such as *Haplothrips* (Mound and Minaei 2007, Minaei and Mound 2008), genera that feed on fungal spores and breed at the base of grasses such as *Nesothrips* and *Carientothrips* (Eow *et al.* 2014) and predatory genera such as *Podothrips*, a coccid predator (Mound and Minaei 2007).

The other major grass thrips family is Thripidae, with many genera feeding and breeding on grass leaves, however some breed in florets such as *Chirothrips* (Mound and Palmer 1972) and *Odontothripella* (Mound 2011). There seems to be distinct host associations between endemic Australian thrips and endemic native grasses. For example, Mound (2011) has observed *Odontothripella* (a floret breeder) species associated with *Danthonia*, *Stipa* and *Themeda* grasses,

and the leaf breeding *Aliceathrips*, *Masamithrips*, *Karphothrips* and *Monothrips* associated with *Chrysopogon*, *Poa*, *Stipa* and *Gahnia* hosts.

Despite these observed associations of thrips and host, there is a lack of records regarding specific host association among grass thrips, even for the more abundant species (Mound 2005). Host plant can also be hard to define, as localised strains of polyphagous thrips may have a strong attachment to a particular plant species (Mound 2005). The loss of native grasslands due to introduction of exotic pasture grasses will have a significant effect on the survival of both specialist and polyphagous thrips, especially when they are displaced under a changing climate.

The Importance of native grasslands

Grasslands and grassy woodlands in Australia have become heavily degraded since European settlement and are often poorly conserved (Cole and Lunt 2005). This has had a significant effect on insect community structure and insect-plant interactions (Landsberg *et al.* 1990). Restoring woodlands often requires significant effort directed towards establishing a native understory for biodiversity conservation (Prober and Thiele 2005) and to improve soil nutrition (Prober *et al.* 2005). This can be difficult as many native species compete poorly against exotic weeds (Cole and Lunt 2005). *Themeda triandra* (Kangaroo grass) and *Poa sieberiana* (Snow grass) are possible exceptions to this and as such, have received considerable attention for use in restoration projects (Adair and McDougall 1987, Phillips 1999). *Themeda triandra* has been successfully established from seed and transplants (Scott 1972, Groves *et al.* 1982, McDougall 1989, Baxter *et al.* 1993) and occurs across a very wide range of climates and habitat types (Cole and Lunt 2005).

Themeda triandra

Themeda (subfamily Panicoideae) is a genus of grass with over 20 species, 3 of which are found in Australia. *Themeda triandra* is the most widespread of these species and has one of the widest distribution ranges compared to all Australian flora (Hayman 1960). When assessing insect communities over a range of climates, it is very useful to keep the host plant constant to reduce the effects of large differences in host plant chemistry and architecture on the results (Leather 1986, Zangerl and Berenbaum 1993). This is often difficult to do when a large climatic range is required as the host of interest may not occur under a sufficient range of climates. Based on its wide distribution and high conservation significance, *T. triandra* was chosen as the main host plant in this project for assessing Thysanoptera populations.

It is important to note that *T. triandra* occurs as five different ploidy levels (Hayman 1960), but most commonly as diploids or tetraploids depending on where it grows (Groves 1965). *Themeda triandra* diploids are mainly found in the higher rainfall belt of eastern Australia and tetraploids are generally

found in the more arid areas of inland Australia (Groves 1965). In terms of major differences between *T. triandra* ploidies, tetraploids have larger cell sizes (increasing the overall size of the plant), different hairiness, presence of different vein classes and different flowering times to the diploids (Woodland 1964, Scott 1972). Arvanitis *et al.* (2010) describe the lack of studies that consider how plant polyploidization is related to interactions with insects. Their results suggest that an increase in ploidy may lead to insect host shifts and that plant ploidy explains insect host use. In newly formed plant polyploids, novel interactions may alter habitat preferences and trait selection.

Recent Advances in Community Analysis

One common method of analysis in the studies that have assessed insect community composition in relation to environmental variables (Leather 1986, Campos *et al.* 2006, Novotny *et al.* 2006), is an algorithmic approach such as a canonical correspondence analysis (ter Braak 1986) or tests based on a distance measure such as Bray-Curtis (Anderson 2001). These methods can be hard to interpret and are difficult to use for model selection (Burnham and Anderson 2004). They are also difficult to use for making specific, quantitative predictions of community abundances (Warton and Hudson 2004). Further, these distance based analyses may not give reliable results due to complications arising from the typical mean-variance relationship seen in ecological data (Taylor 1961). Generally, as mean abundance increases, variance increases, this can affect the way location effects (i.e. differences in mean abundance) and dispersion effects (i.e. differences in variability of abundance) are interpreted, as assessed in Warton *et al.* (2012)

Warton *et al.* (2012) recommends the use of generalised linear modelling approaches, as they explicitly model the mean-variance relationship. A model based approach is quite often used for predicting the responses of a single species to environmental change (Botkin *et al.* 2007, Illán *et al.* 2010, Rebelo *et al.* 2010) or the total abundance and richness of communities (Yamamura *et al.* 2006, Gruner 2007). However, a model based approach is not commonly used for predicting responses of entire communities (but see McCarthy (2011)), this has mainly been due to a lack of

user-friendly methods to help achieve this. A package for R (R Development Core Team 2014) called `mvabund` (Wang *et al.* 2012) now exists to address this issue, this package allows fitting generalised linear models to multivariate abundance datasets (Wang *et al.* 2012) and it is used in the same way as the standard modelling functions in R making it relatively easy to use.

Recent Advances in Morphological Analysis

In order to gain an understanding of what might drive species responses to the environmental variables, it is useful to measure functional traits (behavioural, physiological or morphological) and use this data in an analysis. Many studies have assessed how morphological traits respond to environmental variables (Azevedo *et al.* 1998, Blanckenhorn and Demont 2004, Merrick and Smith 2004). Often, these studies do not consider trait frequencies, but sometimes a measure of trait richness is used (Pavoine and Bonsall 2011). This type of data does not always account for abundance patterns and has the potential to be misleading, the presence of a particular trait in highly abundant species would often be more important than if it was in rarer species (Bêche and Statzner 2009). There have been very few attempts at simultaneously assessing morphological traits along with community abundance data, some use the maximum entropy approach (Mokany and Roxburgh 2010) and others build upon the 'fourth corner problem' (Doledec *et al.* 1996, Legendre *et al.* 1997, Pollock *et al.* 2012). The fourth corner approach needs to take three matrices, one of environmental data, one of species abundance data and one of trait data. Recently, Brown *et al.* (2014) developed a new model based approach to the fourth corner problem using generalised linear models with a LASSO penalty (Hastie *et al.* 2009). Additionally, this has been incorporated into the `mvabund` (Wang *et al.* 2012) package for R (R Development Core Team 2014) to allow this method to be used relatively easily.

Thesis Outline

The work present in this thesis assesses how grassland Thysanoptera communities are shaped by climate both using broad scale climate data and microhabitat (grass tussock level) temperature data. Specifically, *Themeda triandra* dominated grassland communities are assessed in terms of Thysanoptera species composition and morphological characteristics. This provides knowledge of how Thysanoptera associated native Australian grasslands may be affected under a changing climate. The methods used can also be applied more broadly using other taxa and traits. The knowledge gained can be used alongside studies of other taxa in other systems to assist in predicting the consequences of climatic changes.

Three data chapters are included. They are written up as standalone journal manuscripts in preparation for review. In this format, there will be overlap in some of the introduction and methods sections. The chapters are:

Chapter 2: Thysanoptera community composition across a climatic gradient in Themeda triandra dominated grasslands

This chapter examines the response of Thysanoptera (thrips) communities across a climatic gradient. The effects of climate change on thrips has not been given much attention outside of the agricultural/quarantine context. This chapter uses the statistical package `mvabund` to apply generalised linear modelling to a multivariate response matrix. By examining the community as a whole and then focussing on some of the more abundant thrips species, new knowledge was gained regarding the potential impacts of climate change. It was also clear that the use of tussock level microclimate data resulted in much stronger models than relying on weather station data.

Chapter 3: Response of Thysanoptera trait frequencies across a climatic gradient in Themeda triandra dominated grasslands

This chapter uses a combination of morphological trait data, species abundance and environmental data to examine the importance of climate on determining species traits. A recently developed statistical method is used for the simultaneous analysis of three matrices of data. It is a model based method built upon the 'fourth corner' concept that produces coefficients that describe the interaction between environmental variables and morphological trait measurements in determining abundances. An additional allometric analysis (SMATR) was used to assess variability in trait-body size relationships between the three major feeding types identified in grassland thrips (predator, herbivore, fungivore).

Chapter 4: The effects of climate and host plant polyploidy on Thysanoptera colonisation using a transplant experiment

This chapter uses a transplant experiment to investigate the question of how a warmer, drier climate may affect host plant colonization. *Themeda triandra* was used for this experiment, transplanted to three sites that simulate different levels of warming and drying. The level of ploidy found in *Themeda triandra* affects various physiological aspects of the plant, this allowed us to test potential insect preferences of diploid or tetraploids in each of these different climates. The same multivariate modelling method used in chapter 2 was used to analyse this data.

Chapter 5: Thesis Discussion

This final chapter discusses the major themes presented in the thesis and identifies future research that should lead on from this body of work.

Appendix I: This appendix contains supplementary figures and discussion that are not important for the aims of the thesis, but I found interesting enough to explore.

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Chapter 2: Thysanoptera community composition across a climatic gradient in *Themeda triandra* dominated grasslands



This chapter is written as a standalone manuscript, a modified version of this manuscript is intended for submission to a journal

Thysanoptera community composition across a climatic gradient in *Themeda triandra* dominated grasslands

2.1. Introduction

Insect diversity and community structure is shaped strongly by climate variables, both means and extremes, that they are exposed to (Carroll *et al.* 2003, Beaumont *et al.* 2007, Robinson *et al.* 2012, Andrew 2013, Andrew and Terblanche 2013). Changes in climate have been observed in the past and are predicted to continue at a more rapid pace in the future (IPCC 2014), this will continue to have a strong influence on wider ecological communities (Root *et al.* 2003). The average global surface temperature of our planet has increased by up to 0.6°C over the last 100 years (IPCC 2014), this is the highest rate of increase detected over the past 1000 years (Walther *et al.* 2002). By the end of this century, temperatures are likely to increase by 2°C - 5°C in addition to changes in precipitation levels (IPCC 2014). It is also likely that the extreme weather events associated with climate change (Bureau of Meteorology 2014) will affect species composition and the functional attributes of entire ecosystems. The ability of ecosystems to resist and recover from major disturbance events is dependent upon the frequency and duration of the extreme weather event and the evolutionary history of the species (Parmesan *et al.* 2000). It would be expected that the species with wide ranges, and individuals that occur towards the centre of these ranges, would have a greater chance of surviving a change in climate (Bale *et al.* 2002). It is for this reason, that it is important to understand the current spatial patterns of species in relation to climate.

Previous assessments for how insect communities are shaped by climates have used latitudinal (Barlow 1994, Davidowitz and Rosenzweig 1998, Boyero 2002, Andrew and Hughes 2004) and altitudinal (Alonso 1999, Brehm and Fiedler 2003, Escobar *et al.* 2007) gradients as surrogates. Some studies have also looked directly across climatic gradients (Hysell *et al.* 1996, Blanche 2000, Link *et al.* 2003, Bairstow *et al.* 2010, Lessard *et al.* 2010, Yates *et al.* 2011) although these studies are less common. The problem with some gradients is that similar climates are not replicated with large

spatial separation, for example the degree of spatial separation is often correlated with climate differential. This makes it hard to make more broad generalisations from the results. Sampling from a broad area so that areas of similar climate but large spatial separation are sampled helps address this issue. Sampling multiple climate types along the same latitude can also help address the issue of photoperiod differences confounding the results (Fielding *et al.* 1999).

Thysanoptera

The focus of this study is on grassland Thysanoptera (thrips), an insect order comprised of approximately 5,500 species (Mound 2011) that is greatly underrepresented in terms of research (Binns 2016 Chpt 1). The unusual biology of thrips (Crespi 1992, Mound *et al.* 1998, Crespi and Abbot 1999, Mound and Morris 2000, Gilbert *et al.* 2012) makes them useful for investigating interesting biological questions. The community structure of some Thysanoptera communities has occasionally been seen to be influenced by environmental variables such as rainfall and the temperatures experienced by the populations during development (Davidson and Andrewartha 1948, Kirk 1984, Morsello *et al.* 2010, Krumov and Karadjova 2012), although there are very few studies that assess this.

Grass living Thysanoptera are comprised of species with a wide range of feeding behaviours. The majority of species feed on the leaf tissue of the grass (Mound 2011). Other types include thrips that feed and breed in grass inflorescences (Mound and Palmer 1972, Minaei and Mound 2010), predatory thrips that are likely to feed on mites (Pereyra and Mound 2010) and thrips that feed on the fungus within the grass tussock (Mound 1974). Most species of grass thrips are within the family Thripidae and Phlaeothripidae (Mound 2011).

Interestingly, thrips diversity has previously not been found to correlate with floristic diversity (Mound 2004). The assumption that related insect taxa are associated with related plant taxa is often not the case with Thysanoptera (Mound 2004).

Potential mechanisms of host association can be based on plant nutrition (ie nitrogen content (Atakan 2006) and nitrogen content of soil (Stavisky *et al.* 2002, Chow *et al.* 2012)), plant secondary

metabolites and plant architecture (Brodbeck *et al.* 2002). Individual plants within the same patch may even harbour very different numbers of a thrips species, possibly due to small physiological differences in each plant (Mound 2004).

There is evidence that past climate changes have caused significant changes in the distributions of whole communities (Parmesan *et al.* 2000, Coope 2004). Generally, when the climate warms, the shift of species occurs towards the poles (Peters and Darling 1985). These shifts generally don't occur at the same rate, causing mismatches in existing interactions (Bale *et al.* 2002). There is also evidence that communities have very individualistic responses to climate change and this is likely to continue into the future (Graham and Grimm 1990, Davis *et al.* 1998) It is therefore important to assess the individual responses of species in addition to the community as a whole.

