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

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

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4.1. Introduction

Under a changing climate, insect species may adapt to the new conditions and stay where they are through changes to physiological or behavioural traits (Andrew *et al.* 2013a), change their geographic range (Stireman *et al.* 2005) or go extinct (Parmesan *et al.* 2000). Range shifts have been observed and predicted for a number of species (Bale *et al.* 2002, Hill *et al.* 2002, Thomas *et al.* 2004), which leads to altered community structure and phenology in existing ecosystems. Range shifts are rarely synchronous for species within a community (Hodkinson 1997, Hodkinson and Bird 1998). This asynchrony is an important consideration for species with specific feeding requirements as they may respond to climatic changes at a different rate to their host or prey, resulting in a decoupling of interactions (Hughes 2003, Westoby and Burgman 2006).

Themeda triandra

Problems caused by a mismatch between host and insect after a climate change induced range shift can be due to a loss of host species (Bale *et al.* 2002), and sometimes also due to a loss of host plant genotype (Arvanitis *et al.* 2008, Jones *et al.* 2011). Polyploidy is observed in *Themeda triandra*, that is, some populations have more chromosomes than the normal diploid populations (Grant 1981). Polyploidy in plants generally results in an increase in cell size and change in cell surface area (Levin 1983). This can result in changes in leaf and flower morphology (Scott 1972) which will alter insect responses (Dafni *et al.* 1997, Thompson 2001), such as leaf miner preferences for symmetrical leaves (Mller 1995, Cornelissen and Stiling 2005). Polyploidy can also alter cell activity (Weiss *et al.* 1975), slow cell growth and metabolism (Cavalier-Smith 1978) and alter the chemical composition of cells (Levin 1983). This will also alter insect feeding behaviour (Schoonhoven *et al.* 2005), for example (Mattson 1980, Lincoln *et al.* 1986).

Themeda triandra occurs most commonly as diploids or tetraploids, depending on where it grows (Groves 1965): 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 *Themeda 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 (Scott 1972). In addition to observing naturally occurring populations, Scott (1972) conducted a transplant experiment to determine the performance of each population when moved to a different climate, he found that when any of the grasses experienced a different climate they flowered poorly. He also found that when tetraploids were grown in Armidale (cool, temperate climate), where diploids normally grow, they developed even larger cells than normal.

Due to differences in the biology of different ploidy *Themeda triandra*, it is reasonable to expect that they would attract a different suite of insects (Schoonhoven *et al.* 2005). There are examples of how higher ploidy plants are more susceptible to butterfly predation in Brassicaceae (Arvanitis *et al.* 2007, Arvanitis *et al.* 2008) and that different levels of ploidy in Saxifragaceae attract a different suite of insect visitors (Segraves and Thompson 1999) host plant families. Some experimental studies exist that demonstrate that polyploids may be more resistant to attack from insects (Busey and Center 1987) and nematodes (Busey *et al.* 1993), although there are a lack of studies that consider the importance of host ploidy in shaping the insect communities that colonise native Australian grasses.

Transplant Experiments

Many climate change studies 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. A field based transplant experiment can be used to compliment these sorts of field studies as a way to test the effects of a warmer climate on the health and phenology of a host plant in a realistic setting (as opposed to laboratory experiments) (Nooten and Andrew in press). It provides a way to observe what actually happens when a plant is exposed to the conditions of interest (Scott 1972, Bruelheide 2003, Link *et al.* 2003, Angert and Schemske 2005, De Frenne *et al.* 2011). Transplants are also useful for comparing the insect assemblage associated with an 'exotic genotype' plant, to what occurs on plants of a local genotype (Arvanitis *et al.* 2010), by observing the composition of insect colonists when a population of both plants are planted at the same site. Making comparisons between host genotypes will give insight into what might happen when a range shift mismatch occurs. There are some examples of experiments performed to test the effects of climate on shaping the insects communities on transplanted plants or field manipulation experiments (McGeoch *et al.* 2006, Andrew and Hughes 2007, Petrucco-Toffolo and Battisti 2008, Villalpando *et al.* 2009, Nooten *et al.* 2014, Nooten and Hughes 2014) although these experiments are not common. Additionally, many of these experiments found more of an individualistic response of species to simulated climate change so broad scale generalisations will not be useful for predicting community level changes, making it even more important to perform more of these experiments for different community types.

For this experiment we wanted to assess insect composition among a range of climates. To do this, it was important to keep the host plant species constant so that the results are not confounded by variation between species (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. To make a reliable assessment, a host plant had to be carefully selected that fits the requirement of having a wide climatic distribution and well known biology. We chose *Themeda triandra* as it is a very good example of a host plant with a distribution that covers all Australian climates (Hayman 1960, Cole and Lunt 2005).

Thysanoptera

Thysanoptera is an insect order comprised of approximately 5500 species (Mound 2011) that is greatly underrepresented in terms of research (Binns 2016 Chpt1). There appear to be no studies that assess the effect of community level climate change or that answer more specific questions related to range shift mismatch such as assessments of host plant ploidy on Thysanoptera feeding behaviour, although there are detailed descriptions of general feeding behaviour (for example Heming (1978)) that may be used to help explain future ploidy related observations. 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). In addition, the loss of native grasslands due to introduction of exotic pasture grasses may have a significant effect on the survival of both specialist and polyphagous thrips, especially when they shift ranges under a changing climate.

We compared the assemblage of insects, with a focus on Thysanoptera, that colonised transplants of diploid and tetraploid *T. triandra* at three locations based on varying climate (hot/dry semi-arid, warm/dry semi-arid and cool temperate). The assemblages on the transplants were also compared to the assemblages that occurred on the *T. triandra* that grew naturally at the site. This experiment will allow us to investigate broad changes in insect community structure under a warmer and drier climate. The experiment also allows us to test more specifically whether insects have a preference for local or exotic genotypes, and what effect the process of transplantation has on how insects perceive the plant. Answering this will allow us to make predictions regarding insect success both under broad climate change and when mismatched shifting to different ranges causes a loss of host genotype.

It can be expected that insect response to the transplantation of a foreign plant into their natural range would be dependent upon, primarily, whether the insect is a herbivore or pollinivore (directly affected by changes in host plant characteristics), or a carnivore or fungivore (indirectly effected by host plant changes). Secondly, whether the insect is a specialist or generalist will be important in determining their response to a foreign plant: A specialist is likely to prefer a plant of local genotype as they may be more sensitive to changes in host morphology and chemistry; a generalist is likely to prefer the plant with greater nutritional value. The response of the plant to being moved into a new climate will also indirectly influence insect colonisation: Locally adapted plants may be more vulnerable to local insects that have evolved mechanisms to overcome the plant defences (Roy 1998), however if the foreign plant cannot cope with the different climate it may be more vulnerable simply due to reduced health. Due to these reasons, the results are unlikely to be uniform in terms of the direction of insect responses.

4.2. Methods

The native grass, *Themeda triandra* was used for this transplant experiment. *Themeda triandra* is distributed all over Australia, although it appears uncommon in sandstone derived habitats (pers obs). We have previously assessed Thysanoptera communities in established *Themeda triandra* throughout mid to eastern NSW and Victoria in Binns 2016 Chpt2.

One hundred tussocks of *T. triandra* were collected in December 2009 from three sites (Table 1, Figure 1), using the protocols of Whalley and Brown (1973): 1) remove entire plant including a ball of soil around roots, 2) immediately place plant in large plastic bag and clip leaves/culms to 10% of original height, 3) dampen soil with water and seal bag, 4) keep plants shaded during transport. The grass was then grown in a glasshouse in Armidale for twelve months.

Themeda triandra occurring at Garah (hot, dry) and Coonabarabran (warm, dry) are tetraploids and *T. triandra* occurring at Armidale (cool, temperate) are diploids (Hayman 1960, Scott 1972) and confirmed by grass biology specialist Dr Wal Whalley (pers comm 2009).

Study design

Four *T. triandra* tussocks were collected for use within each of three replicates for each transplant treatment, of which there were four treatments (Figure 1). A reciprocal transplant was used at each site to assess the effects of the transplant process on the associated arthropod assemblage (Figure 1). In total, 100 individual *T. triandra* plants were grown in the glasshouse at the University of New England for a year, eighty-four of which were used in the transplant experiment. During glasshouse growth, each tussock was potted into 18 cm diameter pots with a 1:1:1 peat:sand:loam mix. All *T. triandra* tussocks were watered three times a week during their time in the glasshouse.

Table 1: Site characteristics based on weather station data, and ibutton data placed at tussock level for the duration of the transplant experiment (Summer and Autumn 2011).

		Weather Station Data		**Microclimate Data During Experiment Period**		
Site name	**Coordinates**	**Annual mean temperature (˚C)**	**Annual Precipitation (mm)**	**Mean (˚C)**	**Max (˚C) (hours above 50˚C)**	**Min (˚C)**
Garah (Hot, dry) Tetraploids	-28.96423333 149.69415	19.5	590	28.1	67 (160)	7.6
Coonabarabran (Warm, dry) Tetraploids	-30.8445 149.0287	16.4	500	25.4	64 (30)	6
Armidale (Cool, temperate) Diploids	-30.41428333 151.62525	12	755	19.3	53 (15)	4.1

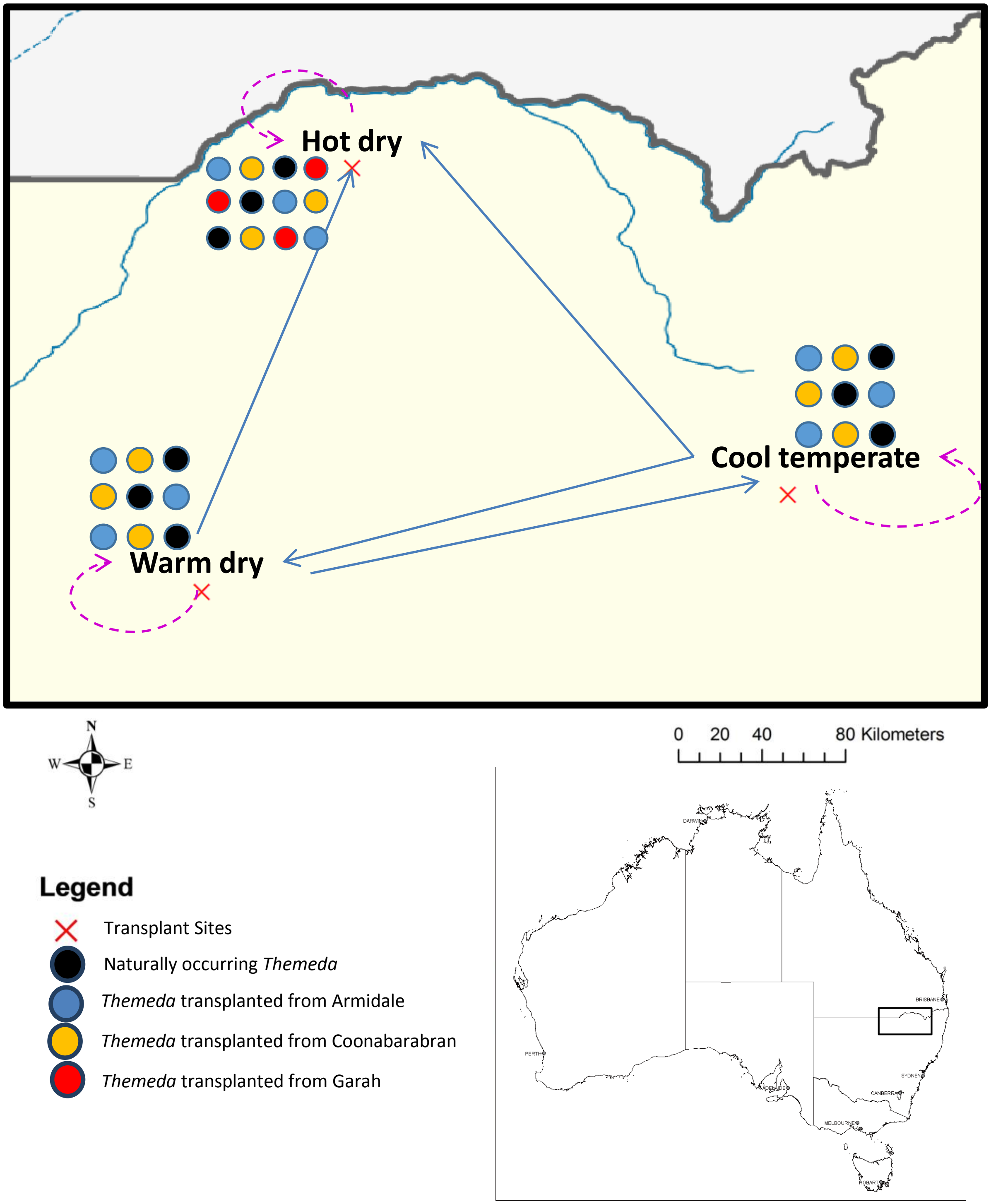

Figure 1: Map showing the transplant site and treatment locations. Solid blue arrow represents tussocks moved from one site to another, dashed purple arrow represents a reciprocal transplant. Each site also includes naturally occurring *in situ* tussocks not exposed to the transplant process, as controls. Each individual coloured circle represents a treatment group of four *Themeda* tussocks.

In November 2010, the patches were planted in a randomised arrangement at each site. Each patch of grass consisted of 4 tussocks and this was replicated three times for each treatment. Prior to de-potting, plants were sprayed with a 0.6% concentrate of synthetic pyrethroid (Kendon Chemical & Manufacture Co Pty Ltd) mixed with tap water, to remove any insects that may have colonised them in the glasshouse. Synthetic pyrethroids have a very rapid rate of degradation, less than 16 hours (Miyamoto 1976) allowing recolonisation to occur soon after transplant. Holes were dug in clear patches of land, the *T. triandra* was removed from the pots and placed in the holes. After planting, each tussock was given two litres of water to assist establishment, but no further watering, to allow the grass to acclimatise to climate conditions.

Table 2: A description of treatments at each site, each treatment was replicated three times with four tussocks per replicate to provide more sweep volume.

Site name	Treatments
Garah (Hot, dry) Tetraploids	*Themeda* from Armidale transplanted into Garah *Themeda* from Coonabarabran transplanted into Garah *Themeda* from Garah transplanted into Garah Naturally occurring *Themeda* at Garah
Coonabarabran (Warm, dry) Tetraploids	*Themeda* from Armidale transplanted into Coonabarabran *Themeda* from Coonabarabran transplanted into Coonabarabran Naturally occurring *Themeda* at Coonabarabran
Armidale (Cool, temperate) Diploids	*Themeda* from Armidale transplanted into Armidale *Themeda* from Coonabarabran transplanted into Armidale Naturally occurring *Themeda* at Armidale

Three soil samples were taken at each site (15 cm diameter x 20 cm depth). Soil samples were dried at 40^{o}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. Two 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)).

The range of soil characteristics (Appendix Table 2) shows similar or narrower fertility ranges for nitrogen and phosphorous when compared to other transplant studies undertaken in eastern Australia (Andrew and Hughes 2007, Nooten and Hughes 2014).

Insect collections and identification

The transplanted *T. triandra* were left in the field for six months to allow colonisation by local insects. Fine, black sweep nets were used to collect grassland invertebrates from the transplanted grass and naturally occurring grass at each site. Each replicate of tussocks was swept ten times. There was a high rate of grass mortality at the hot dry site (60% - mostly diploids sourced from Armidale) due to extremely hot conditions following transplant (December 2010 - January 2011). For this reason the hot dry site was taken out of the analyses.