This research will use the recent advances in multivariate statistical modelling to assess the influence of a range of climatic and plant trait variables on native grassland dwelling Thysanoptera. Due to the diverse nature of Thysanoptera physiological, feeding and behavioural traits it is expected that species within the communities will be affected in a non-uniform manner. For this reason, we will determine what variables cause the most significant changes in overall community composition and then predict how changes in these variables may change the occurrence of particular Thysanoptera species. We also expect that Thysanoptera will be more sensitive to microclimatic variables rather than ambient variables. For this study, we sampled invertebrates from *Themeda triandra* dominated grasslands across a large spatial area that covers a range of different climates and environments in eastern Australia.

2.2. Methods

Site Selection

To assess the effect of climate on grassland insect communities it was important to use a grass species that was easy to find in a large range of climates in order to remove the effects of varying

host plant species. *Themeda triandra* is the grass species chosen for this as it is distributed all over Australia, so it was essential for all sites to contain a sufficient amount of this grass to be sampled. Sites were selected using topographic, vegetation, land use and geological maps, in addition to climate layers created using BIOCLIM and ArcGRID. Using ArcMap to view several climate layers, 44 sites (Figure 1) that encompass a wide range of climates and environment types were chosen. The sites were located between 28.36°S and 37.75°S and 144.7°E and 153.13°E and ranged from 26 m to 1250 m in elevation. The mean annual temperature varied from 9.3°C to 19.4°C and mean annual precipitation ranged from 385 to 1659mm.

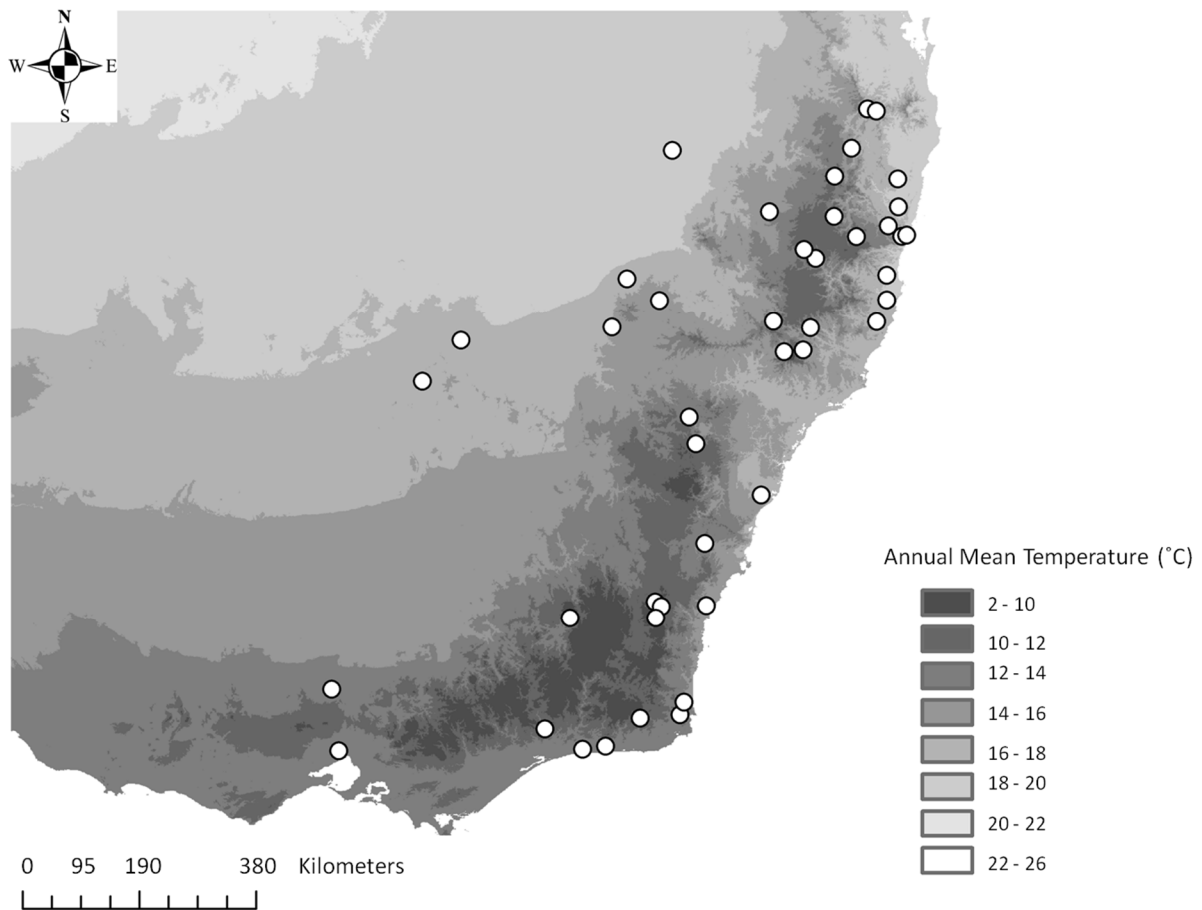


Figure 1: Map of research area, sampling sites are shown as white circles, shading shows mean annual temperature.

Survey of invertebrate communities in eastern Australia

Black, fine mesh sweep nets with a 40cm diameter opening were identified as an efficient method of grassland insect capture after performing a pilot survey. Sampling was conducted between the hours of 08:30 and 17:00, about 2 hours was spend at each site. A 20 m transect line was selected for each sample, at least 50 m from the habitat edge (i.e. road or fenceline) and separated by 20 m from each other. Ninety percent of sites were large uniform grassy areas, so sampling was conducted as close to the centre of the site as possible. A few sites consisted of smaller isolated patches (mainly some sub-tropical forests), so we sampled a line through the centre of each patch and the next closest patch (up to 500 m separation) was selected to provide additional samples at the site. After sweeping each transect, the net contents were washed into a vial with 80% ethanol. There were nine plots at each of the forty four sites, three of which were predominately (>70%) *T. triandra*, three were predominately the local dominant *Poa* species (*Poa sieberiana* at most sites) and three were a mix of other grass species in the area (including exotics). These collections occurred during November to December 2009 (season 1), March to April 2010 (season 2), and March to April 2011 (season 4) so that three seasons worth of data could be collected. The benefit of this was to obtain a seasonal representation of the feeding preferences of individual species, and to account for differences in host plant phenology (flowering, seed formation) and site-specific climatic differences (New 1979). The sampling route was designed to minimise correlation of date with latitude (i.e. sites sampled in a different order each season).

Table 1: Description of codes used to characterise site conditions as used in analyses

	Height	Inter tussock density	Intra tussock density	Disturbance	Flower	Wind	Sun
1	Flat growth form	Up to 3 tussocks per m ²	Very few leaves	Natural habitat with a mixed grassy and shrubby understorey with no signs of human visitation	Dead	Still	Sunny
2	Short tussock (<20 cm)	4-8 tussocks per m ²	Medium density	Natural habitat with a shrubby understorey and signs of occasional human visitation	Very mature	Slight breeze	Some clouds
3	Medium tussock (20-50cm)	>8 tussocks per m ² with separation by bare ground	Moderate density	Natural habitat with a grassy understorey and high human visitation	Mature	Windy	Cloudy
4	Tall tussock (>50cm)	'Sea of grass' (no bare ground)	Extremely dense	Highly modified and unnatural habitat with regular disturbance by humans or domesticated animals	New	Very windy	Overcast

For this study, we used climate data generated by BIOCLIM (Booth 1985, Busby 1986, Busby 1991) to characterise the sites. The downside of BIOCLIM is that it cannot give the exact values of climatic variables at tussock level (Yee and Mitchell 1991), and is based on weather station data which can vary considerably from ground level sensors (Graae *et al.* 2011). To address this, we obtained more precise data by placing three iButton® Hygrochrons/Thermochrons (set to record at hourly intervals) at each site at grass tussock level for temperature and humidity recordings, and used a metal detector to find them, download the data and reset them during the following sampling season. A script for R (R Development Core Team 2014) was written by Professor David Warton (UNSW) that fitted models to the ibutton data to obtain useful variables from the ibutton data, these included: maximum and minimum predicted temperatures, mean predicted temperatures, temperature diurnality, seasonality, temperature at sampling time, temperature during the morning of sampling day, mean temperature during week before sampling, mean temperature during growing season (90

days) before sampling and seasonal noon temperature at time of sampling. Humidity readings from the ibuttons were unfortunately not very useful. The plan was to use them to record rainfall events but recorded 100% after the first rainfall event and did not decrease for over week.

At each site we collected grass leaf samples for chemical analysis and recorded date, time of sampling, ambient humidity, ambient temperature, sun intensity (qualitative), wind strength (qualitative), grassland characteristics (Table 1) such as disturbance based on the classification in (Davies *et al.* 2003), leaf temperature at time of sampling using an IR 'gun', elevation and slope.

Three soil samples were taken at each site (15cm diameter x 20cm depth). Soil samples were dried at 40°C until a constant sample weight was obtained. Each sample was then crushed and passed through a 2 mm sieve. 0.3 grams of soil (ground to 0.5mm), per sample was used in a LECO TruSpec Series Carbon and Nitrogen Analyser. 2 grams of soil per sample was used in an ICP atomic emission spectrometer to analyse Ca, Mg, Na and K concentration (using a method adopted from Rayment and Higginson (1992)). Sodium adsorption ratio (S.A.R.) was calculated using:

$$S.A.R = \frac{Sodium}{\sqrt{\frac{1}{2}(Calcium^2 + Magnesium^2)}}$$

Insect Sorting and Identification

Insects were sorted to major orders (Hemiptera, Coleoptera, Thysanoptera, Hymenoptera) and the other orders were grouped into 'others'. Spiders were separated and assessed in Gibb *et al.* (2015). Thysanoptera was sorted to morphospecies (Oliver and Beattie 1996) based on characteristics used in Thysanoptera keys (Mound 2011, Hoddle *et al.* 2012, Mound *et al.* 2012). A voucher specimen of each morphospecies was photographed using a Leica MZ16a microscope and LAS automontage software. The online Thysanoptera key, Ozthrips, (Mound *et al.* 2012) and a compound microscope were used to identify common thrips to genus or species. Thrips larvae were excluded from the

analysis as they were difficult to associate with adults of the same species. For the more abundant Thysanoptera species, high resolution photographs were sent to expert Thysanoptera taxonomist Dr Laurence Mound (ANIC, Canberra) for additional verification in 2012.

Analysis

Due to time constraints, only the three *T. triandra* samples (out of the nine samples within each site) from seasons one, two and four were analysed. Analyses were performed on the entire Thysanoptera dataset. Species estimation curves were generated using EstimateS 9.1.0 (Colwell 2013) using both the classic and bias-corrected Chao-1 index, which is known to represent the upper bound of true species richness. The estimated coefficient of variation (CV) for abundance distribution was >0.5 for all curves and the classic formula gave larger Chao-1 values than when using the bias-corrected formula, this indicates that the classic formula is more accurate with this data and so I only compared the curves produced using this. These curves indicate how close the actual number of species I found was to the estimated species number based on the same sampling effort.

The three subsamples (each 20m transect) from each site were pooled as the analyses used assume independent samples. A principal components analysis (PCA) and observations of correlations of raw data were used to reduce the number of predictor variables for use in the models (Warton 2008b, Mellin *et al.* 2010). Simultaneous generalised linear models using a negative binomial response (O'Hara and Kotze 2010) were used to determine the effects of the predictor variables used on the whole community dataset. The `mvabund` (Wang *et al.* 2012) package for R 2.15.1 (R Development Core Team 2014) was used for this analysis. In addition to this, post-hoc tests were used to determine individual responses. Quadratic terms were considered in this modelling for the mean and leaf temperature variables, as unimodal responses are often expected in ecological theory (Abrams 1995, Austin 2002). Four level qualitative factors were reduced to two levels to increase interpretability. Residual plots were used in all analyses to ensure the analysis method was

appropriate for the data. The `summary.manyglm` function was used to identify significant variables, this models the variables non-sequentially, so the order of fit is not important. Other parameters used were `resamp="pit.trap"` a form of resampling found to give the most reliable Type 1 error rates (Warton & Wang in review), `test="wald"` (Warton 2008a, Warton 2008c), and `cor.type="shrink"` which allows for correlation between variables when variable number is high compared to sample size (Warton 2008c).

2.3. Results

Approximately 60000 insects were collected from 504 samples of *T. triandra* grasslands over forty-four sites across four sampling seasons. Of these insects, 1354 were Coleoptera, 6734 were Hemiptera, 5557 were Hymenoptera, 5000 were Spiders and 8760 were Thysanoptera, comprised of sixty-seven morphospecies. The remaining 32500 insects comprised a range of orders not analysed in this study. Two species of *Haplothrips* made up half the total abundance of Thysanoptera collected, and *Thrips imaginis* made up about a quarter of all abundance. The Thysanoptera abundance and richness for each site is summarised in figures 2 and 3. To determine the proportion of species sampled compared to the entire beetle assemblage available, the number of actual species sampled (rarefaction curve) was divided by the expected number of species (Chao-1 species estimation curve). For the entire Thysanoptera dataset, across three seasons, 72% of the expected thrips species were sampled (Figure 4).