Insects were sorted to major orders (Hemiptera, Coleoptera, Thysanoptera, Hymenoptera) and the other orders were grouped into ‘others’ (hereafter 'ordinal data'). Spiders (Araneae) were also separated and numbers recorded. Thysanoptera was sorted to morphospecies (Oliver and Beattie 1996) and images of each species were taken using a Leica MZ16a microscope and LAS automontage software. The online key, Ozthrips (Mound *et al.* 2012) was used to identify the thrips to family, genus or 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. Thysanoptera larvae were excluded from the analysis as verification to adult species is unreliable.

Analyses were performed on both the specimens classified to order (hereafter 'ordinal data') and the Thysanoptera species data separately. Simultaneous generalised linear models using a negative binomial response (O’Hara and Kotze 2010) were used to compare assemblages between transplanted and naturally occurring grass, and also to compare assemblages between transplanted diploids and tetraploids. The `mvabund` (Wang *et al.* 2012) package for R 3.1.0 (R Development Core Team 2014) was used for this analysis. `ggplot2` (Wickham 2009) was used for boxplots.

Glasshouse mealybug assessment

During the period of growth in the Armidale glasshouse, some of the plants were colonised by mealybugs. Heavy mealybug infestation was also experienced by Scott (1972) when he grew *Themeda triandra* in Armidale, however there is no data available on host preference for this occurrence. Pyrethrum was used to kill these before they had a chance to reduce plant health. The plants were arranged in the glasshouse haphazardly to reduce location effects (i.e. light intensity, temperature variation). Mealybugs would be expected to colonise and spread to nearby plants however this was not the case. Data was collected on rates of mealybug colonisation and analysed as there appeared to be a preference for plant genotype. A logistic regression was used to compare infestation rates among grass plants from different locations using R 3.1.0 (R Development Core Team 2014).

4.3. Results

In total, 1308 arthropods were collected from the transplanted *Themeda triandra*; 616 from Armidale (cool, temperate), 662 from Coonabarabran (warm, dry) and 30 from Garah (hot, dry). Of these, 22 were Coleoptera, 769 were Hemiptera, 92 were Hymenoptera, 97 were spiders, 113 were Thysanoptera and 215 were unclassified ('Others'). Fifteen species of Thysanoptera were collected; fourteen species were found overall on the natural grass and eight species were found overall on all transplanted grasses. The low numbers (113 individuals) of Thysanoptera causes potential issues with the analyses, many effects will be hard to detect.

Testing the effect of host plant origin on insect order composition

There was on overall significant effect of site on ordinal composition (sum-of-LR = 32.35, p-value = 0.007) as identified by `anova.manyglm (mvabund)`. Univariate results identified a significant interaction effect between the site and the source of the transplants on Thysanoptera abundance (sum-of-LR = 7.162, p-value = 0.043). This interaction effect is due to Thysanoptera abundance being higher on plants sourced from the warm dry site planted at the cool temperate site (Figure 2) and Thysanoptera abundance being the same regardless of host plant origin at the warm dry site (Figure 2). The only other order affected by host plant origin was spiders (sum-of-LR = 6.855, p-value = 0.023). Spider abundance was higher on host plants originating from the cool temperate site at both sites (Figure 2).

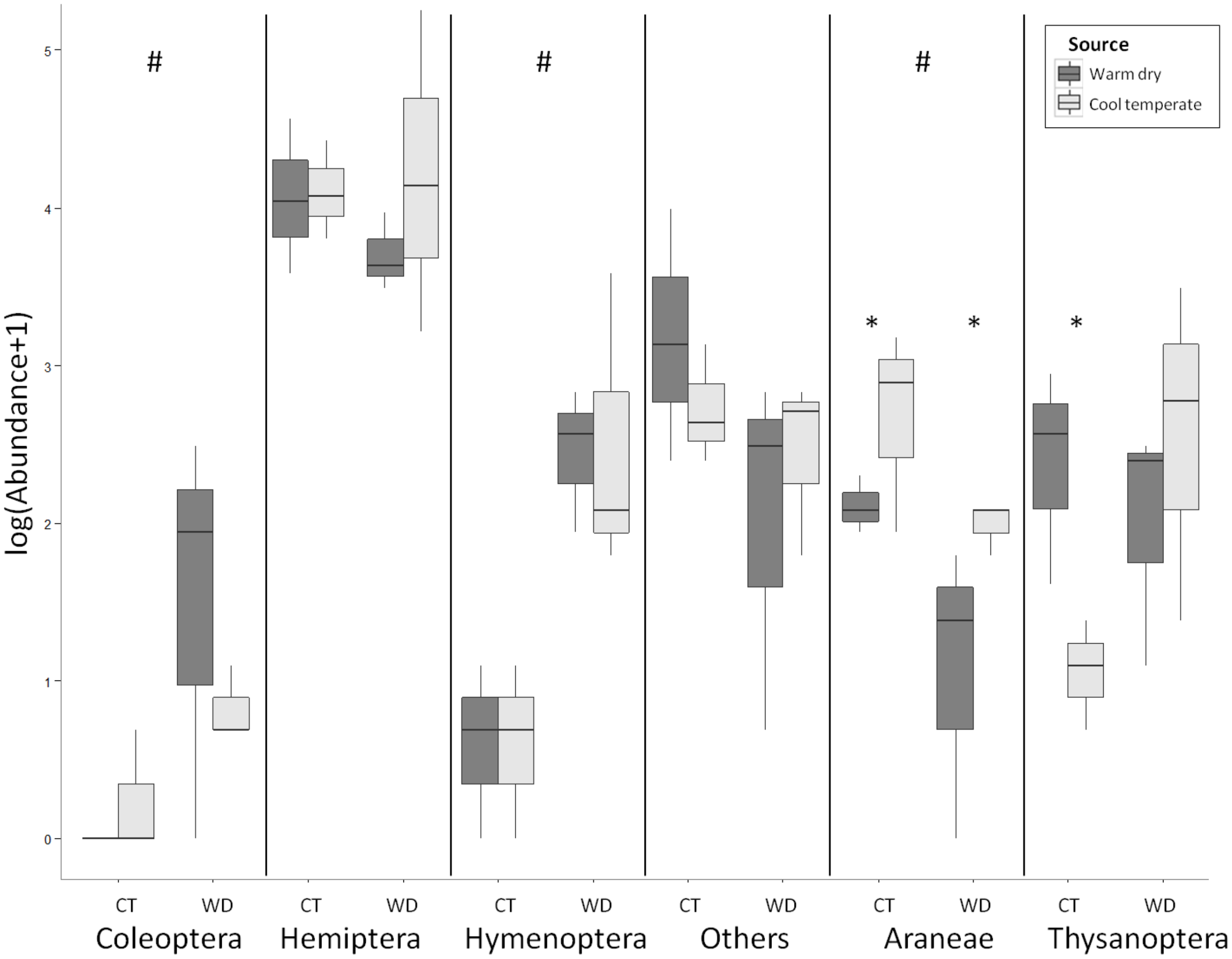

Figure 2: Mean log(abundances + 1) of insect orders on transplanted *Themeda triandra*. Dark boxes indicate plants sourced from the warm dry site, light boxes represent plants sourced from the cool temperate site. X axis shows transplant site (CT = cool temperate, WD = warm dry). Asterisk (*) indicates significant source effect, Hash (#) indicates significant site effect. Boxplot solid line represents median, box covers upper and lower quartiles, whiskers show greatest and least value excluding outliers.

There were significant differences in Coleoptera (sum-of-LR = 7.144, p-value = 0.021), Hymenoptera (sum-of-LR = 14.79, p-value = 0.001) and spider (sum-of-LR = 5.724, p-value = 0.024) abundances between the two transplant sites. Coleoptera and Hymenoptera abundances were higher in the warm dry site, spider abundance was higher in the cool temperate site (Figure 2).

Testing the effect of the transplant process on insect order composition

Results collected from the transplant samples were compared to results obtained from sampling naturally occurring *T. triandra* found at the same site. This comparison revealed that the transplant process had a significant effect that is dependent upon the site for some orders (Figure 3). The transplant effect for Hymenoptera was only observed at the cool temperate site (sum-of-LR = 5.99, p-value = 0.041), in which it was almost absent on transplanted plants (Figure 3). The transplant effect for spiders was only observed at the warm dry site (sum-of-LR = 7.994, p-value = 0.01), in which it was very low on transplanted plants (Figure 3). The transplant effect for Thysanoptera was observed at both sites (sum-of-LR = 55.22, p-value = 0.001) but in different directions. In the warm dry site, more Thysanoptera were found on naturally occurring *Themeda triandra.* In the cool temperate site, more Thysanoptera were found on transplanted grass (Figure 3).

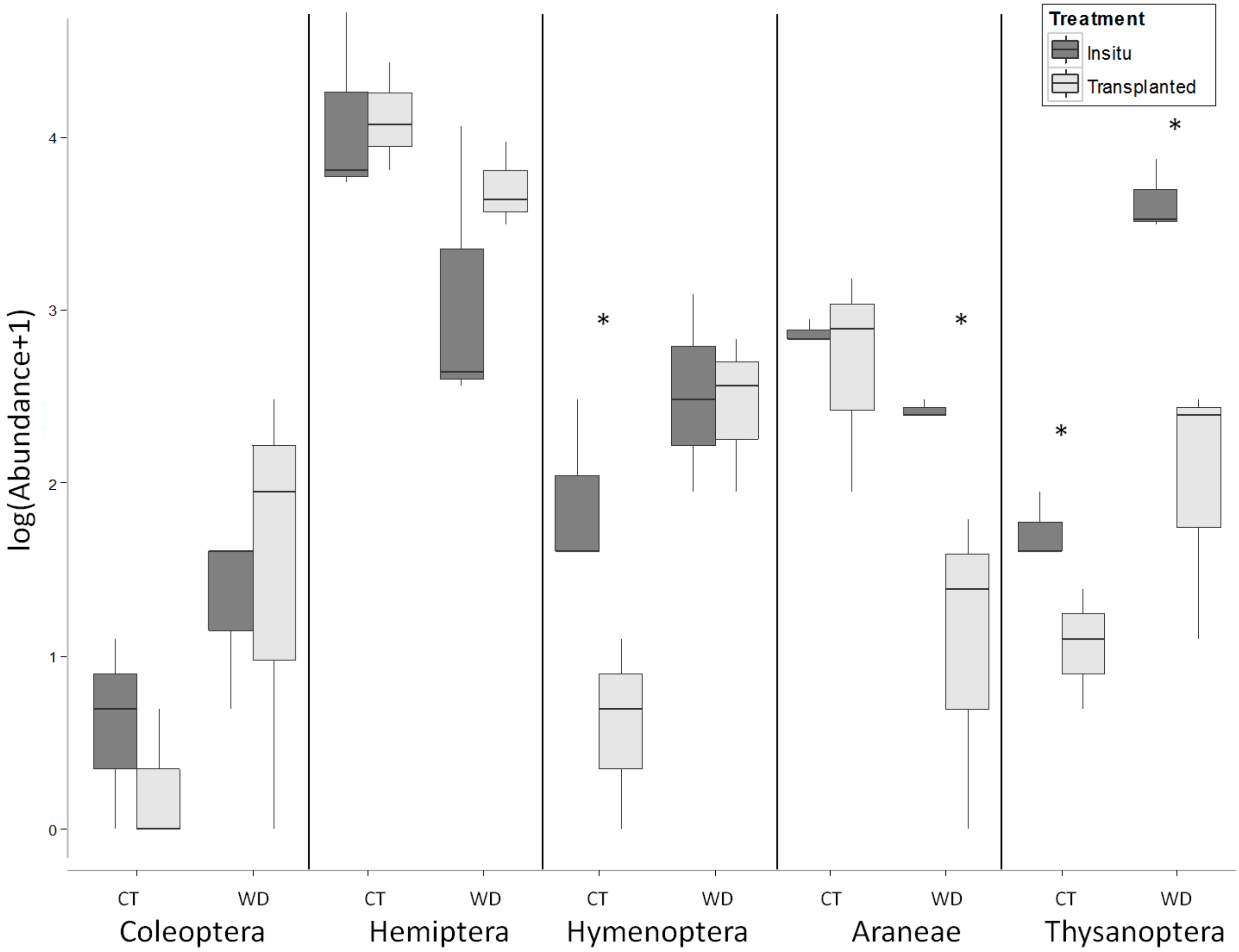

Figure 3: Boxplot showing mean log(abundances + 1) of insect orders on *in situ* versus transplanted *Themeda triandra*. Dark boxes represent samples from in situ plants, light boxes are samples from reciprocal transplants. X axis shows site (CT = cool temperate, WD = warm dry). Asterisk (*) denotes a significant transplant effect. Boxplot solid line represents median, box covers upper and lower quartiles, whiskers show greatest and least value excluding outliers.

Effects of host plant origin and transplant process on Thysanoptera species

An overall interaction effect between the sites and the source of the transplants on thrips community composition (sum-of-LR = 31.66, p-value = 0.001) was identified using `anova.manyglm (mvabund)`. Adjusted univariate results indicate that this effect is due to two species, *Anaphothrips* sp. 2 (sum-of-LR = 20.57, p-value = 0.002) and *Anaphothrips incertus* (sum-of-LR = 5.138, p-value = 0.043). Both species were more abundant in grass that had been transplanted from elsewhere than in host plants of local origin (Figure 4).

Within sites, there was no host plant preference for species other than *Anaphothrips* sp. 2 and *Anaphothrips incertus*. Thripidae sp. 4 was the only thrips that occurred in significantly different numbers between sites (sum-of-LR = 9.105, p-value = 0.011) (Figure 4).

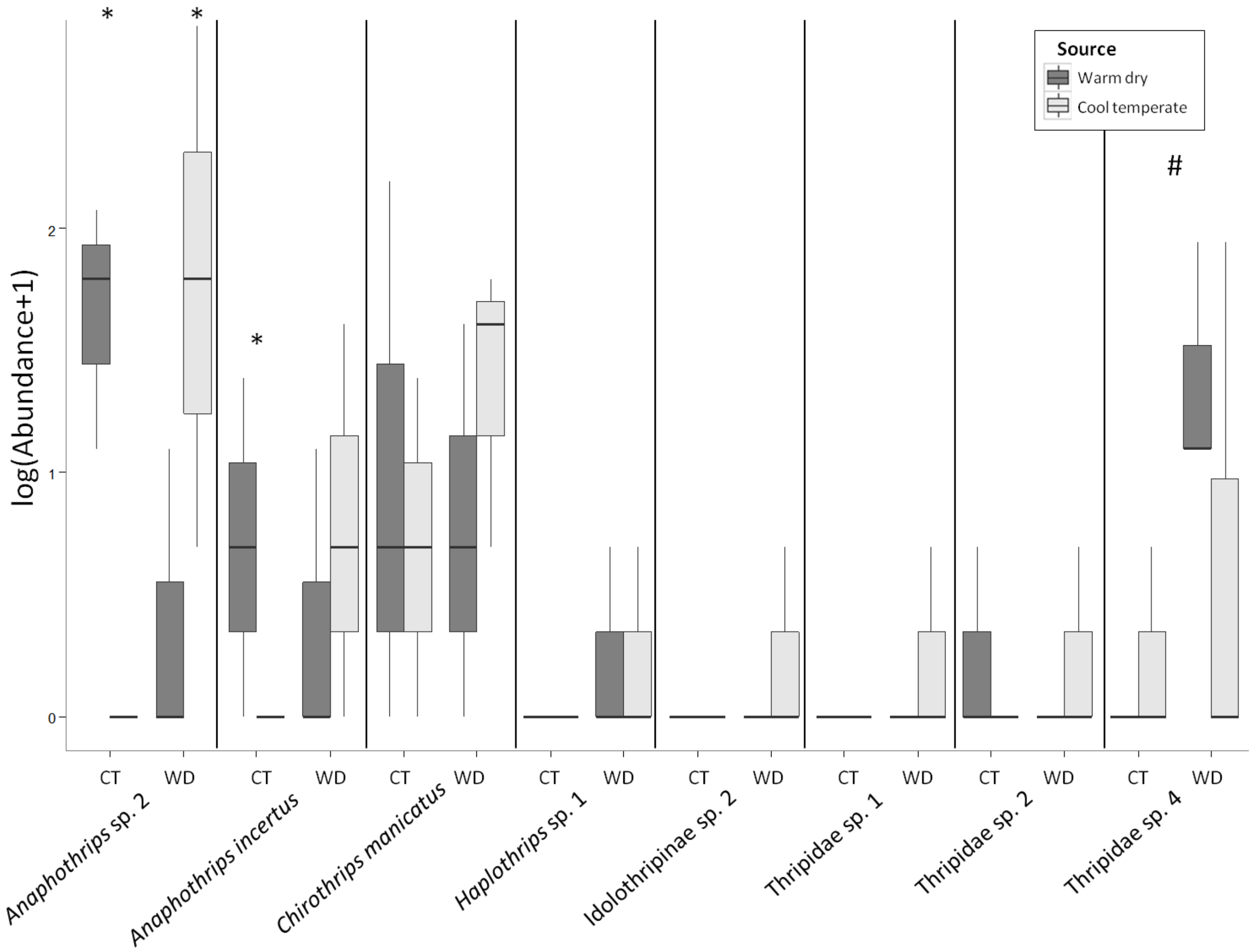

Figure 4: Boxplot showing mean Thysanoptera species log(abundances + 1) on transplanted *Themeda triandra*. Dark boxes indicate plants sourced from the warm dry site, light boxes represent plants sourced from the cool temperate site. X axis shows transplant site (CT = cool temperate, WD = warm dry). Asterisk (*) indicates significant source effect, Hash (#) indicates significant site effect. Boxplot solid line represents median, box covers upper and lower quartiles, whiskers show greatest and least value excluding outliers.

These results provide an indication that perhaps most of the thrips species found during this experiment have no preference for plant genotype (although a lack of numbers makes it hard to say for sure). Two species, *Anaphothrips* sp. 2 and *Anaphothrips incertus,* have a strong preference for the plants sourced from a different climate to the transplant site (Figure 4).

When grass from the cool temperate site was grown at the warm dry site, it was colonised by a large abundance and diversity of thrips (Table 2). Grass from the cool temperate site that had been planted back into cool temperate was colonised by only two thrips species (*Chirothrips manicatus* and Thripidae sp. 4), these species also colonised the naturally occurring cool temperate grass and cool temperate grass transplanted to the warm dry site (Table 2).

When grass from the warm dry site was transplanted to the cool temperate site, it was colonised by a similar diversity of species as when it was transplanted back into warm dry (Table 2). Naturally occurring warm dry grass supported greater thrips diversity than the reciprocally transplanted warm dry grass. Interestingly, *Chirothrips manticus* and Thripidae sp. 4 were only found on grass that had been transplanted (Table 2). Overall, the transplant process significantly affected Thysanoptera abundances (ManyGLM: sum-of-LR = 71.52, p-value = 0.029). Univariate results indicate that three species were responsible for this difference: *Nesothrips propinquus* (sum-of-LR = 8.64, p = 0.026), *Anaphothrips* sp. 2 (sum-of-LR = 13.48, p = 0.001) and *Thrips* sp. 2 (sum-of-LR = 15.84, p = 0.006).

Table 3: Community composition of thrips species across transplanted and naturally occurring *Themeda triandra* from each source and at each site. Each cell shows the number of individuals. Colours represent location and source; green = from/to cool temperate, pink = from/to warm dry, orange = from either warm or cool, moved to an alternative climate.

	Transplants				'*In-situ*' Plants	
Site	Warm dry		Cool temperate			
Source	Cool temperate	Warm dry	Cool temperate	Warm dry	Warm dry	Cool temperate
Anaphothrips sp2	22	2		14	24	4
Chirothrips manicatus	10	5	4	9		2
Anaphothrips incertus	5	2		4	11	
Haplothrips sp1	1	1			8	
Idolothripinae sp1					2	2
Idolothripinae sp2	1				1	
Nesothrips propinquus					7	
Phibalothrips longiceps					1	
Thrips imaginis						2
Thripidae sp1	1				1	
Thripidae sp2	1			1		
Thripidae sp3					1	
Thripidae sp4	6	10	1			1
Thripidae sp5						1
Thrips sp2					28	1
Total	**47**	**20**	**5**	**28**	**84**	**13**

Glasshouse mealybug assessment

Two of the Thysanoptera species assessed in the field experiment appeared to have a preference for host plants with 'exotic' genotypes. This is in contrast to what was observed with the mealybug colonisation during glasshouse growth, where the Armidale mealybugs had a clear preference for colonising plants sourced from the local cool temperate region (deviance = 38.4, $p < 0.0001$) (Figure 5).

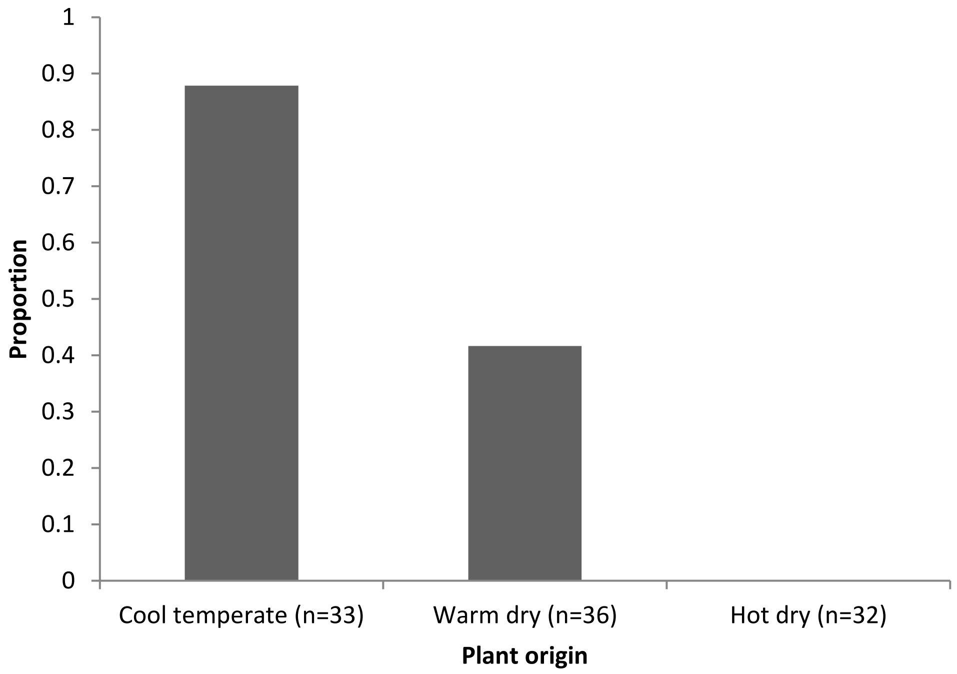

Figure 5: Percentage of mealybug colonisation on *Themeda triandra* during growth stage in an Armidale (cool, temperate) glasshouse.

4.4. Discussion

Asynchrony in range and phenological shifts due to climate change is already a strong driver of species loss and changes in ecosystem dynamics (Cudmore *et al.* 2010, Hillyer and Silman 2010, Zvereva *et al.* 2010, Chen *et al.* 2011, Moser *et al.* 2011). As shifts become more rapid, the changes in communities will become more extreme. The focus of the majority of research has been based on long term observations of natural systems (Abbott and Maitre 2010, Dijkstra *et al.* 2011, Dobson and Randolph 2011, Yang *et al.* 2011, Andrew *et al.* 2013b), or by using laboratory experiments where climatic variables have been manipulated (Diaz *et al.* 1998, Johns and Hughes 2002) or where plants have been translocated but the associated insect assemblages have not been assessed (Angert and Schemske 2005, Villalpando *et al.* 2009, De Boeck and Nijs 2011, De Frenne *et al.* 2011). This research can lead to explanations of what might happen if species become dissociated due to asynchronous shifting, however it does not directly test what happens to insect assemblages if they are presented with a host genotype originating from a different climate (but see Ireson *et al.* (2008)).

In this transplant experiment, spiders and Thysanoptera were the only orders that had a significant preference in terms of the source of the transplanted *Themeda*. Spiders preferentially colonised *Themeda* sourced from the cool dry site at both transplant sites. Spider abundances may be assumed to be related to the abundance of other insects as they are predators (Clarke and Grant 1968). This would not necessarily be related to the insect abundances collected in this experiment, as the sampling method was biased towards insects that live in the *Themeda* tussocks rather than insects passing through. Web weaving spiders are more likely to prey upon insects unrelated to the host plant than hunting spiders (Nyffeler 1999), so classifying spiders as web weavers or hunters would be necessary to come to any worthwhile conclusions regarding this result.

Thysanoptera community structure

The Thysanoptera community structure varied in different ways depending on the source of the transplanted *T. triandra*. When grass from the cool temperate site was grown at the warm dry site, it was colonised by a number of additional species when compared to what is observed at the cool temperate site. Grass sourced from the warm dry site, grown in the cool temperate site did not show this trend. The result that a plant sourced from a temperate climate, grown in a warmer drier climate, are colonised by additional species is consistent with patterns observed for insect assemblages on transplanted *Acacia falcata* by Andrew and Hughes (2007). This could suggest that as areas warm in the future, Thysanoptera diversity may increase on *T. triandra* - although many more observations are needed to truly determine this.

Research on host ploidy preferences among insects is limited, although Arvanitis *et al.* (2010) found that gall midge attacks on the *Cardamine pratensis* herb were restricted to higher ploidy levels. Their explanation for this was that the midge may prefer larger plant parts and/or earlier flowering. This could certainly apply for some thrips as flowers can be very important for their biology (Mound 2005) and tetraploid *T. triandra* is larger than the diploid (Scott 1972), although in this experiment we kept plants at similar sizes to eliminate this factor. Another example was found by Thompson *et al.* (1997) who observed that the moth *Greya politella* were more likely to attack tetraploid *Heuchera grossulariifolia* (Saxifragaceae) than diploid variants in an *in situ* study. Contrary to these observations, in this transplant experiment there appeared to be no consistent preference for higher levels of ploidy by Thysanoptera. This is consistent with Halverson *et al.* (2008) who observed strong but variable ploidy preferences in five species of Dipteran gallmakers on *Solidago altissima* (Asteraceae). Halverson *et al.* (2008) proposes that this variability could be explained by the fact that some insects may respond to plant traits that are a direct consequence of ploidy variation, whereas other insects may respond to plant traits that have evolved differently due to reduced gene flow between ploidies. So these traits may not be directly caused by ploidy, however they are associated with ploidy.

Nesothrips propinquus was only found on naturally occurring *T. triandra* in this experiment. *Nesothrips propinquus* is known to feed on fungal spores but generally breeds at the base of grass tussocks (Hoddle *et al.* 2012). Perhaps naturally occurring *Themeda* provides a safer environment for breeding from the thrips' perspective. This may also be why Idolothripinae species were mostly found on naturally occurring grass, they are presumed to all feed on fungal spores and some use grass tussocks for breeding (Mound *et al.* 2012). Another explanation is due to possible differences in fungal community establishment and species composition between *in situ* and transplanted *Themeda*.

Anaphothrips incertus was found on all *T. triandra* except for grass of cool temperate origin growing at the cool temperate site. *Anaphothrips incertus* is known to feed on native grasses (Mound *et al.* 2012) and many *Anaphothrips* are associated with semi arid areas (Mound and Masumoto 2009). *Anaphothrips* sp. 2 had a similar preference of host plant, although some were found on naturally occurring cool temperate *Themeda*.

Effects of the transplant process on the host plant

When evaluating the comparison of transplants versus established plants, it is important to note the implications of the difference in plant architecture in terms of insect assemblages (Leather 1986). Generally, larger more complex plants are more conspicuous to insects, have a greater range of microclimates and are simply able to better sustain large populations which is likely to increase insect abundance and richness (Lawton 1983, Campos *et al.* 2006). The transplants in this experiment were generally less complex as they only had six months to establish in the field. This is likely to be the reason why in some cases (40% of comparisons) there were lower abundances and species diversity on transplanted grass obtained from the same site. This difference is in contrast to Andrew and Hughes

(2007) who found that, despite differences in plant size and architecture, there were no differences in community composition based on proportional representation of functional groups. Species composition is also likely to be time dependent, generalist herbivores are likely to take less time to adapt to foreign host plants than specialists (Strong *et al.* 1984).

In this experiment, spiders preferred in situ plants but only at the warm dry site. The in situ *Themeda* at the warm dry site was the largest grass, this is consistent with much of the literature. Gibb *et al.* (2015) found high abundances of juvenile spiders in dense *T. triandra* tussocks, Gunnarsson (1990) also found high spider abundances on spruce branches with higher needle densities. Romero and Vasconcellos-Neto (2005) found a species of jumping spider more frequently on larger bromeliads. In this study, Hymenoptera preferred in situ plants, but only at the cool temperate site. This is hard to explain as the in situ plants at the cool temperate site were similar sizes to the reciprocally transplanted cool temperate *Themeda*.

Most Thysanoptera species were more abundant in naturally occurring *T. triandra*, however Thripidae sp. 4 and *Chirothrips manicatus* were actually more abundant on transplants. This result is unexpected, as *Chirothrips manicatus* is known to breed in florets (Nakahara and Foottit 2012) and the non-transplanted plants had more flowers. *Thrips imaginis* also feeds and breeds in flowers, in fact many species in the *Thrips* genus feed on pollen (Mound *et al.* 2012) . *Thrips imaginis* and *Thrips* sp. 2 were only found on naturally occurring *Themeda*, indicating the importance of flowing. These unexpected results may be due to a lack of specimens collected in order to make comparisons, future transplant experiments should ideally be left for longer and be sampled multiple times to increase the strength of the dataset.

Glasshouse conditions may cause different insect responses to natural conditions

In this transplant experiment, it was observed that some thrips preferentially colonised foreign genotype *T. triandra* and that no thrips species had a clear preference for locally sourced *Themeda*. The results from the mealybug colonisation are potentially a contrast to this as they preferentially colonised local grass, although these two observations cannot be directly compared as they were discovered in very different contexts and the mealybug observations were not results of a properly controlled experiment. The thrips were found out in the field sites after the host plants had experienced natural climatic conditions, whereas the mealybugs were found within a temperature regulated glasshouse where the host plants were watered regularly.

The mealybug results could support the ‘rarity advantage’ hypothesis, that plants of a local origin are attacked by herbivores more often than plants of foreign origin (Roy 1998). This would be the case if the herbivorous insects evolved to effectively take advantage of the local plants at a greater rate than the plants evolved defences. The opposite can also occur, that foreign plants have poorer defences against local herbivores. This could explain the preference for foreign genotypes by *Anaphothrips* sp. 2 and *Anaphothrips incertus* observed in this experiment.