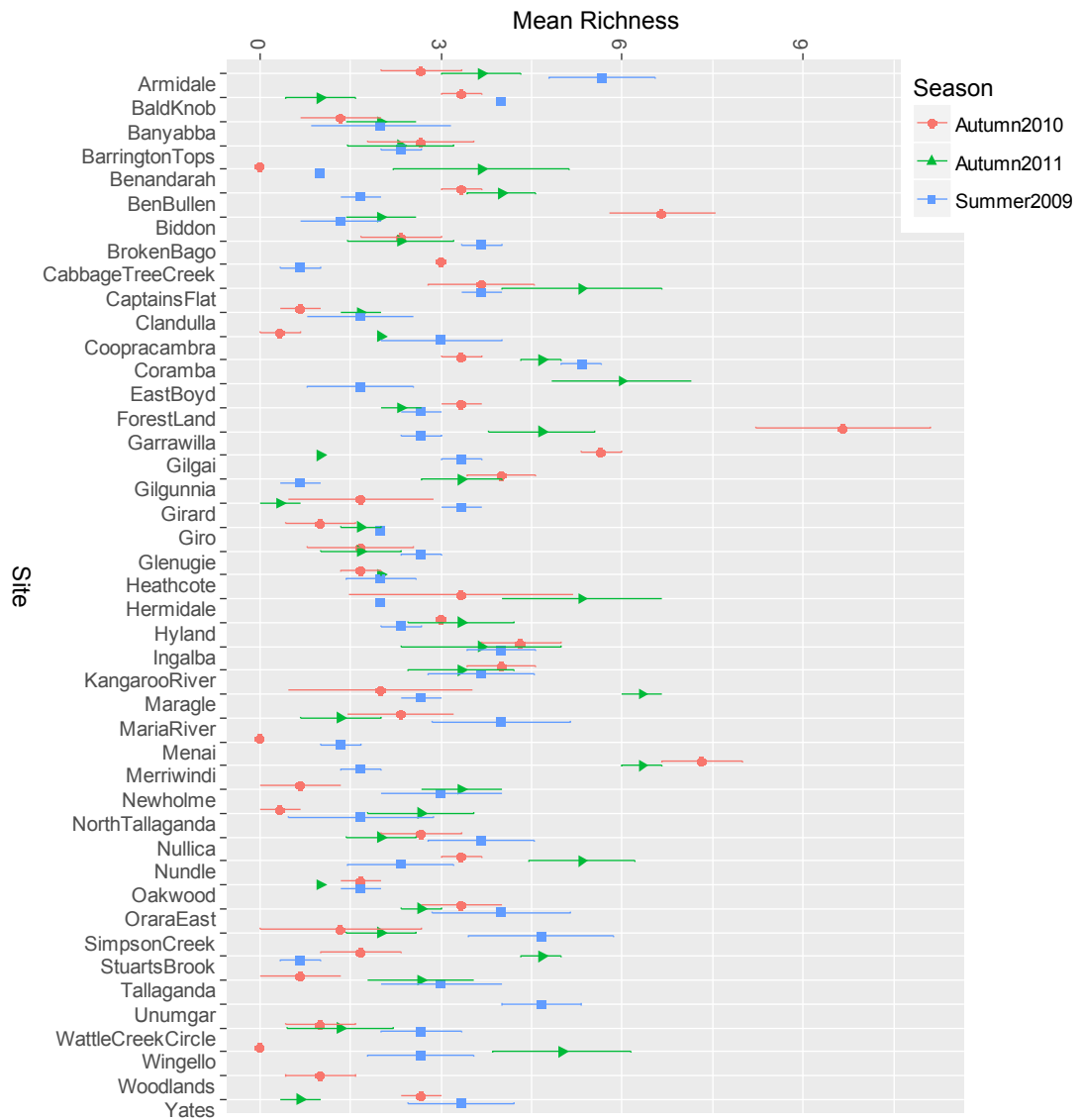


Figure 2: A summary of mean Thysanoptera richness at each site, for each season.

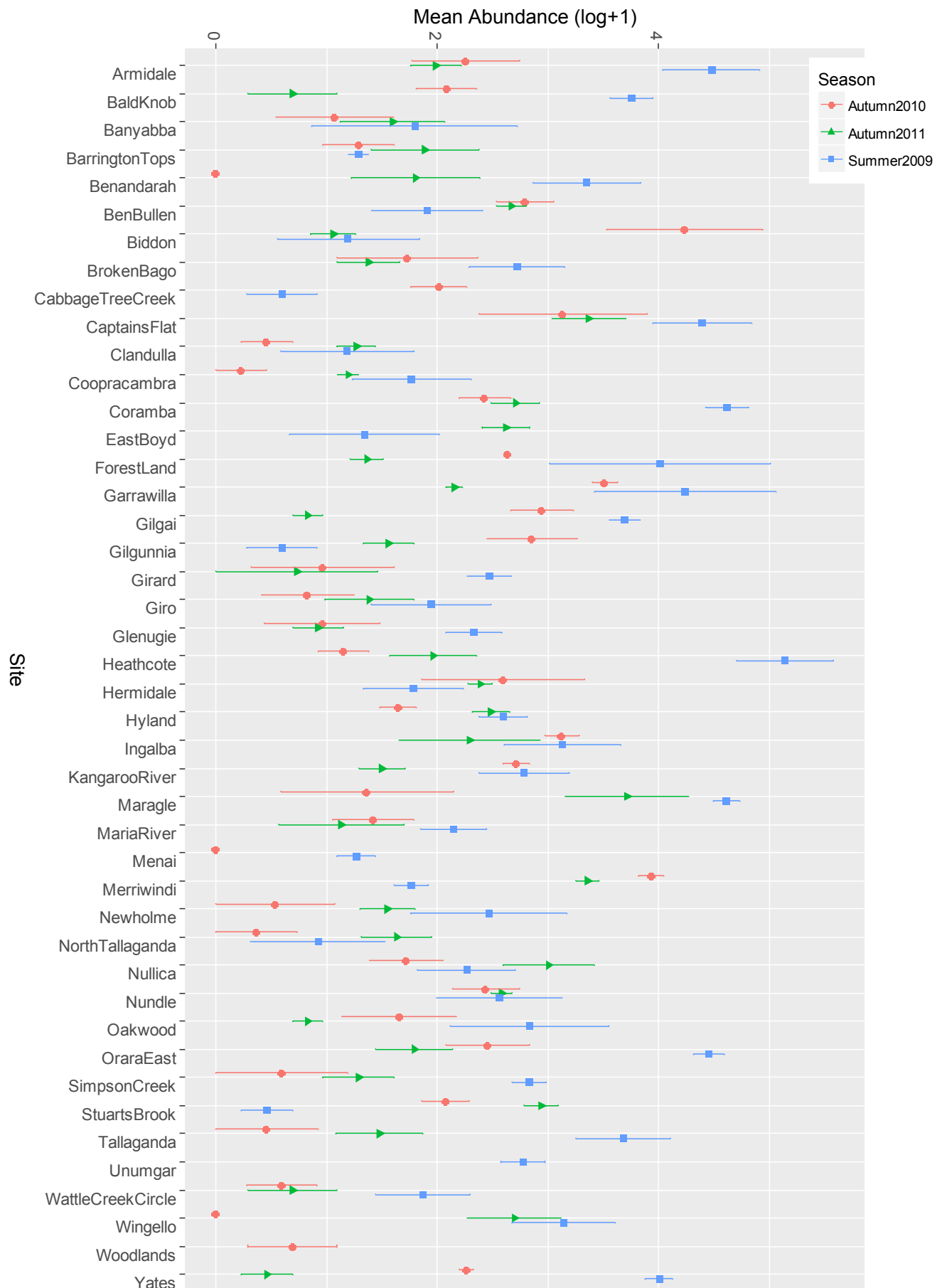


Figure 3: A summary of mean Thysanoptera abundance (log +1) at each site, for each season.

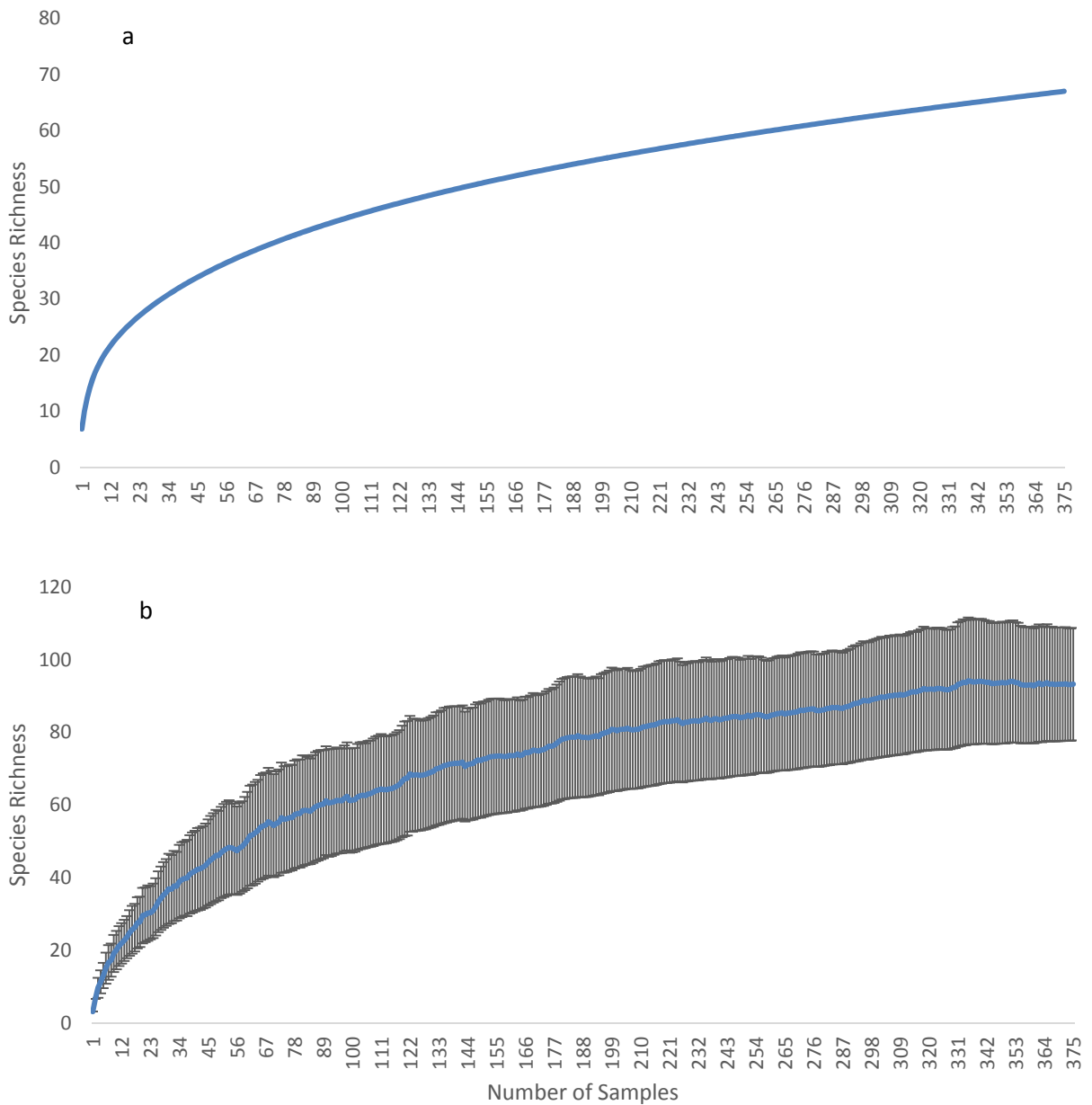


Figure 4: (a): Coleman rarefaction curve of the entire beetle dataset showing the accumulation of new Thysanoptera species found per number of samples. (b): Chao-1 species estimation curve (\pm SD) of the entire Thysanoptera dataset showing the estimated number of thrips species likely to exist per number of samples.

Thysanoptera community

The final model (Wald = 29.14, p-value = 0.006, df = 78) found that season, presence of flowers, inter tussock density, disturbance, ambient temperature and humidity, leaf surface temperature, tussock temperature during the week before sampling, tussock temperature during the growing season,

maximum predicted tussock temperatures, annual precipitation, elevation, latitude and C:N were all significant variables in accounting for the variation in Thysanoptera species composition (Table 2). It appears that the more arid sites have lower total abundances during Summer when compared to Autumn, but the temperate sites have higher abundances during Summer than Autumn (Figure 5).

Table 2: Results from fitting a multivariate generalised linear model, with negative binomial error distribution using a log-link function, to Thysanoptera community data. This tests the relationship between the predictor variables and the assemblage composition, significant predictors shown in bold. A Wald test was used, so the Wald statistic is presented along with the significance (p-value).