Under glasshouse conditions, where no plants were under stress, the ‘rarity advantage’ could be applicable. However in the field, the foreign plants are likely to be attacked to a greater degree due to their reduced fitness from experiencing stress from unusual climatic conditions (Leimu and Fischer 2008, Gutbrodt *et al.* 2011, Bauerfeind and Fischer 2013). This is especially likely with *Anaphothrips* as they are most commonly associated with plants from semi-arid regions (Mound and Masumoto 2009) yet in this experiment they preferentially colonised foreign plants irrespective of originating or current climate.

Conclusion

We found that two species of thrips preferentially colonised foreign *T. triandra* when transplanted in the field. There were differences in abundance and richness of thrips between plants that had been through the transplant process and plants that were naturally growing at the site, this could be due to differences due to establishment time. To accommodate for proper establishment, the plants would ideally be left at a site to grow for several years and planted from seed. The indication that plants of foreign genotype could be particularly attractive to generalist herbivores may imply an increase in herbivory pressure on the plants when insect shift their range to accommodate changing climatic conditions. This may be primarily due to the host plants inability to adapt to the different climate as rapidly as the insects based on differences in generation time, so more long-term studies are needed to determine how long it would take for the plants to ‘catch up’.

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Chapter 5: Thesis Discussion

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). If a species cannot adapt physiologically, morphologically or behaviourally to a rapidly changing climate (Andrew *et al.* 2013), it's geographic range could either shrink or shift (Stireman *et al.* 2005). The extent of the effect of climate differs depending on each species, generally a warming of the climate could favour invasive species over indigenous ones (Chown *et al.* 2007), and generalist species over specialists (Bale *et al.* 2002). Where a species is dependent upon another, this uneven climatic tolerance could decouple this interaction (Hodkinson 1997, Hughes 2003, Westoby and Burgman 2006). Overall trait diversity can also 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). Having more information available in regards to how ecosystems may respond to a changing climate will help us in responding to potential environmental issues.

The aim of this thesis was to determine the ways in which Thysanoptera communities might respond to a changing climate, and attempt to predict what might happen in the future. I did this by examining thysanoptera communities across a climatic gradient and assessing the species composition and frequencies of various morphological traits. I expected microclimate data to be particularly useful for this and invested in a large number of small data loggers to use at each site. I also carried out a transplant experiment to determine how local insects might respond to host plants of exotic genotypes but same species (i.e. a transplant within the host's existing range).

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. Abundances of the more common *Haplothrips* and *Thrips* species were influenced mostly by tussock level temperatures during the week or month before sampling, however the widespread *Haplothrips* had a positive association with this temperature and the generalist *Thrips imaginis* had a negative association.

Assemblage structure changes seasonally as expected, but time of day did not affect what was captured. Habitat characteristics such as host plant height, foliage density and disturbance explained assemblage composition variation, with species responding in various direction. One surprising result for many of the species was a negative association with flowering *Themeda* even in flower-breeding thrips, this may be due to the fact that juvenile thrips were not assessed in this study. Precipitation did not have as much of an effect as microhabitat temperature, and plant nutrition was mostly only important for rarer species.

I also found 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. Traits such as foreleg length were mostly influenced by the physical characteristics of the habitat, whereas body length was influenced by both habitat characteristics and microclimate. Further analysis of my data could be used to assess if trait changes are driven by within species variation, or would a new species that currently exhibits the trait become more dominant. This could potentially change the community dynamics considerably if this new dominant species had a different feeding type or host preference. The use of the fourth corner solution for modelling trait frequency in addition to analysing trait variation within species will improve our ability to answer these sorts of questions for other taxa, in other systems.

I also found that two species of thrips preferentially colonise foreign *T. triandra* when transplanted in the field. Finding that plants of foreign genotype could be particularly attractive to generalist herbivores may imply an increase in herbivory pressure on the plants when insect shift their range to accommodate changing climatic conditions. This may be primarily due to the host plants inability to adapt to the different climate as rapidly as the insects based on differences in generation time. This idea may potentially also apply to some predator/prey relationships.

Limitations and Future Directions

In this thesis, only Thysanoptera were assessed due to their underrepresentation in this field of research despite their relative abundance and trait diversity in ecosystems. As part of this project, all invertebrates captured when sweeping were identified and stored. This provides an opportunity to determine species abundance and trait variation in response to climate across many different insect orders that live in *T. triandra* dominated grasslands.

For this thesis, only *T. triandra* samples were used, primarily to reduce the influence of host plant species in changing insect community dynamics. A limitation of this is the lack of information gained regarding host specificity, existing knowledge of thysanoptera host specificity is very limited so I could not be sure how specific these thrips were to *Themeda*. However, in addition to keeping all other invertebrates, we also sampled from two other hosts when collecting the *T. triandra* samples. Samples from mostly *Poa sieberiana* (or a similar *Poa* or native grass where *P. sieberiana* could not be found) and samples from exotic grasses were collected in the same way and at the same sites. With these samples I can determine how community composition and traits may vary in insects captured from native vs exotic host grass in the future.

The transplant experiment for this thesis was weakened by the death of much of the transplanted grass at the hottest site, this effectively reduced the number of treatment sites to two. The total number of insects collected was also quite small. This type of experiment could be improved by transplanting at a cooler time of year to reduce heat stress related deaths, and by greatly increasing replication and treatments. Allowing a greater time from establishment to sampling may also help, although it would be difficult to increase this past standard 2-3 year project funding cycles.

The use of just sweep netting would influence the type of insects captured, it is likely more active insects would enter the nets and not many ground dwelling insects would enter. Sweep nets were identified as the most efficient method for capturing thysanoptera which is why it was used. Using a combination of methods, such as including pitfall trapping would improve the number of insect types captured.

Overall, the importance of not only microclimate data, but specifically microclimate data during certain periods (such as development period) for predicting trait and abundance variation demonstrates that long term weather station data should not be exclusively relied upon for future studies. The variation in temperature preferences for even the common thysanoptera species shows that generalisations should not be made for communities and that considering both change in assemblage composition and individual responses is important in determining impacts of future climate change. Taking advantage of recent additions to statistical methods such as those contained in the `mvabund` R package make doing this considerably easier and more efficient.

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Appendix I

A.1.1 Equipment

Figure 1: 40cm diameter sweep net used, showing fine black mesh so that small arthropods do not escape (left). An example of short *Themeda triandra* at a sub-tropical site (right).

Figure 2: IR gun used to obtain leaf surface temperatures in *Themeda triandra*

Figure 3: Three ibuttons placed in tussocks at each sampling site, the middle one with a hole can measure humidity in addition to temperature

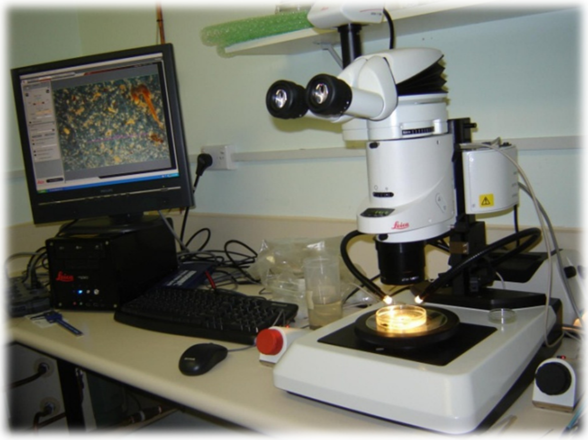

Figure 4: Leica MZ16a used for insect sorting and image capture

A.1.2. Range of soil characteristics

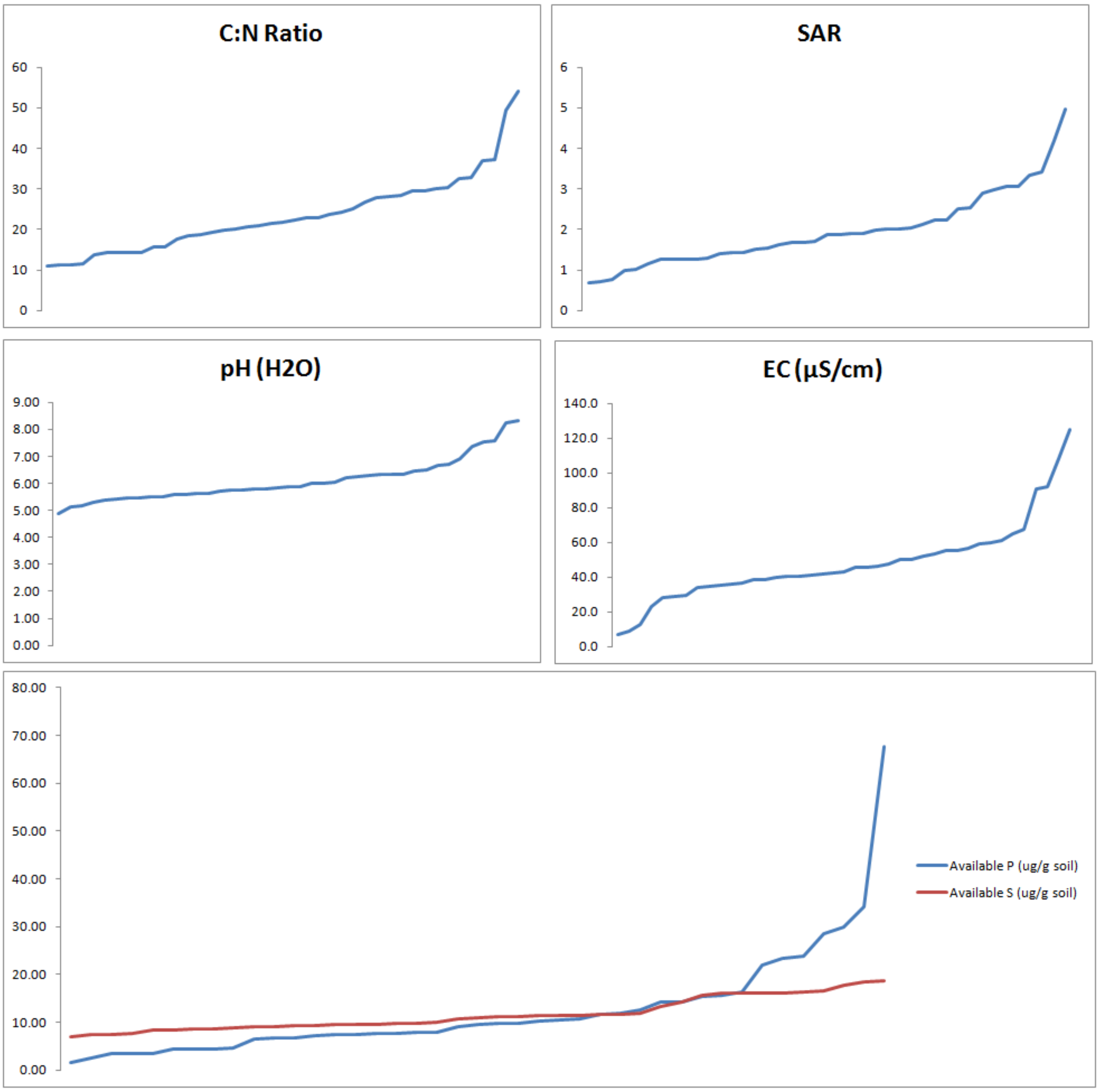

Figure 5: This figure shows the range of soil characteristics across all sites, ranked from lowest to highest values along the x axis

A.2.1. Supplementary Community results based only on order classification

Order composition

Significant terms for determining ordinal composition are shown in Table 1. Season, grass height, tussock density, flowering and leaf temperature were all significant in determining order composition.

Table 1: Results from fitting a multivariate generalised linear model, with negative binomial error distribution using a log-link function, to ordinal data. Significant predictors shown in bold.

	Wald value	Pr(>wald)	
Season2	**4.915**	**0.006**	**
Season4	**6.696**	**0.001**	***
Time of Day	3.226	0.186	
Grass Height	**4.048**	**0.047**	*
Intrasussock Density	**4.143**	**0.04**	*
Intertussock Density	**6.261**	**0.001**	***
Disturbance	2.479	0.48	
Flowering	**4.628**	**0.023**	*
Ambient Humidity	3.343	0.169	
Ambient Temperature	3.738	0.095	.
Leaf Temperature	**4.437**	**0.022**	*
Annual Mean ibutton Temperature	2.192	0.617	
Max ibutton Temperature	3.003	0.293	
Min ibutton Temperature	2.061	0.697	
Growing Season ibutton Temperature	2.575	0.448	
ibutton Temp Week Before Sampling	2.301	0.572	
ibutton Temp at Sampling Time	2.469	0.496	
Annual Mean Temperature	4.067	0.054	.
Annual Precipitation	1.38	0.935	
Elevation	3.585	0.124	
Latitude	3.438	0.16	
C:N	3.34	0.178	
Leaf temperature (quadratic)	3.158	0.235	
Mean ibutton temp (quadratic)	1.909	0.789	

The significant coefficients associated with the final model are shown in Figure 6, there is clear seasonal variation in some orders. Hemiptera were more abundant in Autumn 2010 and 2011 than Summer 2009, Hymenoptera most abundant in Autumn 2010 and spiders most abundant in Autumn 2011 (Figure 7).

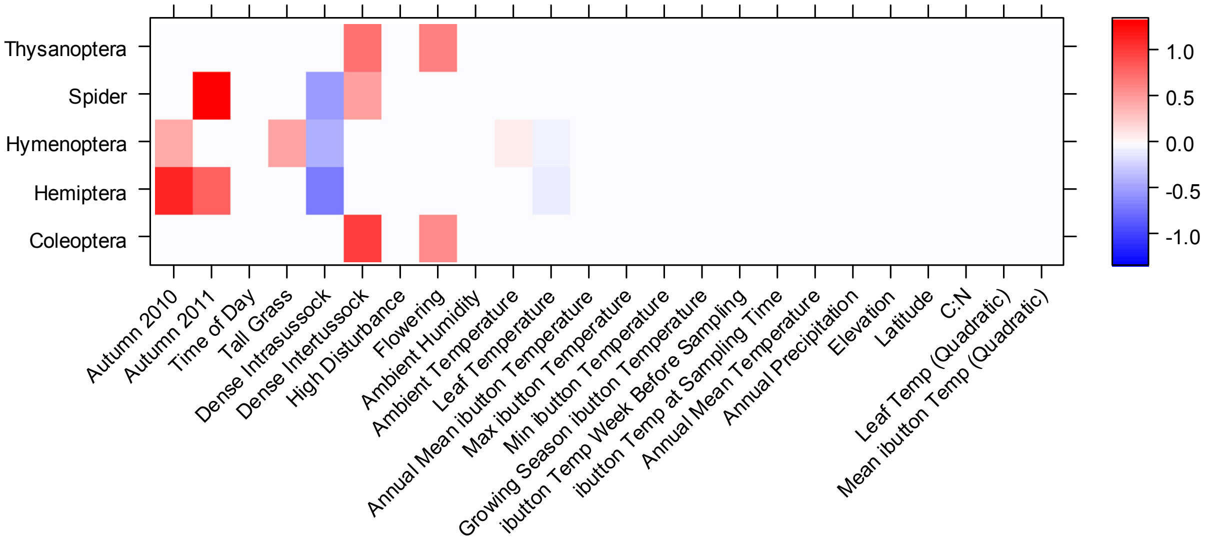

Figure 6: Univariate results from fitting multiple generalised linear models to insect orders, with negative binomial error distribution using a log-link function. The colour represents the coefficients for the significant predictor variables (p <0.05) for each order.