	Wald value	p-value
Season	5.778	0.016
Time of Day	3.884	0.503
Grass Height	4.493	0.152
Intrasussock Density	4.271	0.248
Intertussock Density	6.903	0.005
Disturbance	5.961	0.008
Flowering	7.405	0.002
Ambient Humidity	6.377	0.008
Ambient Temperature	5.513	0.036
Leaf Temperature	5.47	0.036
Annual Mean ibutton Temperature	5.156	0.072
Max ibutton Temperature	6.67	0.006
Min ibutton Temperature	3.473	0.593
Growing Season ibutton Temperature	7.09	0.001
ibutton Temp Week Before Sampling	6.529	0.012
ibutton Temp at Sampling Time	5.896	0.032
Annual Mean Temperature	5.345	0.079
Annual Precipitation	7.965	0.001
Elevation	6.312	0.007
Latitude	6.17	0.008
C:N	6.003	0.014
Leaf temperature (quadratic)	4.514	0.172
Mean ibutton temp (quadratic)	4.005	0.39

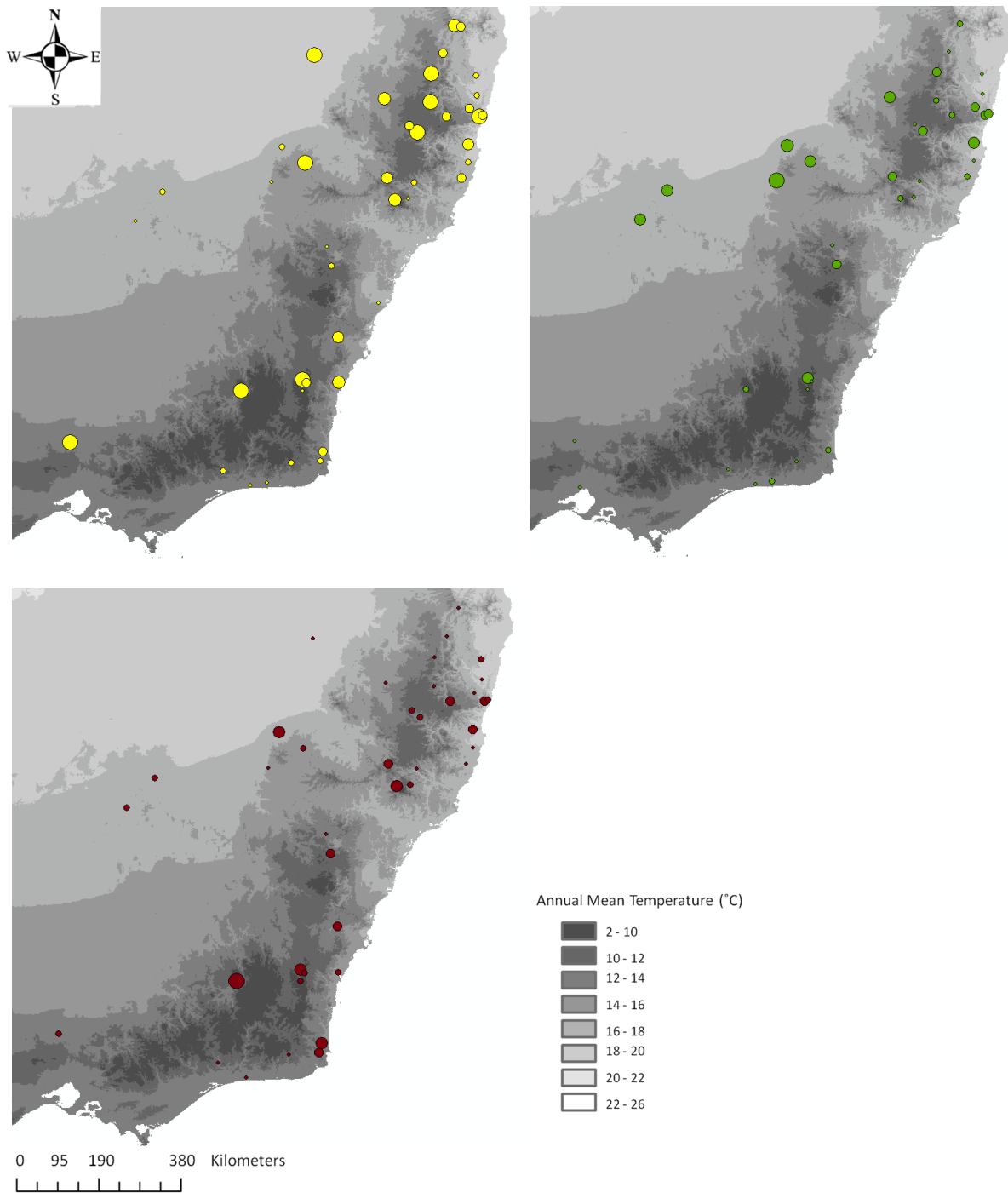


Figure 5: The change in total Thysanoptera abundance between season 1 (Summer 2009, yellow circles), season 2 (Autumn 2010, green circles) and season 4 (Autumn 2011, red circles). There are six different circles sizes for each colour, representing abundances ranging from (smallest to largest circle): 1-10, 11-30, 31-50, 51-100, 100-150, 150+. Background shading shows mean annual temperature.

Seasonal variation in some species of thrips, in various directions is shown in Figure 6. The rare thrips species are not shown in the univariate result table (Figure 6), as the univariate analyses need a sufficient level of abundance for meaningful results. Variables that were not significant for explaining the abundances of any individual species were time of day and ambient humidity. Annual precipitation and elevation was only identified as having a small effect on *Anaphothrips* sp 3. The presence of flowers has a negative association with many species which is unexpected. The temperature data has a variable effect on species abundance (Figure 6), so some of the more common species are assessed in more detail below. One general pattern of note, is that for species significantly affected by ambient temperature at time of sampling, there was often a significant influence of leaf temperature in the opposite direction.

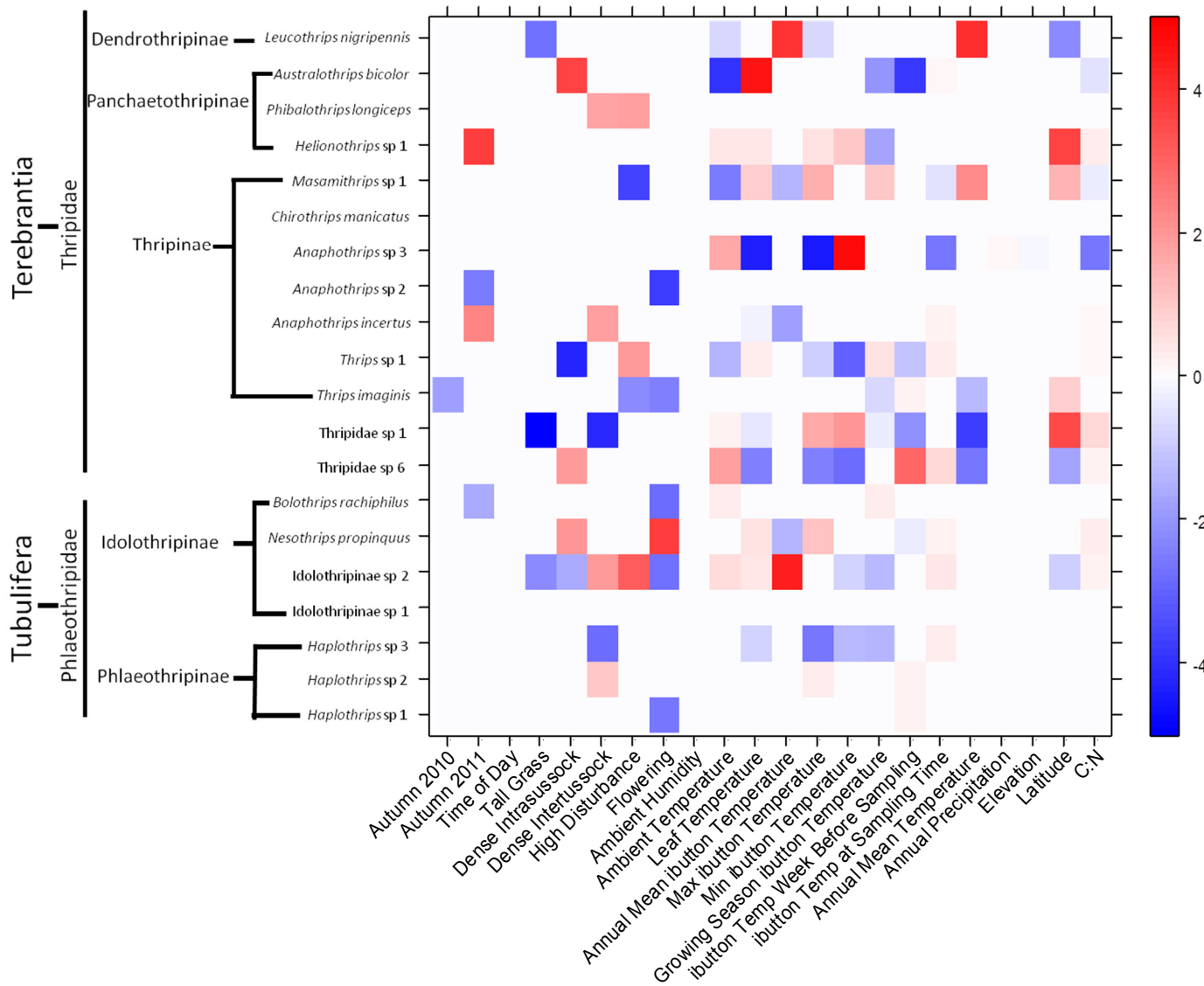


Figure 6: Univariate results from fitting multiple generalised linear models to the most commonly found Thysanoptera species, with negative binomial error distribution using a log-link function. Terms are not sequential, so each one shows the variation explained taking into account all other terms in the model. The colour represents the coefficients for the significant predictor variables for each species. Brighter red indicate stronger positive relationship; brighter blue indicate stronger negative relationship.

Individual responses for common Thysanoptera species

The following sections take the results from the multivariate model and provide figures to help predict how abundances may change if certain environmental variables change (with all others remaining constant).

Family Phlaeothripidae

Subfamily Phlaeothripinae

Haplothrips sp. 1

Haplothrips sp. 1 had a very wide distribution, found in all climate types sampled (Figure 6). During season 1 (Summer 2009), most *Haplothrips* were found in the north east corner of NSW, but in seasons 2 and 3 (Autumn 2010 and 2011) there was a more evenly spread distribution including more abundance in semi-arid areas (Appendix Figure 9). *Haplothrips* sp 1 were more likely to be found on non-flowering *Themeda triandra* and when tussock temperature during the week before sampling is high (Figure 6 and 7a).

Haplothrips sp. 2

Haplothrips sp. 2 had a very wide distribution, found in all climate types sampled. During Summer 2009, higher abundances were found in more northern temperate and sub-tropical areas, however the distribution was more evenly spread in Autumn 2010 and 2011 (Appendix Figure 11).

Haplothrips sp. 2 is expected to be found in higher numbers when tussock density within a plot is high (Figure 6). More *Haplothrips* sp. 2 are expected to be found when the maximum predicted tussock temperature is high and when tussock temperature during the week before sampling is high (Figure 6 and 7b).

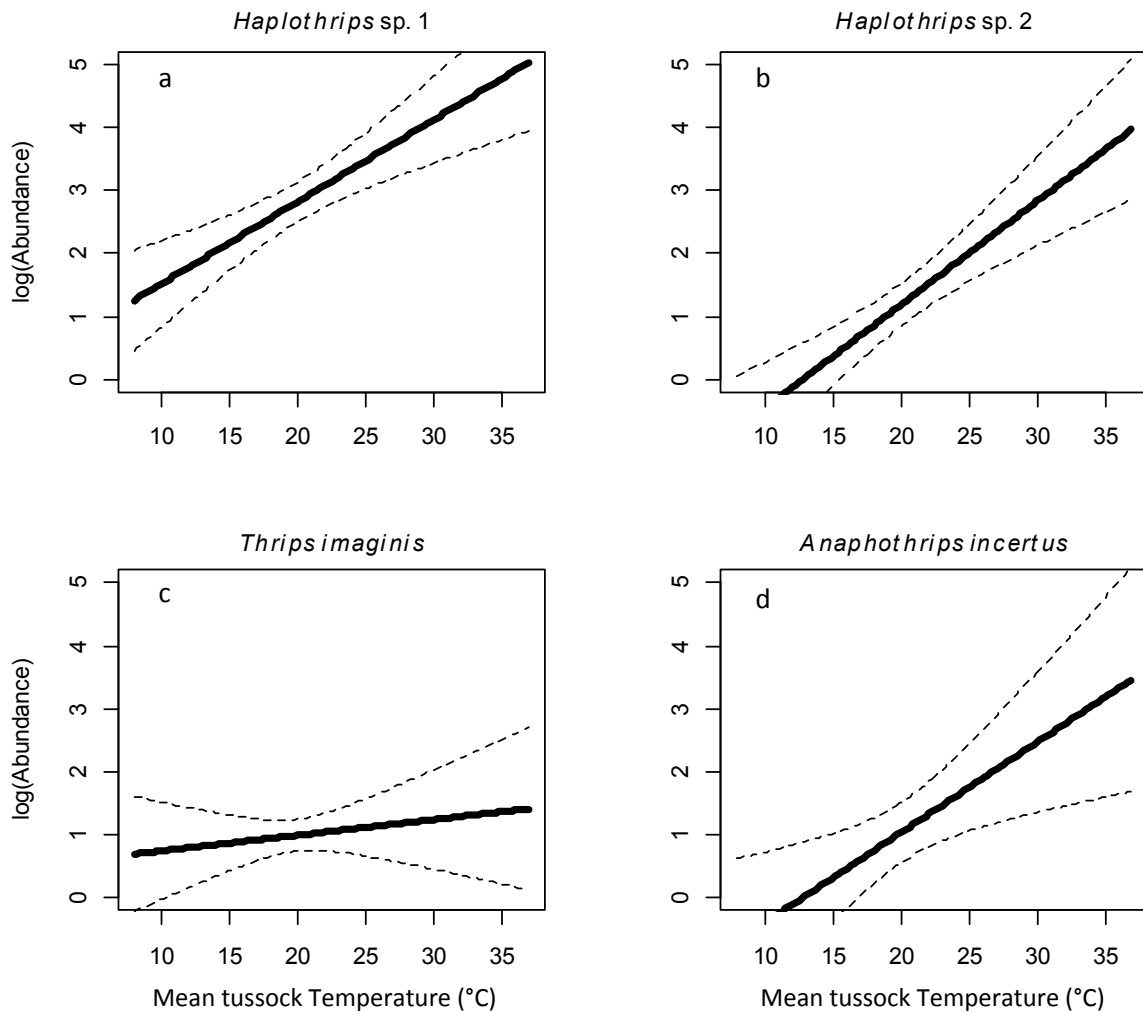


Figure 7: Predicted values (solid black line) of four common Thysanoptera species (a - *Haplothrips* sp. 1, b - *Haplothrips* sp. 2, c - *Thrips imaginis*, d - *Anaphothrips incertus*) abundance as a response to the mean tussock temperature (°C) during the week before sampling. Dashed line is the prediction interval, all other model variables fixed at mean values.

Family Thripidae

Subfamily Thripinae

Thrips imaginis

Thrips imaginis had a very wide distribution during Summer 2009, however it was quite restricted to north east NSW in low abundances during Autumn 2010. Numbers seemed to increase by Autumn 2011 (Appendix Figure 13, Figure 6). *Thrips imaginis* abundance was lowest in season 2 (Autumn 2010) (Figure 6). Fewer *Thrips imaginis* are predicted to occur in highly disturbed sites and when the

Themeda is flowering. More *Thrips imaginis* are expected when the tussock temperature during growing season and annual mean weather station temperature is low, but when the tussock temperature during week before sampling is high (Figure 6 and 7c). A small positive relationship between latitude and abundance is seen in *Thrips imaginis*.