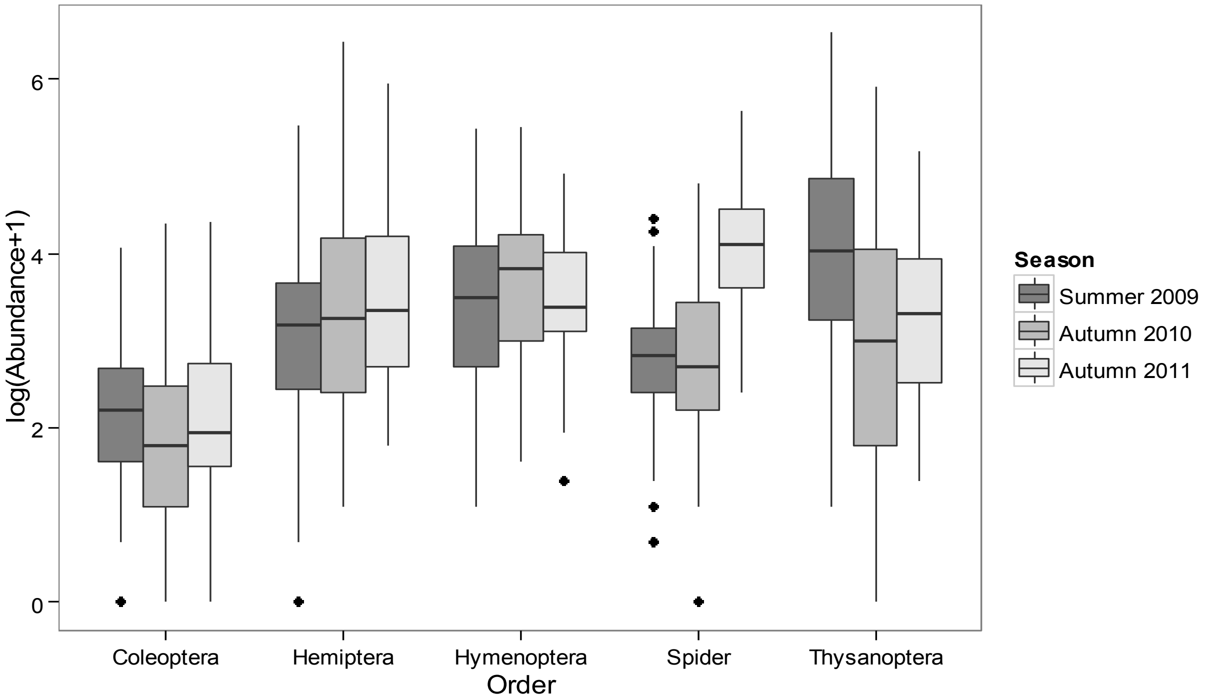

Figure 7: Abundances (log(x+1)) for each order based on season. Boxplot solid line represents median, box covers upper and lower quartiles, whiskers show greatest and least value excluding outliers.

Figure 6 indicates Hymenoptera are most abundant in tall grass tussocks. Hymenoptera, spiders and Hemiptera are are least abundant when intratussock density is low. Thysanoptera, spiders and Coleoptera are most abundant when intertussock density is high. Thysanoptera and Coleoptera are more abundant in flowering *Themeda*. More Hymenoptera are found when ambient temperature is high, but fewer Hymenoptera and Hemiptera are found when the leaf surface temperature is high (Figure 8).

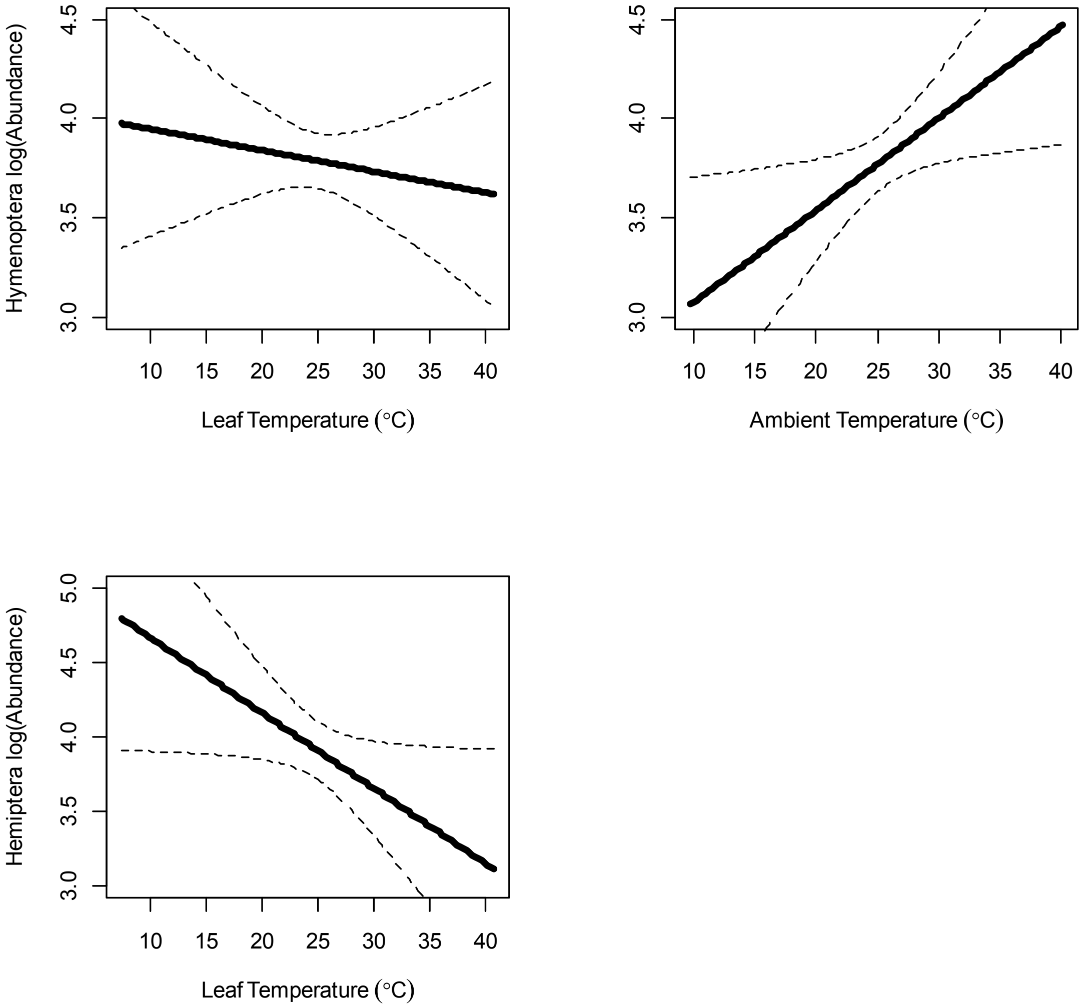

Figure 8: Predicted values (solid black line) of Hymenoptera (top) and Hemiptera (bottom) abundance as a response to significant explanatory variables. Dashed line is the prediction interval.

A.2.2. Supplementary Discussion based only on order classification

There is evidence that past climate changes have caused significant changes in the distributions of whole communities. 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. It is therefore important to assess the individual responses of species in addition to the community as a whole.

Ordinal composition

Temporal variability in numbers of arthropods and plants is well documented (Lowman 1985; Gaston and McArdle 1994; Heatwole *et al.* 1997) so it was no surprise to see that season significantly affected ordinal composition. Generally more insects were found in season 2 (Autumn 2010) and season 4 (Autumn 2011) than season 1 (Summer 2009). The higher temperatures in summer are often considered to cause more rapid insect growth (Bale *et al.* 2002) which would result in shorter generation times and higher abundances, although in this project Autumn mostly had the higher abundances.

Host plant size and density can be considered a measure of complexity, it was found that taller, dense *Themeda* growing in denser patches supported higher abundances of some orders. Host plant complexity has previously been determined as important in determining (generally increasing) insect abundance and richness (Leather 1986).

The nutritional value of a host plant is generally determined by the soil nutrition (Atakan 2006; Chow *et al.* 2012). Plant nitrogen content generally has positive effects on an insects development (Majer *et al.* 1992; Kyto *et al.* 1996) although this is not always the case. More nitrogen availability can sometimes increase the concentration of defensive nitrogen based secondary metabolites which can be very harmful to an insect herbivore (Kyto *et al.* 1996). The carbon to nitrogen ratio was not found to be important for explaining ordinal composition for this project.

Conditions during time of sampling can affect the type of insects captured, as activity of insects is generally suppressed at low temperatures (Drake 1994) and high humidity (Lewis 1963). The influence of high ambient temperature was positive for Hymenoptera abundance, but leaf temperature had a negative relationship with both Hymenoptera and Hemiptera. Leaf temperature has previously been measured at up to 10 degrees higher or lower than ambient depending on the needs of the plant (Ferro *et al.* 1979; Potter *et al.* 2009). Ambient humidity was not identified as being important.

The presence of flowers on a host plant is important for attracting certain insects the feed and breed in flowers (van Asch and Visser 2007). The presence of flowers was identified as an important predictor of ordinal composition. The univariate analysis indicates that flower presence is associated with an increase in the abundances of Coleoptera and Thysanoptera.

Annual mean temperature was negatively associated with order abundances which is not what was expected based on previous research (Beaver 1979; Gaston and Williams 1996; Yamamura *et al.* 2006). This negative association is partially consistent with Novotny *et al.* (2006) who explains that it may be due to increased predation in the tropics.

A.3 Individual Thysanoptera responses supplementary figures

Overal multivariate glm fit

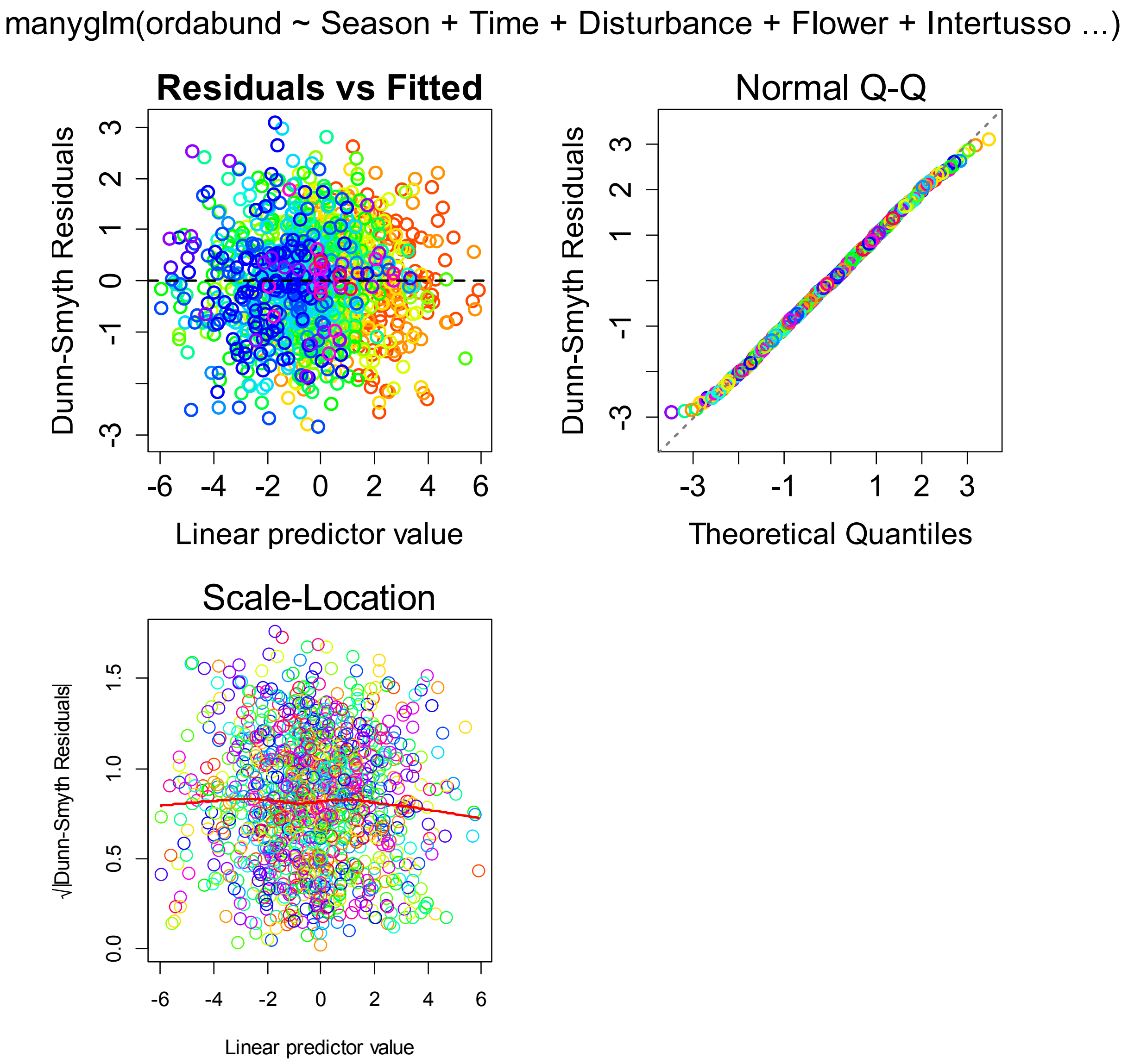

Figure 8: Diagnostic plots for the manyglm model used for Thysanoptera community analysis. They show a good fit for the data.