Anaphothrips incertus

Anaphothrips incertus had a very wide distribution during Autumn 2011, found in all climate types sampled (Appendix Figure 15). During Summer 2009, *A. incertus* was restricted mainly to the sub-tropical sites of north east NSW, and during Autumn 2010 it was fairly scattered (Appendix Figure 15). *Anaphothrips incertus* abundance was highest in season 4 (Autumn 2011). *Anaphothrips incertus* abundance was higher when plots contained high tussock density (Figure 6). *Anaphothrips incertus* abundances are predicted to be higher when the tussock temperature during sampling is higher, but when leaf temperature and annual mean tussock temperature is lower (Figure 6 and 7d). There is also a positive relationship between *Anaphothrips incertus* abundance and C:N.

Anaphothrips sp. 2

Anaphothrips sp. 2 were found mostly in north-east NSW (including semi-arid inland and sub-tropical coast), with smaller numbers in the south-east (Appendix Figure 17). *Anaphothrips sp 2* were found in lowest abundances during season 4 (Autumn 2011) (Figure 6). More *Anaphothrips sp 2* were found in non-flowering *Themeda triandra* (Figure 6). *Anaphothrips sp 2* abundances are not significantly affected by the climatic variables measured.

Anaphothrips sp. 3

Anaphothrips sp 3 was mainly found in north-east NSW close to the coast, and slightly inland in the south east (Appendix Figure 18). *Anaphothrips sp 3* was not affected by seasonal variation, it was found in higher numbers on non-flowering *Themeda triandra* that was tall and sparsely distributed within sampling plot (Figure 6). *Anaphothrips sp 3* is predicted to be found in higher abundances when the maximum temperatures are low and minimums are high (low variability). *Anaphothrips sp*

3 is also one of the few species predicted to be affected by soil nutrition, with higher abundances on *Themeda* growing in soil with higher nitrogen content (Figure 6).

Chirothrips manicatus

Chirothrips manicatus was found mostly in drier regions in both northern and southern parts of NSW, but had a presence in a wide range of climates (Appendix Figure 19). *Chirothrips manicatus* was not affected by seasonal variation, or site characteristics. *Chirothrips manicatus* had a unimodal (Appendix Figure 20) response to mean ibutton temperature, meaning it is predicted to be found in higher abundances when tussocks are exposed to temperature extremes (high maximums and low minimums) (Figure 6).

2.4. Discussion

Thysanoptera Community Response

When assessing the Thysanoptera community as a whole, seasonal variation was important for explaining community composition. The univariate analysis reveals that seasonal variation had significant effects on the abundance of some of the more common species. Latitude was a significant predictor for determining Thysanoptera community composition, likely due to spatial autocorrelation (Legendre 1993). Variation due to time of day was not a significant predictor for any of the species or overall composition, this variation was probably captured more directly by ambient temperature measurements. The only host structure variable that was significant in explaining Thysanoptera composition was intertussock density. At the individual species level, both inter and intra densities had variable effects on a range of different thrips. Tussock height had a negative association with three species of thrips, this is unexpected as larger plants generally have the capacity to harbour more insects (Leather 1986).

Sites were categorised into disturbed/undisturbed, the effect of disturbance and landscape modification can often reduce habitat availability to support complex communities

(Ananthkrishnan 2000, Price *et al.* 2011, Gerisch *et al.* 2012). Disturbance was identified as an important factor in this study for the composition of Thysanoptera communities. The direction of response was variable, and there were significant associations with both common and rare species. In this study, higher overall abundances of Thysanoptera were found on flowering grass. Flowering grass provides the extra habitat and nutrients required for thrips that feed and breed in inflorescences (Mound and Palmer 1972, Mound 2005), meaning a greater variety of thrips should be supported. The presence of flowers was also identified as being important for determining overall Thysanoptera community composition. The importance of flowers in shaping population dynamics of insects is common across many groups (Dicks *et al.* 2002, Schoonhoven *et al.* 2005, Elzinga *et al.* 2007). Many flower-dependent insects also rely on consistent flowering times and lengths to complete their life cycles (Sobhian and Zwölfer 1985, Del-Claro *et al.* 1997, Bartomeus *et al.* 2013). One of the effects of a changing climate is an alteration of plant and insect phenology (van Asch and Visser 2007, Andrew 2013). This is unlikely to occur in synchrony, potentially resulting in a failure of the insect to complete certain life stages (Westoby and Burgman 2006). Phenological shifts should be considered as important for Thysanoptera due to the fact that flower presence was found to be a significant predictor of community composition.

The direction of response to flowering found in the species specific univariate analyses however was mostly negative when a significant relationship was found. The negative response was seen in *Haplothrips*, *Anaphothrips*, *Idolothripinae*, *Bolothrips* and *Thrips imaginis*. *Haplothrips* are thought to breed in flowers of Poaceae and Cyperaceae, but are not believed to be flower feeders – in fact many species are considered to be predatory (Mound and Minaei 2007). *Anaphothrips* are thought to generally feed and breed on Poaceae leaves, with no known association with flowers (Mound and Masumoto 2009). *Thrips imaginis* is known to feed and breed in flowers of dicots, but not necessarily grasses (Kirk 1984). One potential explanation for this is that Thysanoptera larvae were not assessed in this study. There is a chance that *Haplothrips* larvae were collected from flowering

Themeda, but not many adults, maybe the lack of adults near flowering *Themeda* is a strategy to reduce resource competition (Lawrence *et al.* 2003). Another factor to consider is how ripe the seed is. *Themeda* seeds ripen more rapidly in hot dry conditions (McDougall 1989), and while a subjective measure of ripeness was recorded during this project, it is not certain what stage of ripeness would be preferable for each species of thrips.

Ambient and leaf temperature at time of sampling was identified as important in explaining captured Thysanoptera community composition. The direction of response of a species was often not the same between ambient and leaf temperature, nor was there consistency across all species, although there were more positive than negative relationships. This is likely related to conditions required for flight take-off being warm and relatively dry (Mellanby 1939, Lewis 1963, Taylor 1963), and the negative associations could be due to the thermal limit for dispersal activity (Andrewartha 1936, Janiszewski 1984). It was interesting that ambient humidity had no species specific interactions, but it was significant in explaining the overall thrips community composition that was sampled.

Tropical and sub-tropical climates are generally thought to harbour the greatest amount of ecological diversity (Beaver 1979, Rinker and Lowman 2004, Novotny *et al.* 2006). Tropical climates are characterised by low temperature variability (Janzen 1967) and far greater host plant diversity per area (Novotny *et al.* 2006). In this project, maximum predicted temperature (i.e. a measure of temperature variability) was important in explaining community composition.

Much of the Thysanoptera community composition was explained by the shorter term microclimate variables; growing season temperature, temperature the week before sampling and temperature at the time of sampling. Long term maximum temperature was also significant at explaining community composition, but the minimum was not. The microhabitat climate variables have varying influences depending on the species of Thysanoptera, implying they have fairly different climatic tolerances.

Detailed responses of the eight most abundant species were assessed to help explain how they

might respond to a climatic shift. The rarer species did not have enough observations for this to be meaningful.

Individual species responses

Family Phlaeothripidae

Subfamily Phlaeothripinae

***Haplothrips* species**

Haplothrips are one of the most commonly encountered Thysanoptera genera in Australia (Mound and Minaei 2007), and indeed were the most commonly collected thrips in this study. *Haplothrips* are presumed to breed in flowers and some species are associated with Poaceae but can be polyphagous (Hoddle *et al.* 2012) and often predaceous (Mound and Minaei 2007). When comparing the distribution maps, there are similarities in extent of range and abundances within species over the sites and seasons, implying the two common *Haplothrips* species in this analysis shared similar climatic preferences. *Haplothrips* sp 1 had a significant association with flowering, lower abundances are expected when *Themeda triandra* is flowering. Perhaps *Haplothrips* juveniles (not used in analysis) were found in flowering *Themeda*, displacing the adults. Another explanation is that most 'non-flowering' *Themeda* still retained its dead flowers, perhaps adult *Haplothrips* develop in fresh flowers and by the time they are adults the flowers have died.

The mean temperature during the week before sampling explained *Haplothrips* sp. 1 and sp. 2 abundance, the higher temperature would probably reduce the development time of this species leading to higher abundances (Andrewartha 1936, McDonald *et al.* 1998, Rhainds *et al.* 2007, Pakyari *et al.* 2011). More *Haplothrips* sp3 were collected in cooler climates and when the ambient temperature was higher, which is expected as higher temperatures are required for increased activity such as flight (Lewis 1963). There was no association with humidity, generally the thrips would be expected to be lower in the tussock as dispersal is often suppressed in high humidity (Morsello *et al.* 2010). The sweep netting technique involved sweeping down to the base of the

tussocks which was done to catch insects even if they did show this behaviour. Rainfall (i.e. 100% humidity) can also be associated with lower thrips abundance (Morsello *et al.* 2008, Riley *et al.* 2011), also no sampling was done in the rain (or even after recent rain as the grass was too wet for sweep net sampling).

Subfamily Idolothripinae

***Nesothrips* species**

Nesothrips propinquus are fungal spore feeding thrips that often feed at the base of grass tussocks (Hoddle *et al.* 2012, Eow *et al.* 2014), they were rarely captured in this project. This was the only species with a positive association with flowering *Themeda*, despite not being known to feed on pollen. This species also showed a positive association with lower nitrogen, perhaps plant nutrition is not important for fungus feeders. This species was also associated with cooler climates, but more were captured when temperature at the time of sampling was high.

***Bolothrips* species**

Bolothrips rachiphilus originates from western USA, feeds on fungal spores and is assumed to breed at the base of grasses (Hoddle *et al.* 2012), they were rarely captured in this project. This species had positive associations with ambient temperature and growing season temperature, and a negative association with flowering.

Family Thripidae

Subfamily Thripinae

Thrips imuginis

Thrips imuginis is a very common, generalist species – the most likely species to be found when sampling flowers of most plants (pers obs). A very detailed study on the population dynamics of adult *T. imuginis* on garden roses in Adelaide is described in Davidson and Andrewartha (1948).

Thrips imuginis numbers were recorded almost every day from 1932-46, it was found that density is largely determined by weather during Autumn and to a lesser extent, rainfall and temperature during early spring. The development of *T. imuginis* slows during winter due to lower temperatures.

Davidson and Andrewartha (1948) also determined that *T. imaginis* was more active during warm, dry days. The responses of *T. imaginis* to climatic variables in our study was that higher abundances were observed when the tussock-level temperatures during development were low and when the annual climate is cooler, *T. imaginis* is known to have high mortality during hot, dry periods (Davidson and Andrewartha 1948).

Thrips imaginis does not produce eggs without pollen consumption (Andrewartha 1935), with a single second instar larvae of *T. imaginis* observed to consume 1626 pollen grains in one day (Kirk 1987). It is surprising then, that *T. imaginis* had a negative association with the presence of *Themeda* flowers. These observations of *T. imaginis* were in dicot flowers (roses), so perhaps grass pollen is not a good food source for them.

Anaphothrips incertus

Anaphothrips incertus is a native species (Mound *et al.* 2012) that has been observed in a range of native Australian grasses, but not exotic pasture grasses. It has been observed in a wide range of climates ranging from arid to sub-tropic in eastern Australia (Mound and Masumoto 2009). Here, the abundances of *A. incertus* are primarily explained by seasonal variation and *Themeda* tussock density. This supports the observation by Mound and Masumoto (2009) of its wide climatic tolerance. There is however a weak negative association with annual mean microclimate temperatures.

***Anaphothrips* species**

Anaphothrips are generally associated with grass in semi-arid areas, on leaves rather than the flowers (Mound and Masumoto 2009). *Anaphothrips incertus* has been described above as occurring in a wide range of climates but more so in warmer climates. *Anaphothrips* sp.2 abundance was poorly explained by the climatic variables used, this is supported by the distribution map where high abundances can occur in a wide range of climates. Higher abundances of *Anaphothrips* sp. 3 are expected when the microclimate temperatures have a low maximum and high minimum (ie lower

variability). Higher nitrogen availability in the soil is also associated with higher numbers of *Anaphothrips* sp. 3, nitrogen is an important resource for thrips (Chau *et al.* 2005, Atakan 2006, Chow *et al.* 2012).

Chirothrips manticus

Chirothrips manticus is known to breed within florets of Poaceae (Nakahara and Foottit 2012) and is generally observed in temperate areas throughout the world (Mound and Palmer 1972). In this survey, *Chirothrips manticus* abundance was only explained by the quadratic annual mean tussock temperature term. Lowest abundances are expected at temperatures near 17 degrees, with most being found in cool climates.

***Masamithrips* species**

Masamithrips breed on leaves of native grasses (Mound 2011). More were found during lower ambient temperatures, perhaps they have a low thermal limit for dispersal activity (Andrewartha 1936, Janiszewski 1984). More were also found when temperature during the growing season was higher, which would have favoured their population growth (Morsello *et al.* 2010). Interestingly, *Masamithrips* abundance had a positive association with annual mean temperature derived from weather station data, but a negative association with tussock level mean temperature.

Subfamily Panchaethripinae

***Phibalthrips* species**

Phibalthrips longiceps are widespread across Australia, they live on grass leaves and breed on poaceae (Mound *et al.* 2012). *Phibalthrips longiceps* was not captured often in this project, but when it was it was from densely growing *Themeda* in highly disturbed sites.