Family Phlaeothripidae

Subfamily Phlaeothripinae

***Haplothrips* sp. 1**

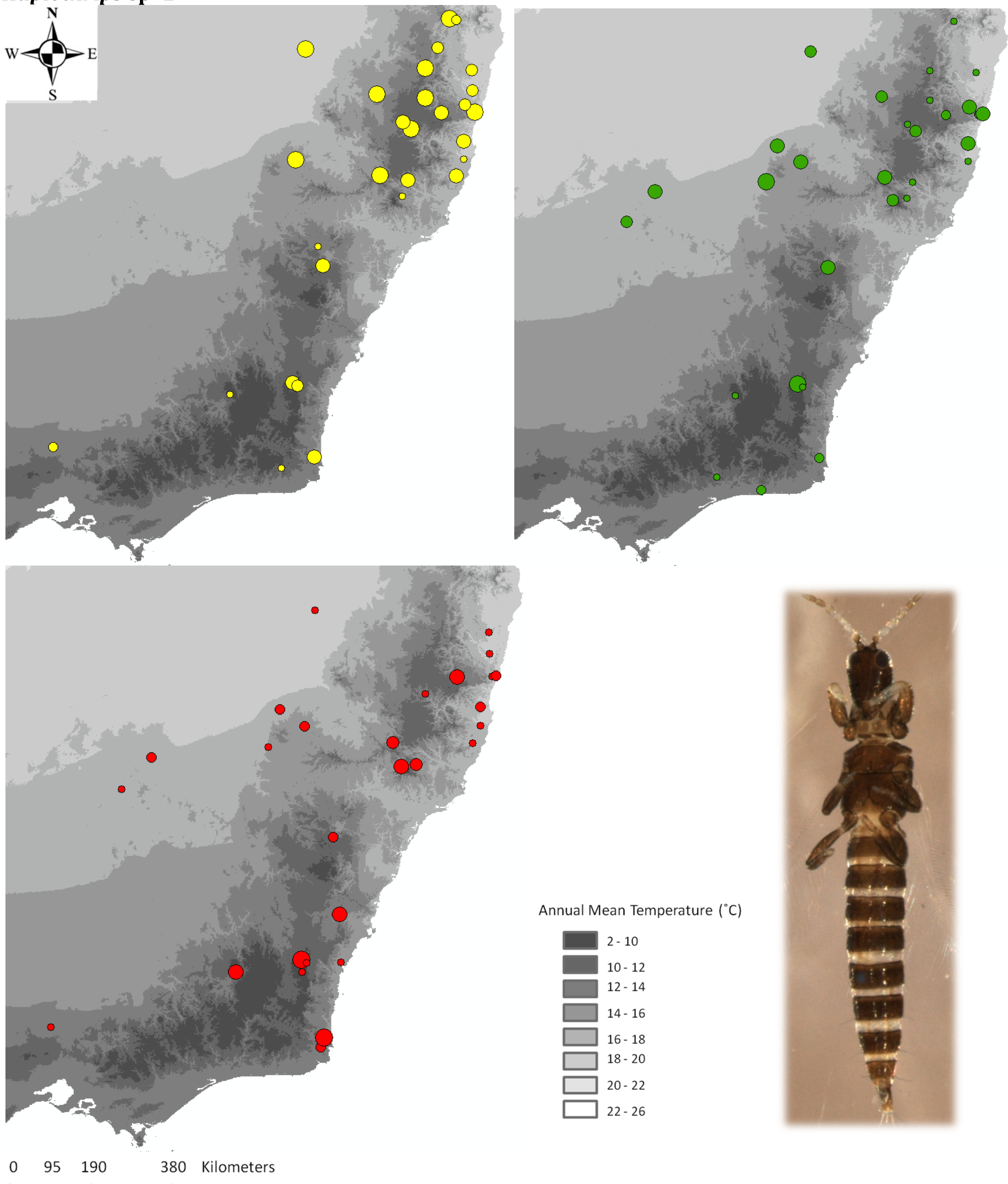

Figure 9: The change in total *Haplothrips* species 1 abundance between season 1 (summer, yellow circles), season 2 (autumn, green circles) and season 4 (autumn, red circles). There are five different circles sizes for each colour, representing abundances ranging from: 1-5, 6-10, 11-20, 21-50, 50+. Background shading shows mean annual temperature.

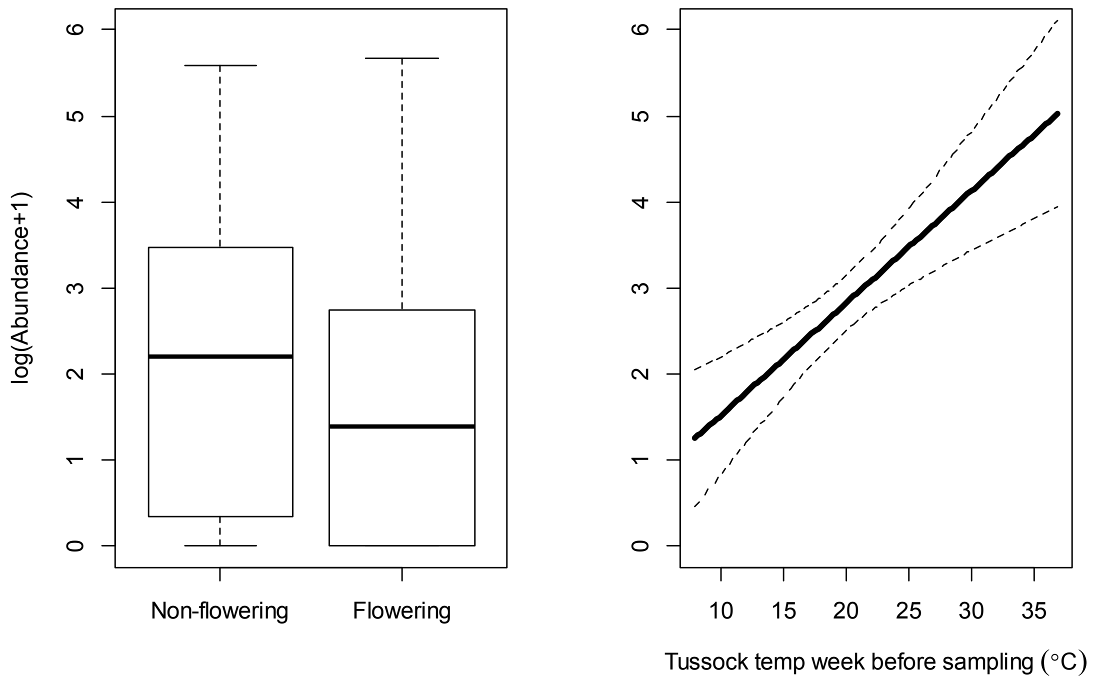

Figure 10: Predicted values (solid black line) of *Haplothrips* sp 1 abundance as a response to significant explanatory variables. Dashed line is the prediction interval. Boxplot solid line represents median, box covers upper and lower quartiles, whiskers show greatest and least value excluding outliers.

Haplothrips sp. 2

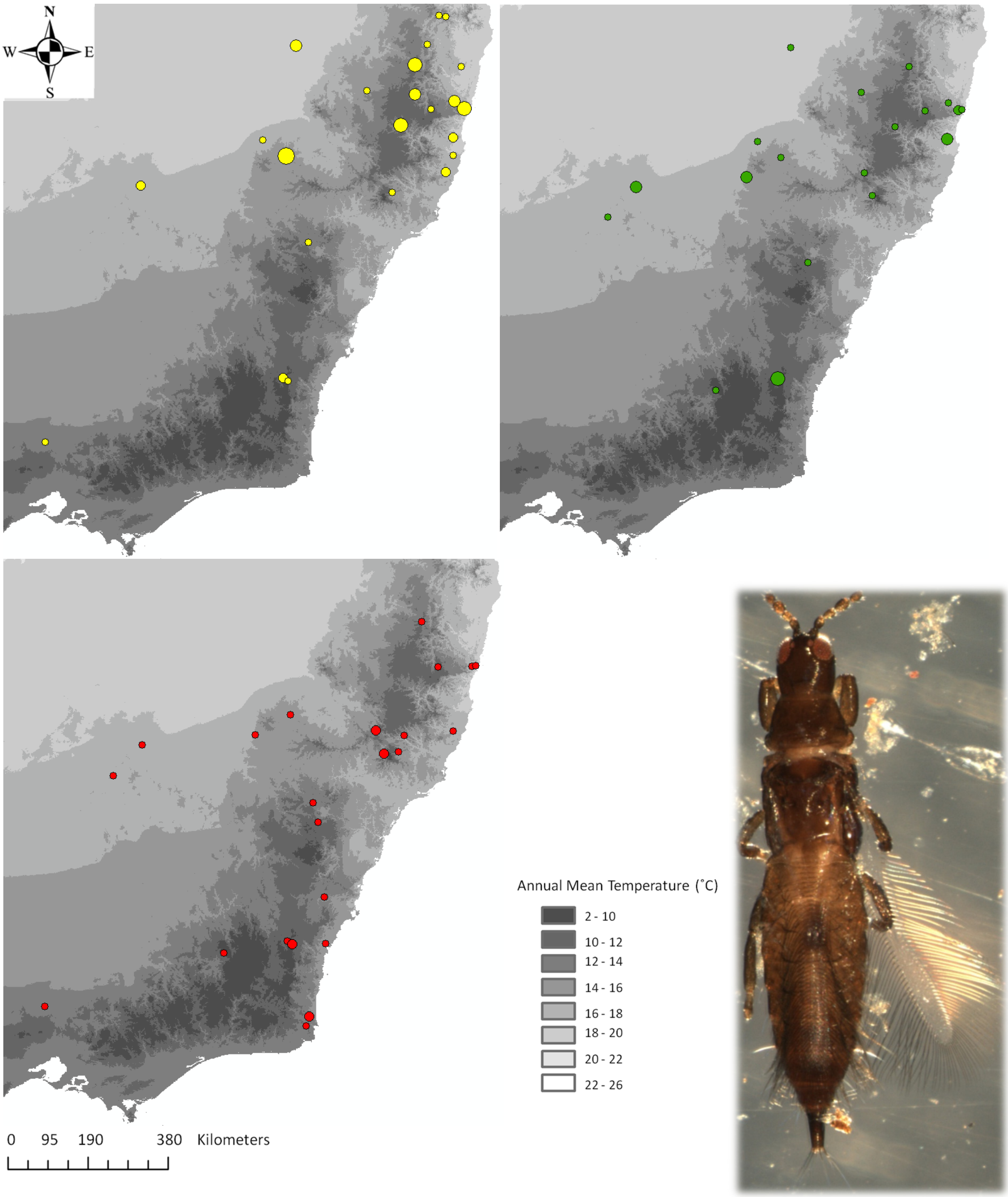

Figure 11: The change in total *Haplothrips* species 2 abundance between season 1 (summer, yellow circles), season 2 (autumn, green circles) and season 4 (autumn, red circles). There are five different circles sizes for each colour, representing abundances ranging from: 1-5, 6-10, 11-20, 21-50, 50+. Background shading shows mean annual temperature.

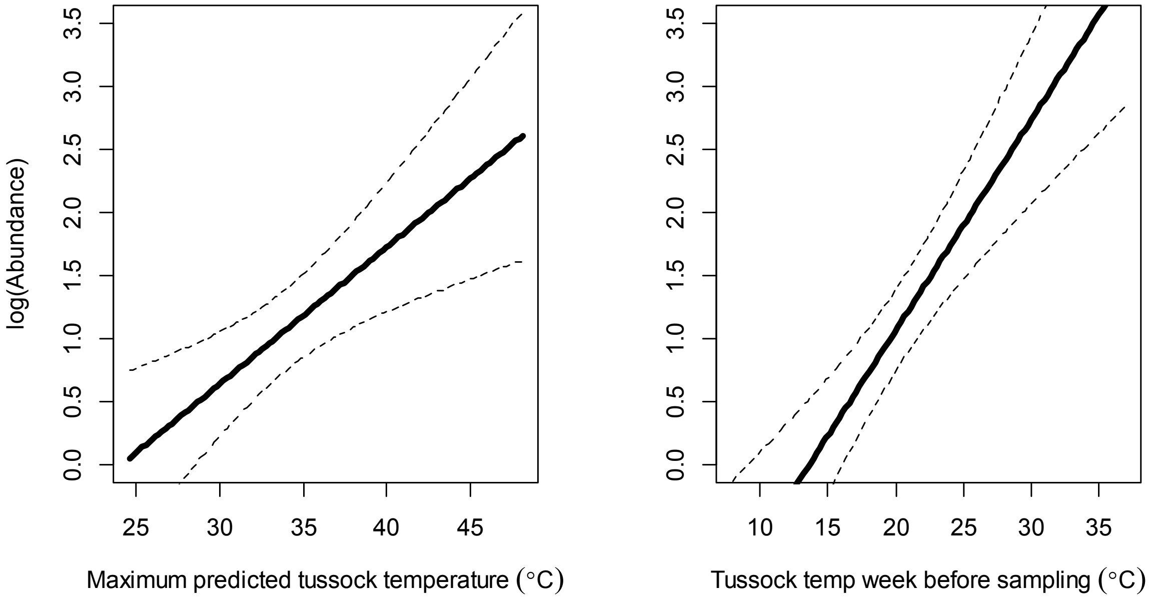

Figure 12: Predicted values (solid black line) of *Haplothrips* sp 2 abundance as a response to significant explanatory variables. Dashed line is the prediction interval.

Family Thripidae

Subfamily Thripinae

Thrips imaginis

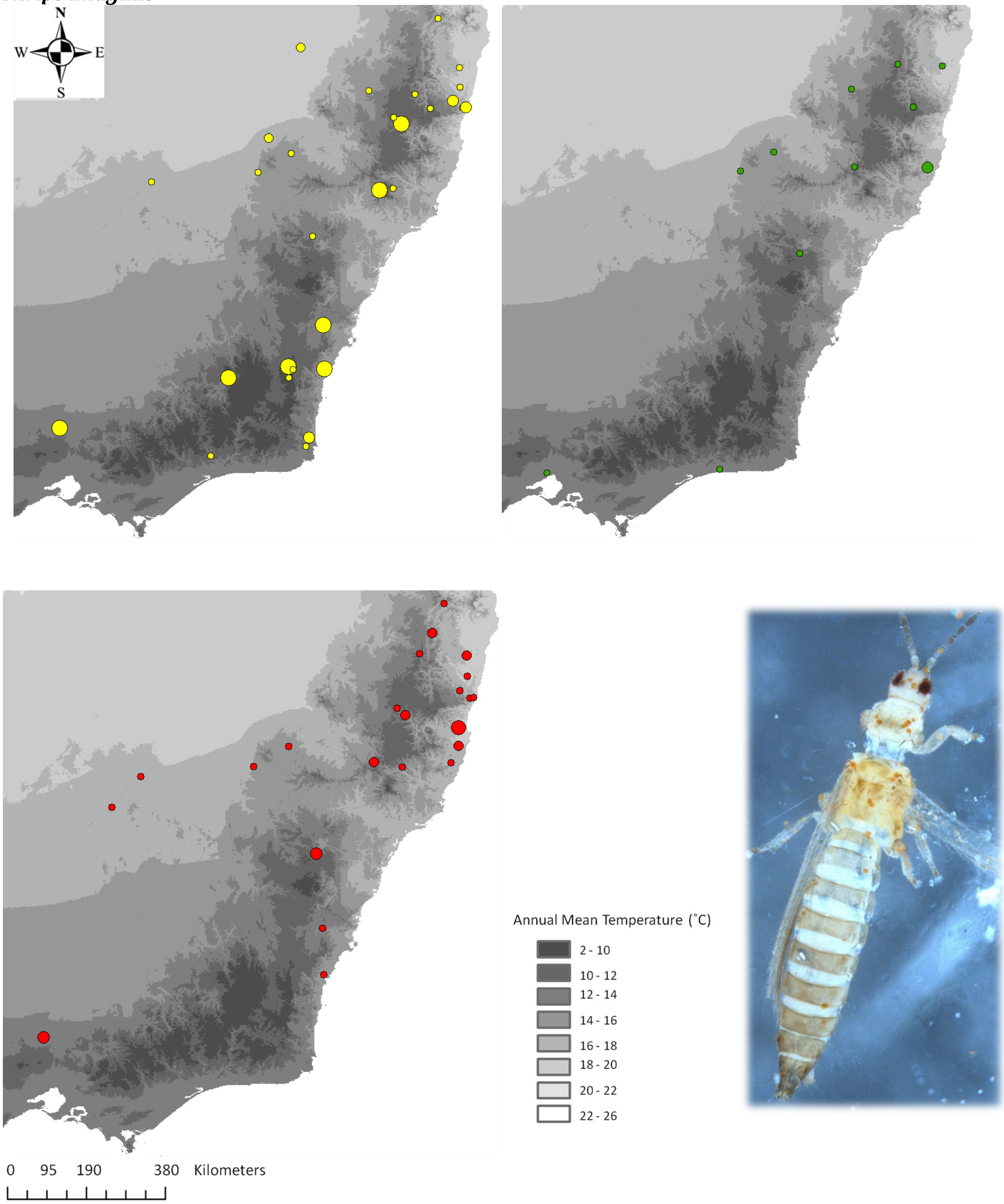

Figure 13: The change in total *Thrips imaginis* abundance between season 1 (summer, yellow circles), season 2 (autumn, green circles) and season 4 (autumn, red circles). There are five different circles sizes for each colour, representing abundances ranging from: 1-5, 6-10, 11-20, 21-50, 50+. Background shading shows mean annual temperature.