Tourist species

The following three species captured were likely to be 'tourist' species not associated with *Themeda*. *Helionothrips* contain native species common in Eucalyptus forests of eastern Australia (Mound *et al.* 2012). *Australothrips bicolor* is widespread across Australia, it feeds on mature leaves of Myrtaceae

(Marullo and Mound 1997, Mound 2004). *Leucothrips nigripennis* is an introduced pest species normally associated with the cultivated fern *Pteris cretica*, mostly near Sydney (Mound 1999). *Leucothrips nigripennis* has also been recorded in wildflowers in Brazil (Monteiro 2002).

Conclusion

We found, through multivariate modelling, that tussock level microclimate data was the most consistent at explaining the variation in Thysanoptera abundances. Overall, there were enough differences in the direction and extent of responses of Thysanoptera to predictor variables to make it beneficial to look more closely at how some of the individual species respond. The influence of not only microclimate data, but specifically microclimate data during certain periods (such as development period) demonstrates that long term weather station data should not be exclusively relied upon. The negative response that many species had to flowering *Themeda* was surprising, especially as some of these species were pollen feeders and some may breed in flowers. Grass morphology was also important in determining Thysanoptera abundances in terms of overall size and density. Interestingly, leaf temperature and ambient temperature often had different effects on Thysanoptera numbers captured – this supports the complexity of microclimate variability on insect behaviour. By using `mvabund` to handle a large dataset while accounting for the dependence between species, we have identified key environmental variables that could be used to predict Thysanoptera community response to a changing climate. Future research could apply the same methods to additional insects groups.

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Chapter 3: Response of Thysanoptera trait frequencies across a climatic gradient in *Themeda triandra* dominated grasslands



This chapter is written as a standalone manuscript, a modified version of this manuscript with additional analyses is intended for submission to a journal

Response of Thysanoptera trait frequencies across a climatic gradient in *Themeda triandra* dominated grasslands

3.1. Introduction

In ecology, a trait is normally defined as a measurable property of an organism that can be taken at an individual level and used as a comparison across species or within species (McGill *et al.* 2006). The occurrence of a species in a certain habitat is often determined by the relationship between its traits and the characteristics of the habitat (Pavoine and Bonsall 2011). These traits are the product of the evolutionary history of adaptation to that habitat and shorter term phenotypic plasticity (Ribera *et al.* 2001, Webb *et al.* 2010), hence it is reasonable to predict that insects that exist under similar conditions will display similar traits (within phylogenetic constraints). It is also reasonable to expect that a diverse range of traits in a community may increase its resilience to environmental change (Bêche and Statzner 2009, Eronen *et al.* 2010, Angert *et al.* 2011, Pavoine and Bonsall 2011).

Additionally, multiple species with similar traits can be important in maintaining functional redundancy (Mayfield *et al.* 2010). If a change in environmental conditions causes a species to go locally extinct, having redundancy (that is, other species that can take up the functional role in the community) might be beneficial (McCann 2000).

The use of functional traits to characterize diversity and interactions within a community has become increasingly common in literature (Larsson and Kustvall 1990, Gibb *et al.* 2006, McGill *et al.* 2006, Cunningham and Murray 2007, Barton *et al.* 2011, Yates *et al.* 2014, Gibb *et al.* 2015). This is often because the information derived from directly measuring traits can potentially provide more information for some insect groups than identifying them as species, or predicting their traits based on their phylogenetic position (Hunt *et al.* 2007, Kraft *et al.* 2007, Menezes *et al.* 2010, Pavoine and Bonsall 2011).

Research into trait diversity over large scales using fine scale measurements is still uncommon. Often the large scale trait studies that do exist classify species into broad functional groups or use meta-

analyses (Davies *et al.* 2003, Stevens *et al.* 2003, Bêche and Statzner 2009, Ingram and Shurin 2009), rather than taking consistent measurements at an individual level. This limits both information able to be derived and consistency between measurements and study designs. The assessment of trait diversity in addition to community assemblage over a large spatial gradient is important to disentangle the traits selected as part of environmental filtering (Webb *et al.* 2010) and those selected due to localised effects of resource availability (Stevens *et al.* 2003, Gibb and Parr 2013). This is particularly important when predicting how communities respond to broad scale climate change (Thuiller *et al.* 2008, Andrew 2013, Andrew and Terblanche 2013).

Fourth corner modelling

To gain an understanding of what might drive species responses to the environmental variables, it is useful to measure functional traits (behavioural, physiological or morphological) and use this data in an analysis. Many studies have assessed how morphological traits respond to environmental variables (Azevedo *et al.* 1998, Blanckenhorn and Demont 2004, Merrick and Smith 2004). Often, these studies do not consider trait frequencies, but sometimes a measure of trait richness is used (Pavoine and Bonsall 2011). Trait richness data does not account for abundance patterns and has the potential to be misleading, the presence of a particular trait in highly abundant species would often be more significant than if it was in rarer species (Bêche and Statzner 2009). The use of highly complex datasets such as this does require more advanced analytical techniques.

There have been very few attempts at simultaneously assessing morphological traits along with insect community abundance data: however those who have, use the maximum entropy approach (Mokany and Roxburgh 2010) and others build upon the 'fourth corner problem' (Doledec *et al.* 1996, Legendre *et al.* 1997, Pollock *et al.* 2012). The fourth corner approach needs to take three matrices, one of environmental data, one of species abundance data and one of trait data. Recently, Brown *et al.* (2014) developed a new model based approach to the fourth corner problem using generalised linear models with a LASSO penalty (Hastie *et al.* 2009). This method has been used

previously in Gibb *et al.* (2015) and Yates *et al.* (2014) as an efficient way to determine how both quantitative and qualitative environmental variables effect the trait frequencies of spider and ant communities.

Allometry

The relationship between the size of an insect's body parts to its overall size is often used to determine how an insects perceives its environment and how it might interact with other components of an ecosystem. One commonly cited hypothesis is the size-grain hypothesis (Kaspari and Weiser 1999) which states that as terrestrial walking organisms decrease in size, they perceive their environment as more rugose and the benefits of having proportionately longer legs outweigh the costs.

Static allometry is the scaling relationship among individuals within a species between two body parts at a specific developmental stage, evolutionary allometry is the same relationship but across different species (Stern and Emlen 1999). It is important to make comparisons among individuals at the same stage of development as allometry can change as an insect grows (referred to as ontogenetic allometry) (Stern and Emlen 1999).The type of slope is most often either isometric (size of the trait scales linearly with body size), steep (traits become relatively larger with increasing body size), or shallow (traits become relatively smaller with increasing body size) (Shingleton et al. 2007).

Static allometry can be used to answer questions about how environmental variables affect an insect's morphology. Nutrient availability, temperature, humidity and larval density/competition are all significant factors that determine the growth of an individual (Emlen and Nijhout 2000).

Aim

Here, we aim to model changes in morphological trait frequencies in Thysanoptera (Thrips) communities across a gradient of climate and habitat structure in *Themeda triandra* (Kangaroo Grass) dominated environments. We will use this model to answer the question of how macro and microhabitat variables might influence the dominance of certain morphological traits. It is expected

that climatic variables are likely to influence overall body size and that plant architecture will influence locomotive and sensory traits. We will also use data on allometry to describe differences in morphology for thrips based on their feeding types.

3.2. Methods

Site Selection

To assess the effect of climate on grassland insect communities it was important to use a grass species that was easy to find in a large range of climates in order to remove the effects of varying host plant species. *Themeda triandra* is the grass species chosen for this as it is distributed all over Australia, so it was essential for all sites to contain a sufficient amount of this grass to be sampled. Sites were selected using topographic, vegetation, land use and geological maps, in addition to climate layers created using BIOCLIM and ArcGRID. Using ArcMap to view several climate layers, 44 sites (Figure 1) that encompass a wide range of climates and environment types were chosen. The sites were located between 28.36°S and 37.75°S and 144.7°E and 153.13°E and ranged from 26 m to 1250 m in elevation. The mean annual temperature varied from 9.3°C to 19.4°C and mean annual precipitation ranged from 385 to 1659mm (Figure 1).

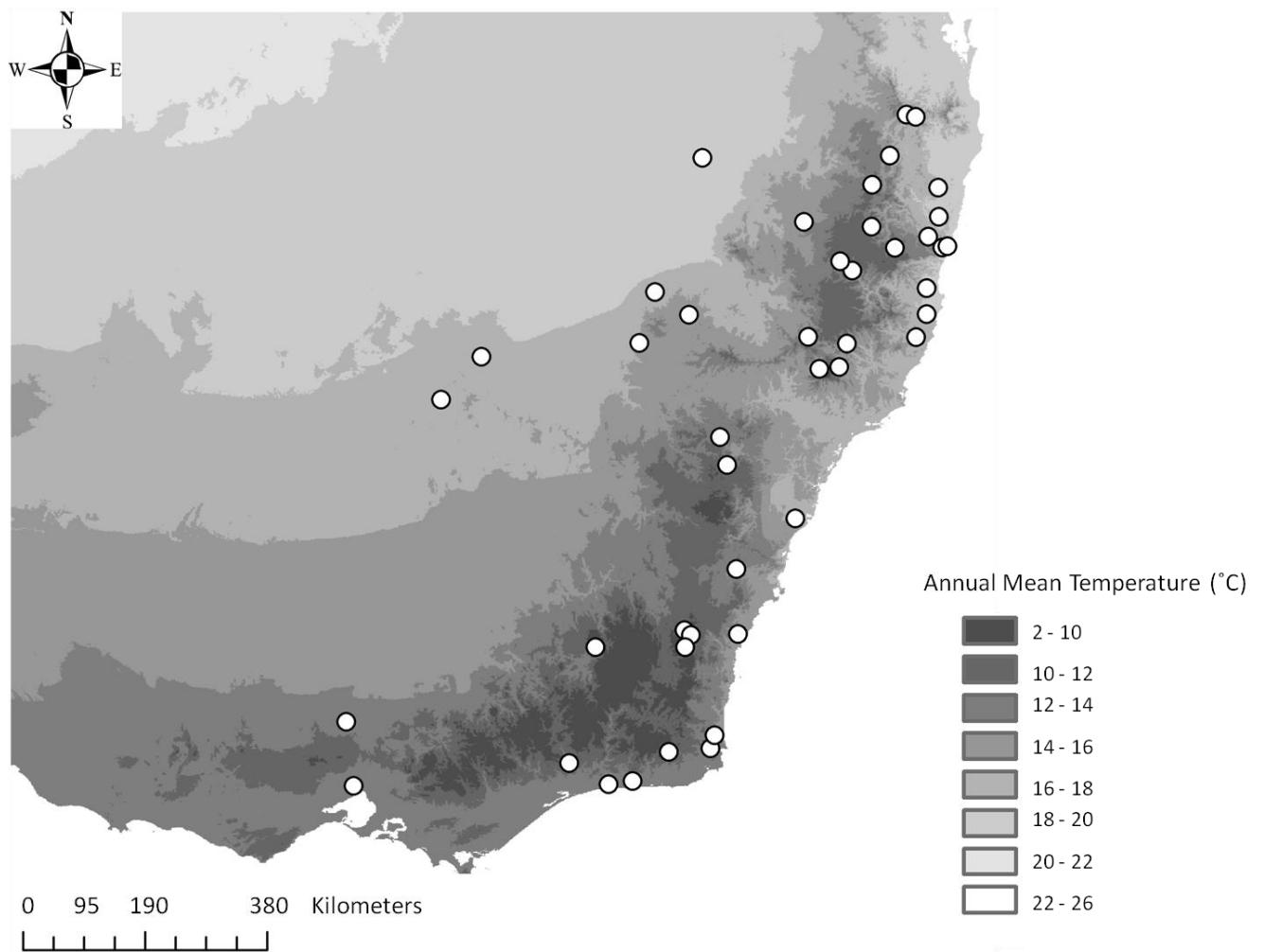


Figure 1: Map of research area, sampling sites are shown as white circles, shading shows mean annual temperature.

Survey of invertebrate communities in eastern Australia

Black, fine mesh sweep nets with a 40cm diameter opening were identified as an efficient method of grassland insect capture after performing a pilot survey. Sampling was conducted between the hours of 08:30 and 17:00, about 2 hours spent at each site. A 20 m transect line was selected for each sample, at least 50 m from the habitat edge (road or fenceline) and separated by 20 m from each other. Ninety percent of sites were large uniform grassy areas, so sampling was conducted as close to the centre of the site as possible. A few sites consisted of smaller isolated patches (mainly some sub-tropical forests), so we sampled a line through the centre of each patch and the next closest patch (up to 500 m separation) was selected to provide additional samples at the site. After sweeping each transect, the net contents were washed into a vial with 80% ethanol. There were

nine plots at each of the forty four sites, three of which were predominately (>70%) *Themeda triandra*, three were predominately the local dominant *Poa* species (*Poa sieberiana* at most sites) and three were a mix of other grass species in the area (including exotics). These collections occurred during November to December 2009 (season 1), March to April 2010 (season 2), and March to April 2011 (season 4) so that three seasons worth of data could be collected. The benefit of this was to obtain a seasonal representation of the feeding preferences of individual species, and to account for differences in host plant phenology (flowering, seed formation) and site-specific climatic differences (New 1979). The sampling route was designed to minimise correlation of date with latitude (i.e. sites sampled in a different order each season).

Table 1: Description of codes used to characterise site conditions as used in analyses

	Height	Inter tussock density	Intra tussock density	Disturbance	Flower	Wind	Sun
1	Flat growth form	Up to 3 tussocks per m ²	Very few leaves	Natural habitat with a mixed grassy and shrubby understorey with no signs of human visitation	Dead	Still	Sunny
2	Short tussock (<20 cm)	4-8 tussocks per m ²	Medium density	Natural habitat with a shrubby understorey and signs of occasional human visitation	Very mature	Slight breeze	Some clouds
3	Medium tussock (20-50cm)	>8 tussocks per m ² with separation by bare ground	Moderate density	Natural habitat with a grassy understorey and high human visitation	Mature	Windy	Cloudy
4	Tall tussock (>50cm)	'Sea of grass' (no bare ground)	Extremely dense	Highly modified and unnatural habitat with regular disturbance by humans or domesticated animals	New	Very windy	Overcast

For this study, we used climate data generated by BIOCLIM (Booth 1985, Busby 1986, Busby 1991) to characterise the sites. The downside of BIOCLIM is that it cannot give the exact values of climatic variables at tussock level (Yee and Mitchell 1991), and is based on weather station data which can

vary considerably from ground level sensors (Graae *et al.* 2011). To address this, we obtained more precise data by placing three iButton® Hygrochrons/Thermochrons at each site at grass tussock level for temperature and humidity recordings (at hourly intervals), and used a metal detector to find them during the next sampling season. A script for R (R Development Core Team 2014) was written by Professor David Warton (UNSW) that fitted models to the ibutton data to obtain useful variables from the ibutton data, these included: maximum and minimum predicted temperatures, mean predicted temperatures, temperature diurnality, seasonality, temperature at sampling time, temperature during the morning of sampling day, mean temperature during week before sampling, mean temperature during growing season (90 days) before sampling and seasonal noon temperature at time of sampling. Humidity readings from the ibuttons were unfortunately not very useful. The plan was to use them to record rainfall events but recorded 100% after the first rainfall event and did not decrease for over week.

At each site we collected grass leaf samples for chemical analysis and recorded date, time of sampling, ambient humidity, ambient temperature, sun intensity (qualitative), wind strength (qualitative), grassland characteristics (Table 1) such as disturbance based on the classification in (Davies *et al.* 2003), leaf temperature at time of sampling using an IR 'gun', elevation and slope.

Three soil samples were taken at each site (15cm diameter x 20cm depth). Soil samples were dried at 40°C until a constant sample weight was obtained. Each sample was then crushed and passed through a 2 mm sieve. 0.3 grams of soil (ground to 0.5mm), per sample was used in a LECO TruSpec Series Carbon and Nitrogen Analyser. 2 grams of soil per sample was used in an ICP atomic emission spectrometer to analyse Ca, Mg, Na and K concentration (using a method adopted from Rayment and Higginson (1992)). Sodium adsorption ratio (S.A.R.) was calculated using:

$$S.A.R = \frac{Sodium}{\sqrt{\frac{1}{2}(Calcium^2 + Magnesium^2)}}$$

Insect Sorting and Identification

Insects were sorted to major orders (Hemiptera, Coleoptera, Thysanoptera, Hymenoptera) and the other orders were grouped into 'others'. Spiders were separated and assessed in Gibb *et al.* (2015). Thysanoptera was sorted to morphospecies (Oliver and Beattie 1996) based on characteristics used in Thysanoptera keys (Mound 2011, Hoddle *et al.* 2012, Mound *et al.* 2012). A voucher specimen of each morphospecies was photographed using a Leica MZ16a microscope and LAS automontage software. The online Thysanoptera key, Ozthrips (Mound *et al.* 2012) and a compound microscope were used to identify common thrips to genus or species. Thrips larvae were excluded from the analysis as they were difficult to associate with adults of the same species. For the more abundant Thysanoptera species, high resolution photographs were sent to expert Thysanoptera taxonomist Dr Laurence Mound (ANIC, Canberra) for additional verification in 2012.

Morphological Traits

Once morphospecies had been identified, a range of metric morphological traits were measured for each morphospecies per collection per site using the measurement module of the Leica application suite with the Leica MZ16a. The morphological traits were related to ecological functional roles and dispersal (Ribera *et al.* 2001, Talarico *et al.* 2007), including traits related to body size, diet (e.g. head shape), locomotion, flight, acuity of vision and antennae.

Only adult thrips were measured, nine different morphological traits were measured from 15 individuals of each morphospecies from each site, as this was considered more than enough to capture intraspecific variation based on initial measurements. For species that occurred in fewer numbers, all individuals at the site were measured. Species where only one or two individuals per site could be measured were only used in the allometric analysis and removed from the fourth corner modelling. The traits measured were: body length, body width, head length, head width, antenna length, eye separation, hind leg length, foreleg length and wing length. For the initial samples, each measurement was taken four times to assess variability among repeated measures.

The variability was considered negligible at less than 1% so all further measurements were only taken once.

Analysis

Due to time constraints, only the three *Themeda triandra* samples from seasons one, two and four were analysed. A principal components analysis (PCA) and observations of correlations of raw data were used to reduce the number of predictor variables for use in the models (Warton 2008, Mellin *et al.* 2010).

To assess how environmental variables influenced the abundance of Thysanoptera morphological traits, a fourth corner modelling approach (Legendre *et al.* 1997) as described in Brown *et al.* (2014) was applied to a matrix of species abundances at each site (**L**), a matrix of environmental variables at each site (**R**) and a matrix of Thysanoptera traits for each species (**Q**) using R 2.15.1 (R Development Core Team 2012). The model used is a generalised linear model (Nelder and Wedderburn 1972), and we selected the negative binomial family because our count data was overdispersed (O'Hara and Kotze 2010).

This fourth corner approach uses LASSO model selection (Tibshirani 1996) with an algorithm to allow the use of a negative binomial option (Brown *et al.* 2014). LASSO uses a penalty term to shrink some coefficients and set others to exactly zero and this produces an easily interpretable solution for large datasets (Tibshirani 1996). In our case, the penalty term is estimated by the use of cross-validation (Brown *et al.* 2014). The method uses forward selection, so it is unlikely to select multiple highly collinear terms, providing resistance to the problem of multicollinearity (Graham 2003). The resulting coefficients for the trait and variable association represents the strength of the association as well as the direction (positive or negative). Only species with more than two individuals found at a site and ten individuals found in total were used in this model in order to reduce false positive detection.

Allometric relationships were analysed among Thysanoptera feeding guilds using SMATR (Standardised Major Axis Tests and Routines) version 3.4 (Warton *et al.* 2012) for R 3.1.0 (R Development Core Team 2014). Only Thysanoptera species with known feeding styles described in literature were used for this analysis. The Thysanoptera were grouped into Fungivores, Herbivores and Omnivores (for those known to feed on other arthropods as well as their host plant). A detailed description of how the SMATR package analyses slopes is found in Warton *et al.* (2006).

3.3. Results

Approximately 60000 insects were collected from 504 samples of *Themeda triandra* grasslands over forty-four sites across four sampling seasons. Of these insects, 1354 were Coleoptera, 6734 were Hemiptera, 5557 were Hymenoptera, 5000 were Spiders and 8760 were Thysanoptera, comprised of sixty-seven morphospecies. The remaining 32500 insects comprised a range of orders not analysed in this study. From three seasons worth of samples, we measured nine different morphological traits from almost 3000 individual thrips across 67 thrips species, the most common species being two from the *Haplothrips* genus and *Thrips imaginis*. Body length was used as a measure of Thysanoptera size, mean body length across all species was 1.5mm with the smallest thrips measuring 0.62mm and the largest measuring 3.8mm.

Trait abundance using the fourth corner model

The fourth corner model (Figure 2) predicts seasonal variation in body length (more shorter thrips in season 1), foreleg length (more thrips with long forelegs in season 2), hind leg length (more thrips with long hind legs in season 4) and eye separation (more thrips with narrow eyes in season 4).

The physical structure of the *Themeda* sampled has an effect on body length, foreleg length and wing length (Figure 2). A greater number of short thrips and thrips with short forelegs are expected to be found in tall grass, and more thrips with short wings are expected to be found in dense patches of grass (ie short distance between tussocks). The state of flowering has no effect on morphological

trait frequency. The level of disturbance that a tussock experience has a small effect on foreleg length, more thrips with short forelegs are expected to be found in disturbed sites.

Leaf temperature at the time of sampling, has no effect on morphological trait frequency (Figure 2).

When the ambient humidity at the time of sampling is high, more thrips with long antennae and more larger thrips are expected to be found.

Tussock level microclimate data had varying effects on the types of morphology found (Figure 2).

Sites with small temperature variation (ie low maximum and high minimum temperatures) are expected to produce more thrips with long antennae. Sites with low minimum temperatures harbour more thrips with short hind legs. The temperature during week before sampling was not identified as important. The temperature during the growing season (90 days) before sampling is expected to have a small effect on body size, more large thrips are expected after a warm growing season. Annual mean temperature at the tussock level explains body length and eye separation.

Sites that experience high mean temperatures are expected to harbour more large thrips and thrips with widely separated eyes.

The interpolated ANUCLIM data was not particularly useful at explaining morphological trait frequency when microclimate data are provided, although sites that experience high annual precipitation are expected to contain more thrips with short forelegs.

The nutritional content of the soil was not identified as important in predicting the frequency of morphological traits (Figure 2).

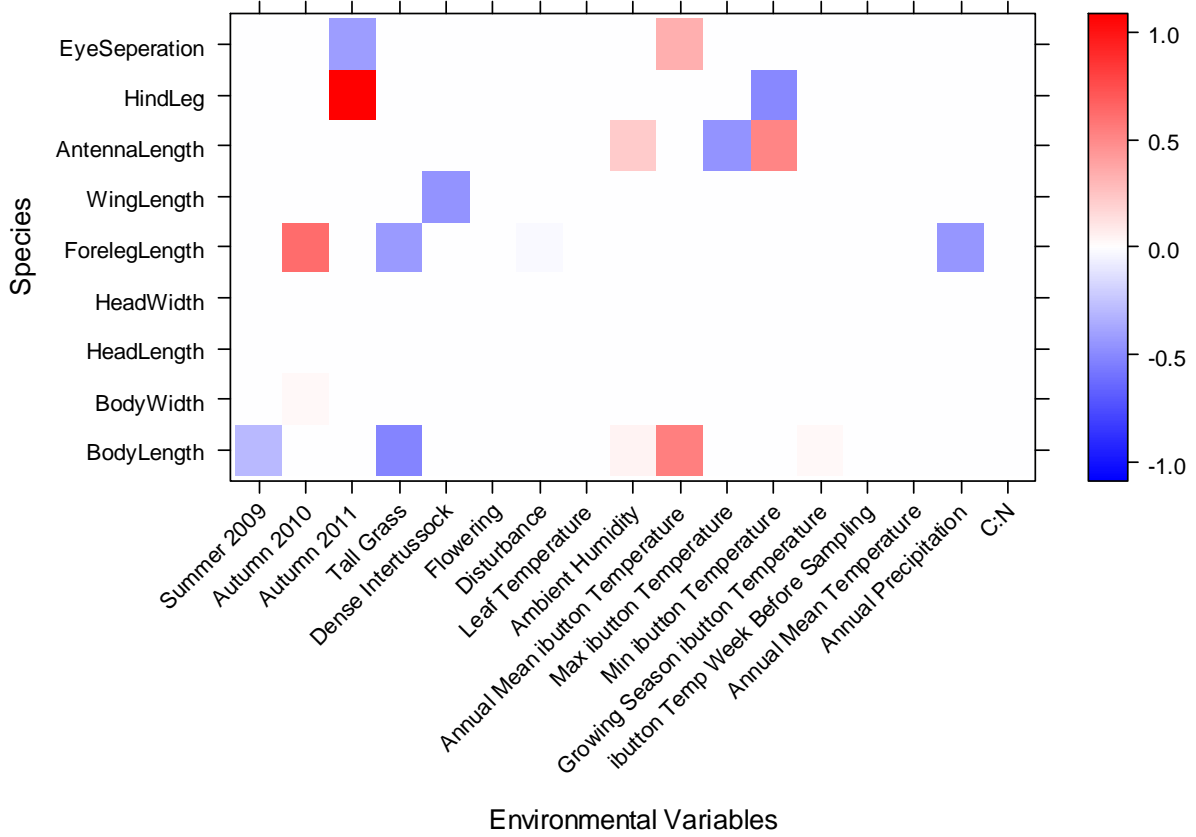


Figure 2: Graphical representation of the 4th corner interaction coefficients for the relationship between Thyranoptera traits and environmental variables. Red indicates a significant positive interaction, and blue represents a significant negative interaction.

Allometry among Thysanoptera feeding guilds

The overall body shape and wing loading of the three Thysanoptera guilds are shown in (Figure 3a&b). Overall, Herbivorous thrips are the smallest, predatory thrips are medium sizes and fungivorous thrips are the largest. In terms of body width/length allometry, fungivores and predators shared similar slopes of around 1.5 while herbivores were not as steep at 1.25. This means that as thrips body length increased, the body width did not increase as much, producing long skinny thrips. Herbivore scaling was the same direction but not quite as severe.

Most fungivores collected in this project were wingless (Figure 3b). Slopes for wing loading allometry between herbivores and predators were significantly different, long predators had proportionately smaller wings (slope: 1.5) than long herbivores (slope: 1.27).