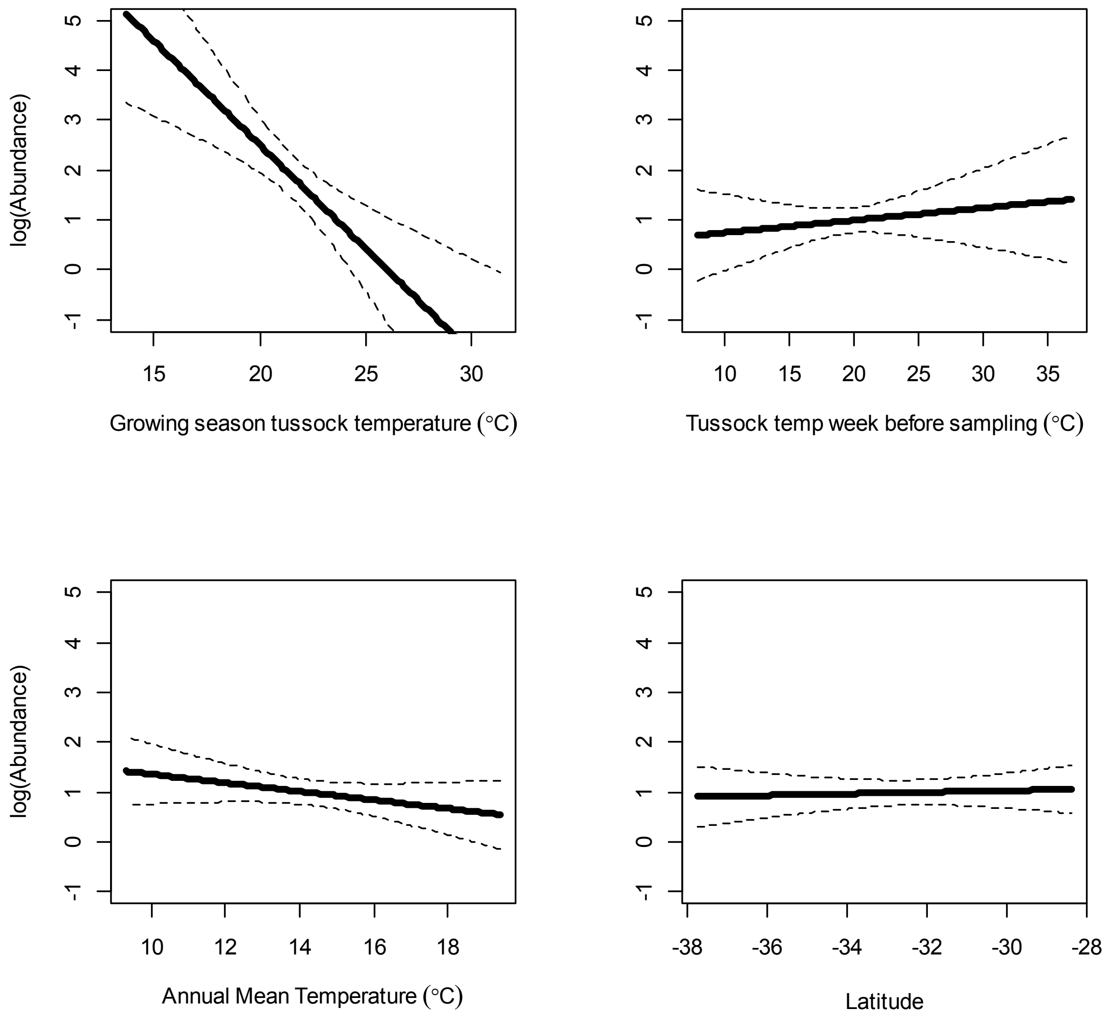

Figure 14: Predicted values (solid black line) of *Thrips imaginis* abundance as a response to significant explanatory variables. Dashed line is the prediction interval.

Anaphothrips incertus

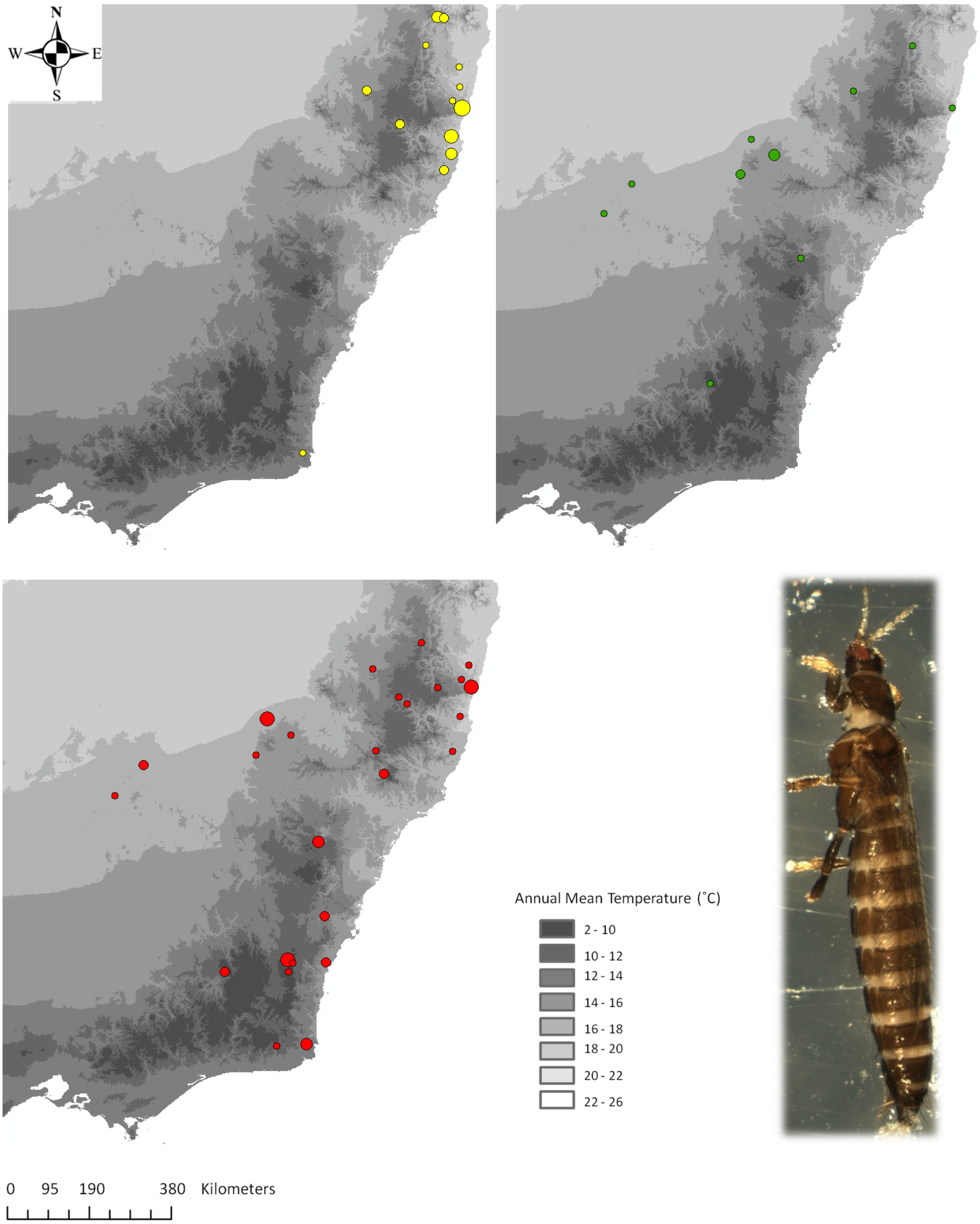

Figure 15: The change in total *Anaphothrips incertus* abundance between season 1 (summer, yellow circles), season 2 (autumn, green circles) and season 4 (autumn, red circles). There are five different circles sizes for each colour, representing abundances ranging from: 1-5, 6-10, 11-20, 21-50, 50+. Background shading shows mean annual temperature.

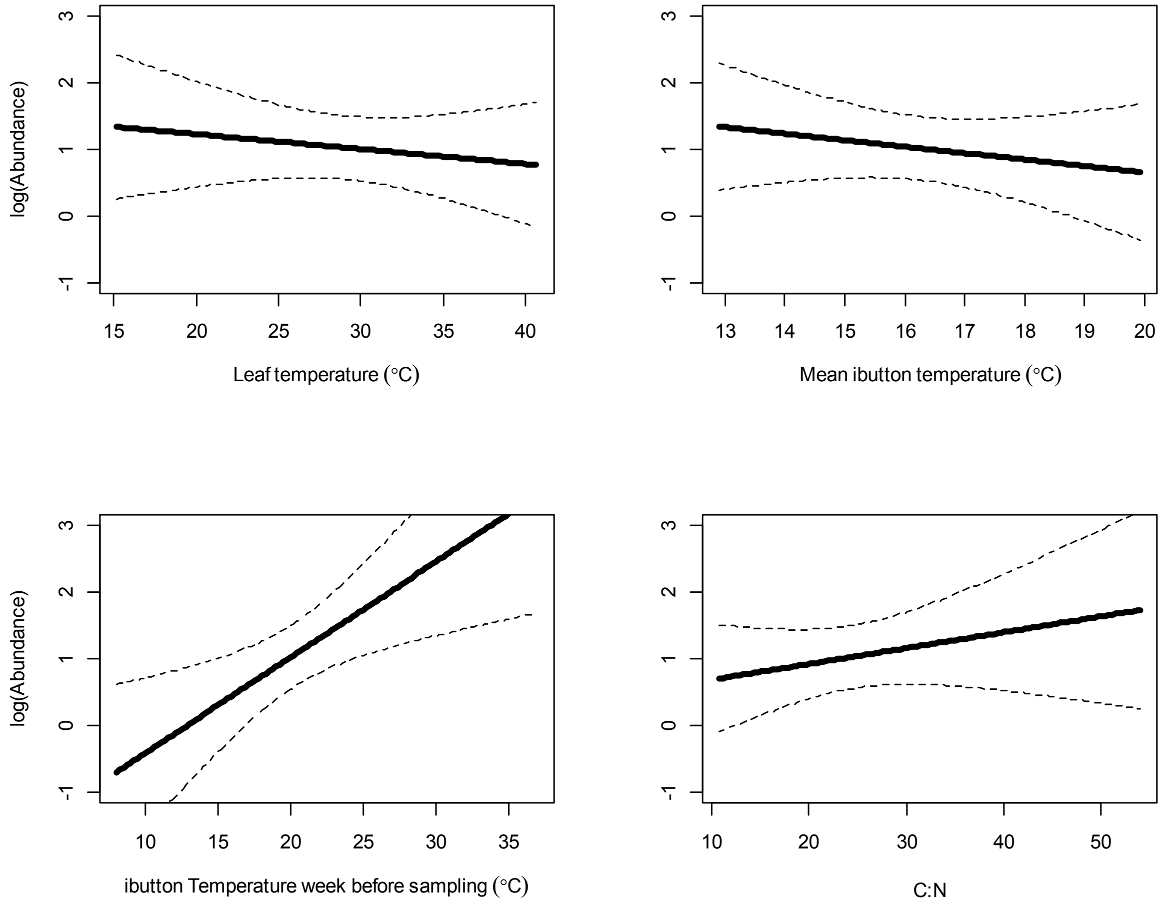

Figure 16: Predicted values (solid black line) of *Anaphothrips incertus* abundance as a response to significant explanatory variables. Dashed line is the prediction interval.

Anaphothrips sp. 2

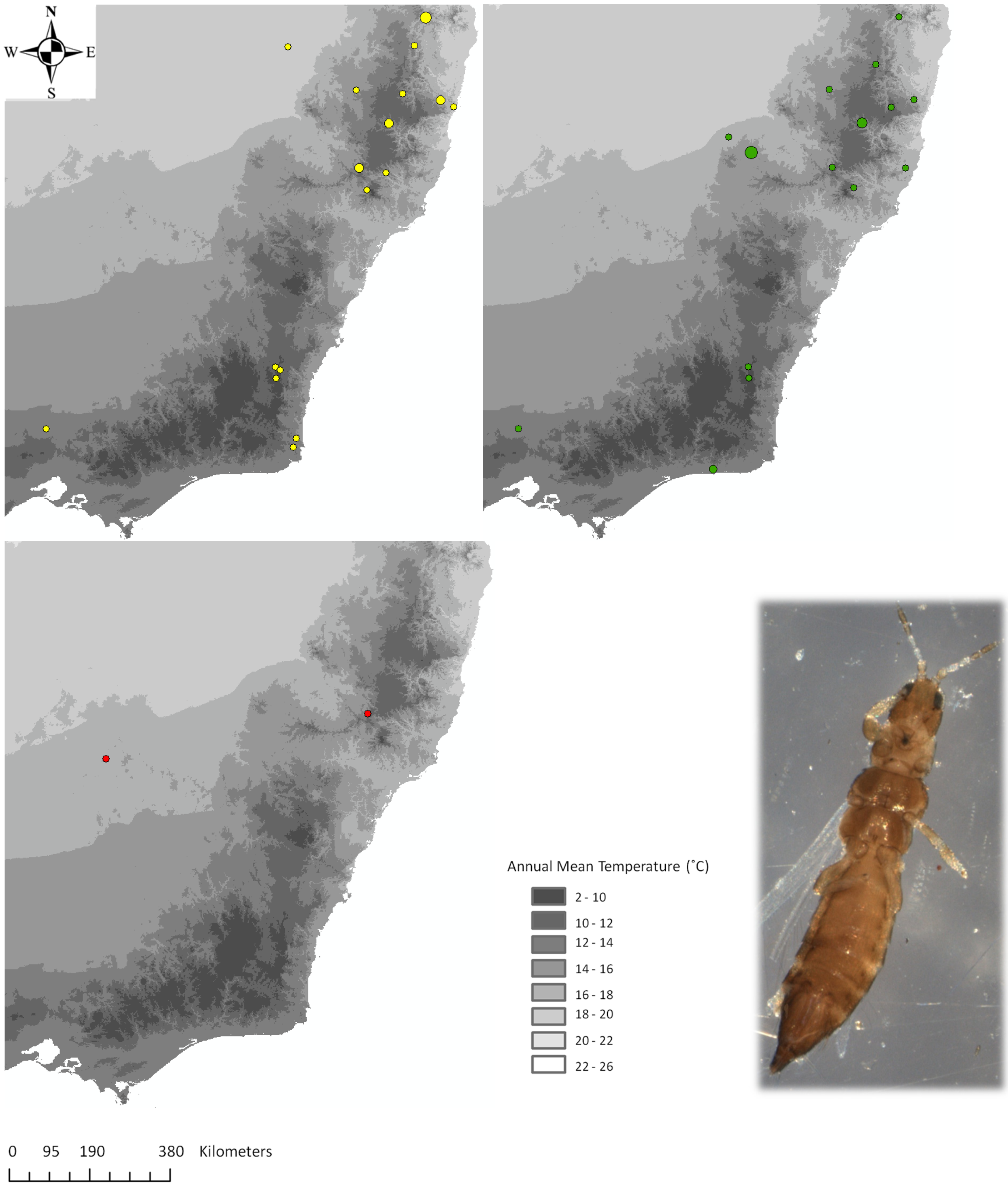

Figure 17: The change in total *Anaphothrips* species 2 abundance between season 1 (summer, yellow circles), season 2 (autumn, green circles) and season 4 (autumn, red circles). There are five different circles sizes for each colour, representing abundances ranging from: 1-5, 6-10, 11-20, 21-50, 50+. Background shading shows mean annual temperature.