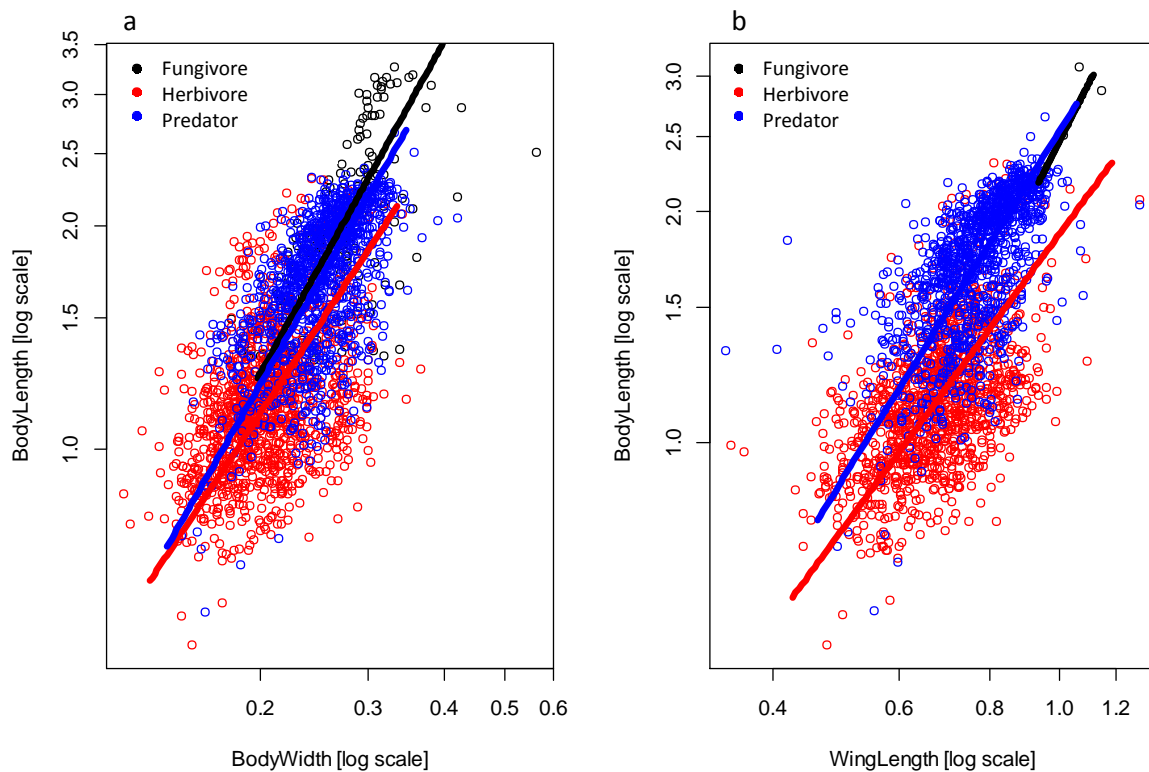


Figure 3: Morphological scaling of body length to body width (a) and body length to wing length (b) for the three identified Thysanoptera feeding groups.

Head morphology

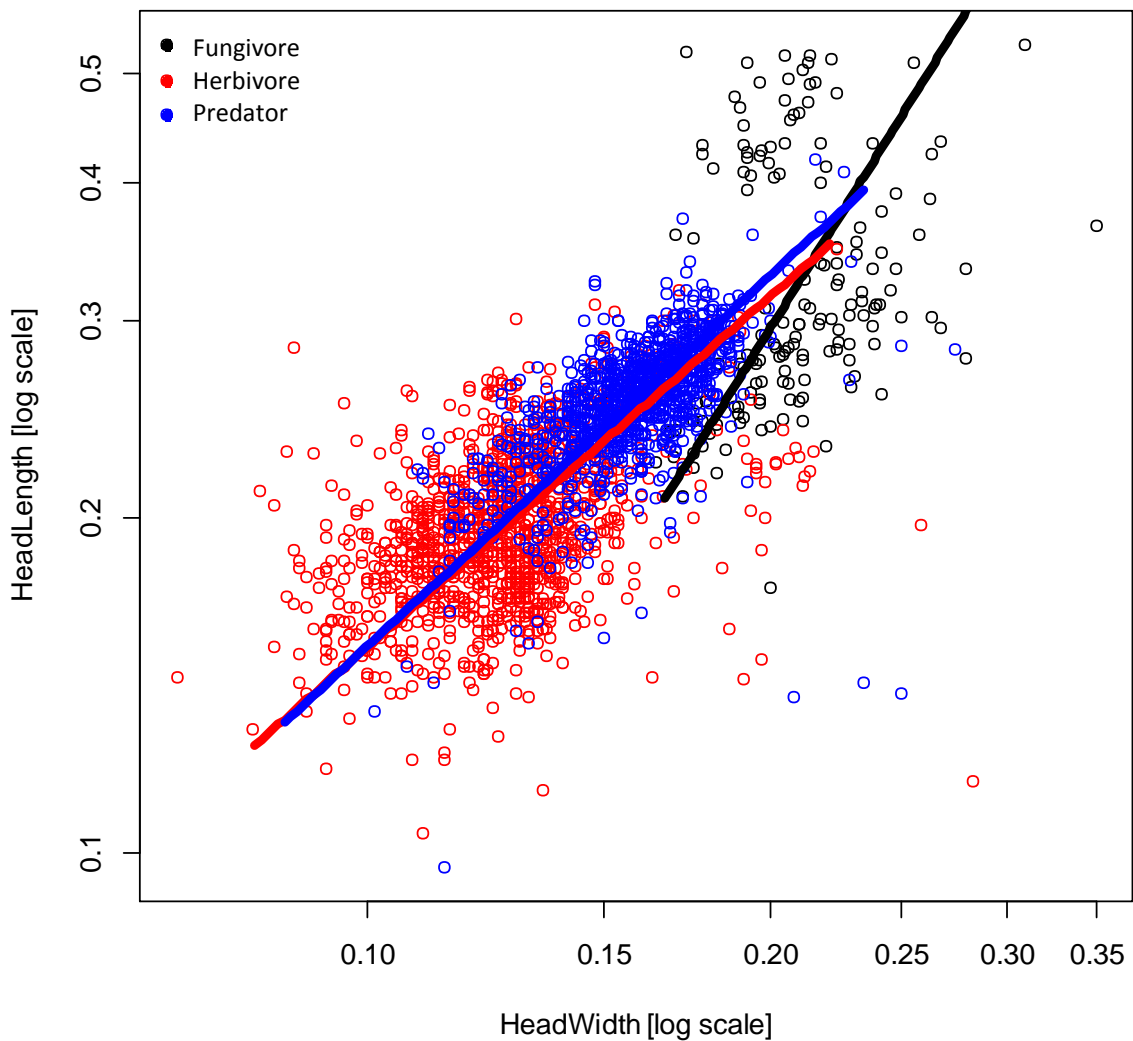


Figure 4: Morphological scaling of head length to head width for the three identified Thysanoptera feeding groups.

Herbivores and predators have the same head scaling which is close to linear meaning the head shape stays the same no matter how long or wide it gets (Figure 4). Head shape scaling is very different for fungivores, the slope is 1.94 meaning head width stays narrow as the head length increases in size.

3.4. Discussion

We were able to describe the relationship between abundance, morphological traits and environmental variables in grassland Thysanoptera by using the recently developed fourth corner modelling method (Brown *et al.* 2014). A combination of plant characteristics and microclimate variables were identified as having importance in explaining the occurrence of morphological traits in thrips. We also determined fungivorous thrips have different head shape scaling to herbivorous and predatory thrips.

Microhabitat structure

In areas where grass tussocks are tall and/or dense, smaller thrips with shorter legs and wings are expected to be more common. This is consistent with other findings that leg length in ants (Gibb and Parr 2013) and body size in beetles (Ribera *et al.* 2001, Barton *et al.* 2011) is related to microhabitat use. It is reasonable to expect that thrips living in dense, complex vegetation would be at an advantage if they are smaller, this would allow them to move through the small spaces more efficiently (Gibb and Parr 2010). Some studies suggest that large leg size relative to small body size would help when hunting prey or escaping hunters (Krasnov *et al.* 1996, Kaspari and Weiser 1999), however this may not be so relevant in Thysanoptera communities due to the relative scarcity of predatory thrips that target fast moving prey in *Themeda* dwelling thrips.

Thrips sensory traits were not identified as being shaped by dense vegetation. Wider eye separation was found to be important for ants living in complex vegetation in Gibb and Parr (2013), but perhaps the advantages of thrips having wider heads may be cancelled by the disadvantages, such as lack of mobility when navigating dense environments.

Habitat disturbance was only associated with foreleg length, more thrips with short forelegs were found in more highly disturbed sites. This contrasts with what is normally observed, our highly disturbed sites have less complex vegetation, so theory would predict that proportionately larger legs are advantageous (Kaspari and Weiser 1999). Perhaps this is indicative of a trade-off where

flight is more important in disturbed habitats (often characterised by sparse vegetation) than walking (Taylor and Merriam 1995, Gibb *et al.* 2006). It could also be due to variations in the relative importance of fighting ability over mobility due to scarce resources in disturbed habitats (Crespi 1986, Crespi 1988).

Wing length was not identified as a significant trait associated with habitat disturbance. This may be due to the fact that flight is important in more than just long distance dispersal (Ribera *et al.* 2001), and more complicated than simply 'big wings = strong flight'. Long wings may not indicate overall 'flight strength' (Roff 1991) when speed and agility are required during short flights (Hill *et al.* 1999). Another factor to consider is that Thysanoptera have a fairly unique 'feathered' wing, this allows them to have a greater effective wing surface area relative to their small size without being cumbersome when not in use (Ellington 1980).

Microclimate

Under sampling conditions of high humidity, most thrips collected are predicted to have long antennae, which suggests sensory ability is more important when humid. Some insect sensilla is thought to be involved in the perception of humidity variations (Romani *et al.* 2009), these sensilla would take up room on the antennae, potentially making them longer. A greater number of large thrips were predicted to be captured in humid conditions, perhaps due to having additional strength beneficial for mobility when humid.

The long term ibutton derived temperature data explained frequencies of body length, antenna length, hind leg length and eye separation traits. Longer thrips had a positive association with both warm annual and growing season temperatures. This is consistent with the general trend that larger body size in terrestrial arthropods is associated with warm temperatures (Gillooly *et al.* 2002, Chown and Klok 2003). Of particular interest is the positive association of temperature experienced during thrips development on body size during the 'growing season'. Higher temperatures can greatly shorten development time of thrips (Riley *et al.* 2011), which may result in a smaller final body size.

Blanckenhorn and Demont (2004) observe that this shortened development time in warmer latitudes mainly seems to affect larger insect species, and that smaller species (like thrips) generally have an increased body size at warmer latitudes (consistent with our results).

Hind leg length was negatively associated with minimum recorded minimum temperatures, this means that a greater number of thrips with short hindlegs were captured at sites with lower minimum temperatures. Temperature has been shown to influence appendage proportions (van den Heuvel 1963), for example wing size decreased with increasing temperature during development in *Drosophila* (Azevedo *et al.* 1998). The abundance of short legged Thysanoptera at sites that experience more extreme minimum temperatures may be due to thermoregulation. Insects need to keep their bodies at certain temperature ranges in order to operate. The body temperature of smaller insects such as thrips changes very quickly with the ambient temperature due to their higher surface-volume ratio (Yamamura *et al.* 2006), therefore reducing their surface area by having smaller limbs may help retain heat. Additionally, thrips in cold conditions may disperse more with flight (making long limbs unnecessary) as more heat is produced when the flight muscles need to keep working (Merrick and Smith 2004).

Antenna length had a positive association with more stable climates (characterised by lower maximum and higher minimum temperatures) and eye separation was positively associated with warmer climates. Tropical climates typically have more stable temperatures (Janzen 1967), perhaps additional sensory receptors are required in more tropical and sub-tropical climates due to the increased complexity of finding mates and the increased importance of avoiding predators (Novotny *et al.* 2006). Higher insect richness in the tropics (Beaver 1979, Rinker and Lowman 2004) may mean more complex pheromones are required during mate searching, hence the longer antennae.

Annual precipitation had a negative association with foreleg length, meaning there were fewer thrips with long forelegs in arid climates. This may potentially assist with desiccation resistance by reducing surface area in arid climates (Schoener and Janzen 1968).

The soil chemistry results do not explain much in this study, soil with higher C:N is likely to be associated with plants of lower nutritional quality (Atakan 2006, Chow *et al.* 2012). A host of high nutritional quality can be associated with larger insects (Majer *et al.* 1992, Schoonhoven *et al.* 2005), however the results we obtained showed no association with any body size parameters.

Allometry

The thrips identified in this project could be classified broadly as herbivores, fungivores and omnivores. Discriminating between feeding types based on body size has previously been seen in beetles (Grimbacher and Stork 2007, Barton *et al.* 2011), and it seems a similar separation can be made among Thysanoptera feeding groups. Herbivores were the smallest overall, with a relatively short-fat body shape and fungivores were the largest thrips. An opposite trend was seen in Grimbacher and Stork (2007), herbivorous beetles were the largest, followed by predatory beetles, with fungivores being the smallest. Fungivorous thrips may be larger due to the relative importance of male/male combat (Mound 2002) or the importance of parental protection and 'herding' of juvenile thrips to feeding sites among these species (Kiestner and Strates 1984).

Body size can also be related to host specificity (Loder *et al.* 1998), or range size (Gaston and Blackburn 1996). Unfortunately not enough information was known about many of the thrips collected regarding hosts and ranges. This can also help explain wing morphology, specialist fungal feeders may require mobility between hosts that harbour the fungus. Diverse fungal feeders are unlikely to need to move at all as long as the microhabitat is suitable for them and a range of fungus is available (Ananthakrishnan and Suresh 1983).

Head Morphology

Generally, head size got proportionately smaller as body size increased. Head shape remained consistent as size increased for herbivores and predators, however fungivore head shape tended to remain narrow as length increased. Thysanoptera feed on fungus by ingesting whole spores (Mound and Teulon 1995) normally found on dry grass leaves (Ananthakrishnan and Suresh 1983). Wider

heads are likely to be unnecessary for this feeding style as the spores are unlikely to require larger muscles to ingest (Bernays 1986). Fungivorous thrips have been observed as having a lack of interest in the mycelia of the fungus and a preference for Coelomycete and Hyphomycete forms possibly for nutritional reasons (Ananthakrishnan and Suresh 1983, Jones 2006), this may require specialised, narrow mouth morphology.

Conclusions

The association of species traits with their environment is of increasing interest to ecologists. We have shown that morphological traits are associated with both climate and habitat structure, which has significant implications regarding the prediction of functional diversity in a changing climate. We also show the importance of obtaining microclimate data, it is far more relevant for predicting community changes than broader data. The unique morphology of thrips make it important to study trait-climate associations specific to this order, rather than making generalisations from other orders. We also gave an overview of allometric scaling across the three major Thysanoptera feeding groups with distinct separations. How this scaling is affected by climatic conditions during developmental stages will require further research, however it is clear that generalisations should not be made for large groups without considering their feeding behaviour. Using a model based approach to the 'fourth corner problem' we demonstrated the additional predictive power gained over simply using species diversity measures.

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