Anaphothrips sp. 3

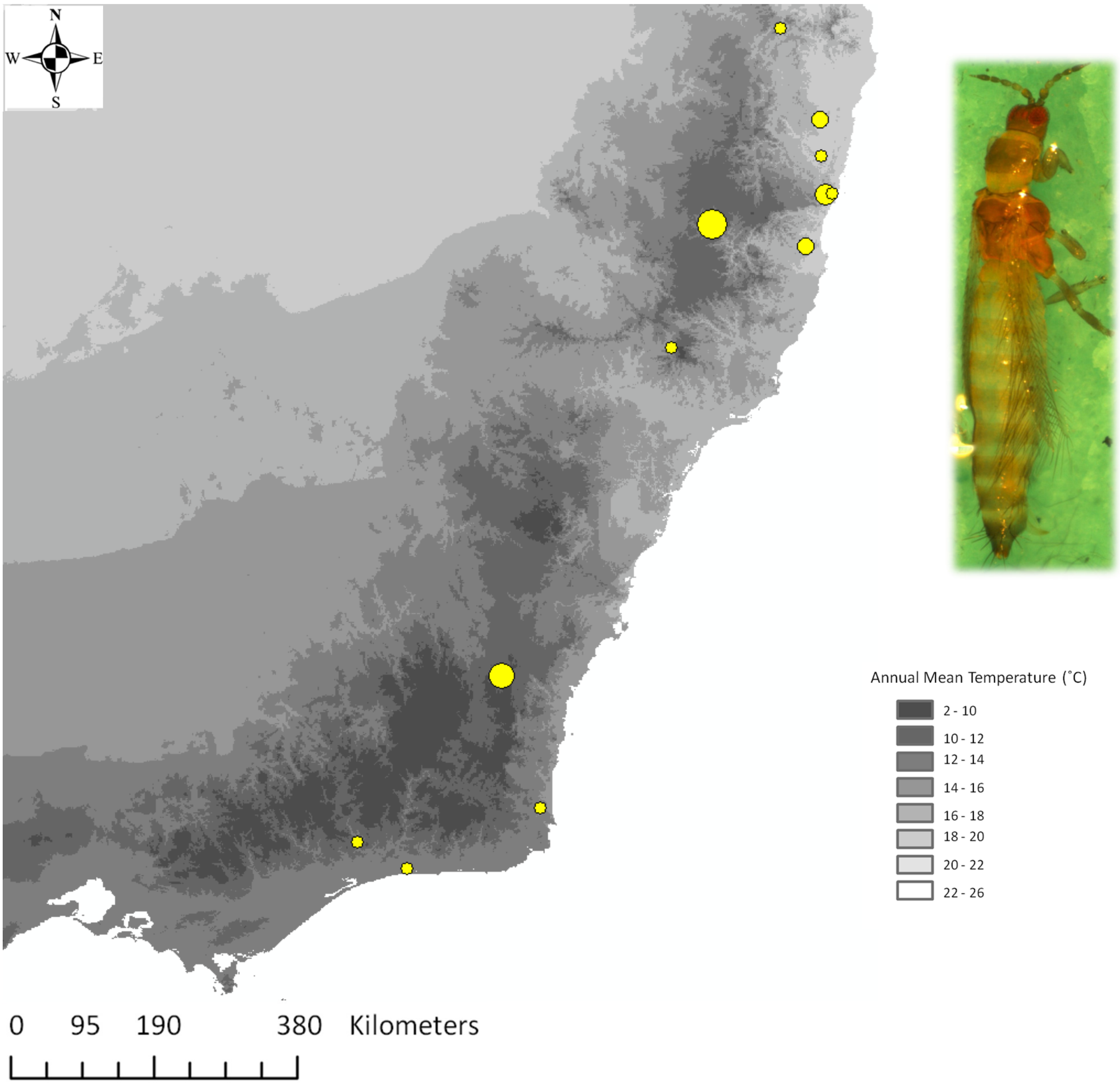

Figure 18: *Anaphothrips* sp 3 distribution map, the size of the yellow circles represents abundance across all seasons. There are five different circles sizes for each colour, representing abundances ranging from: 1-5, 6-10, 11-20, 21-50, 50+. Background shading shows mean annual temperature.

Chirothrips manicatus

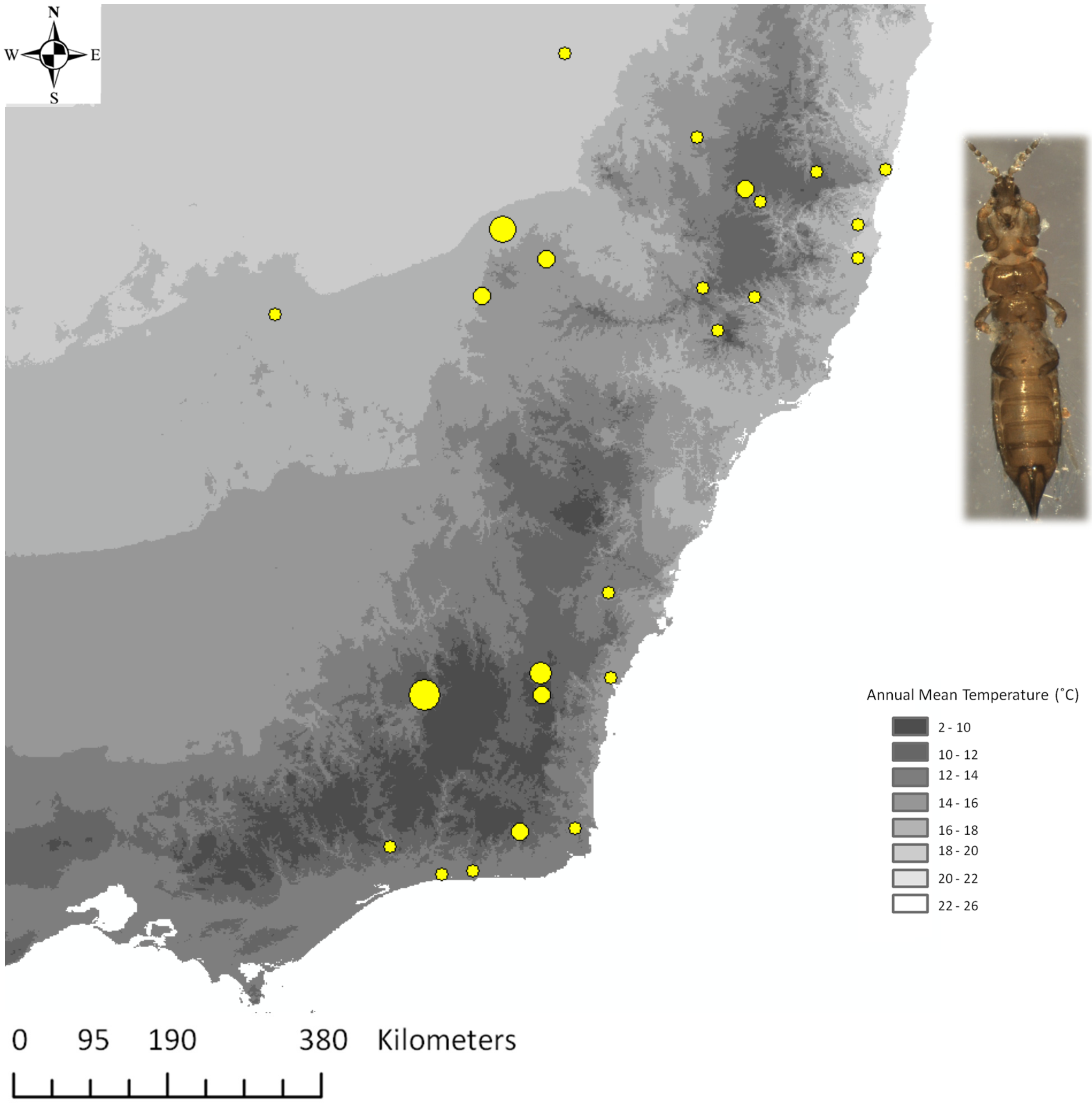

Figure 19: *Chirothrips manicatus* distribution map, the size of the yellow circles represents abundance across all seasons. There are five different circles sizes for each colour, representing abundances ranging from: 1-5, 6-10, 11-20, 21-50, 50+. Background shading shows mean annual temperature.

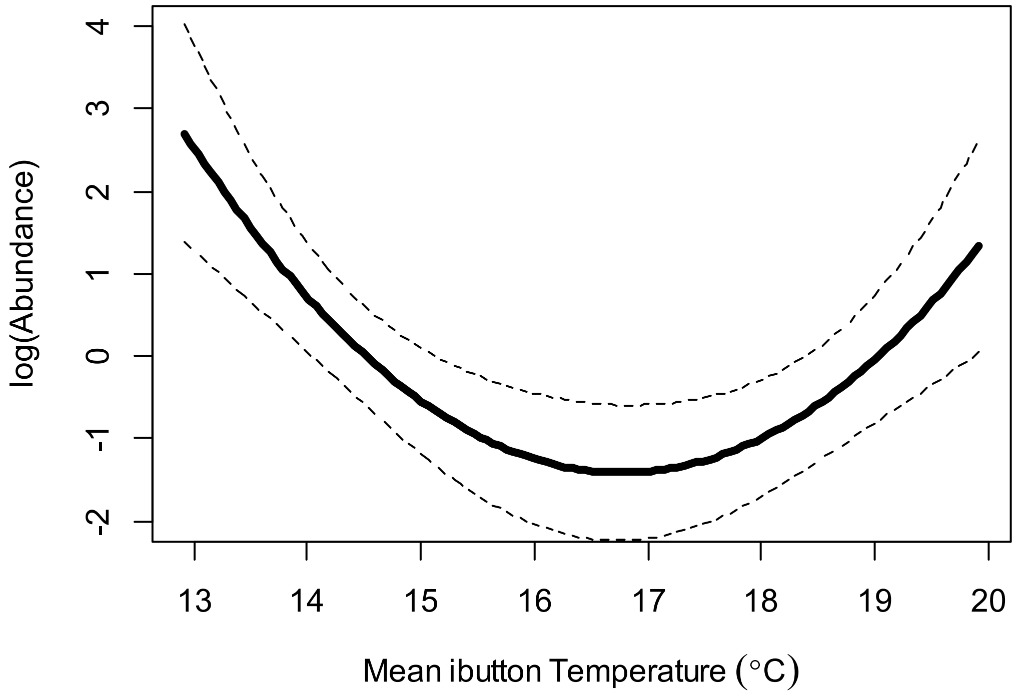

Figure 20: Predicted values (solid black line) of *Chirothrips manicatus* abundance as a response to significant explanatory variables. Dashed line is the prediction interval.

A.4.1. Allometry among Thysanoptera feeding guilds supplementary results

Head morphology

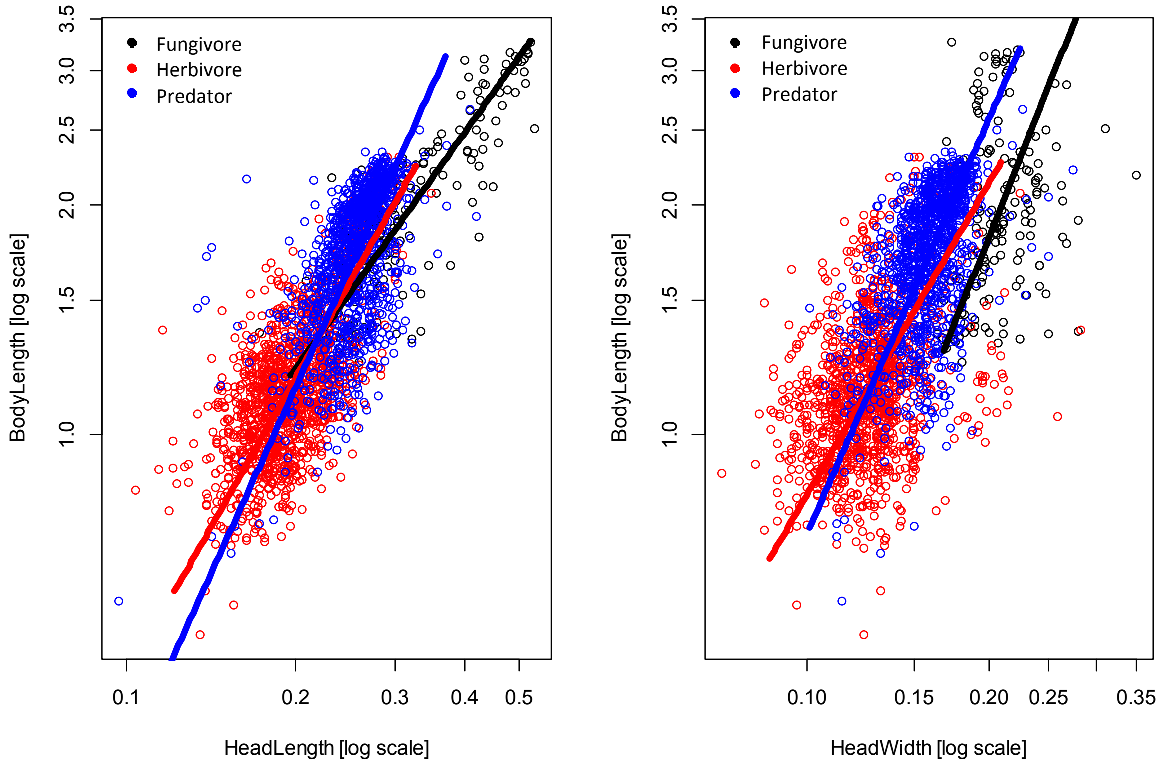

Figure 21: Morphological scaling of body length to head length (left) and body length to head width (right) for the three identified thysanoptera feeding groups.

Thysanoptera head size relative to body length is examined in (Figure 21). The scaling of head length to body length differed across all three feeding groups. Predators had the steepest slope (1.62) meaning as thrips get longer their head size became proportionately smaller. Herbivores had the second steepest slope (1.3) and fungivores had a slope of about 1, meaning their head length scaled almost linearly with body length.

The scaling of head width to body length was very similar between fungivores and predators (slope of about 2), meaning as the body got larger the heads got proportionally skinnier. The herbivore scaling was not as severe (slope: 1.36).

Sensory receptor morphology

The scaling of Thysanoptera body size to sensory morphology is shown in (Figure 22). The scaling slope of Herbivores and fungivores was the same at about 1.1. It is much steeper than predators (slope: 0.5) meaning the antennae of herbivores and fungivores becomes proportionately smaller as body size increases, and the antennae of predators becomes proportionately larger as body size increases. This is mainly due to the predators with very small antennae, overall all thrips had similar antennae length.

Fungivores had the steepest slope for eye separation to body size scaling (Figure 22), meaning eye separation was proportionately narrower in larger fungivores. Predators had the next steepest slope (1.17) and herbivores had an almost linear scaling (0.95).

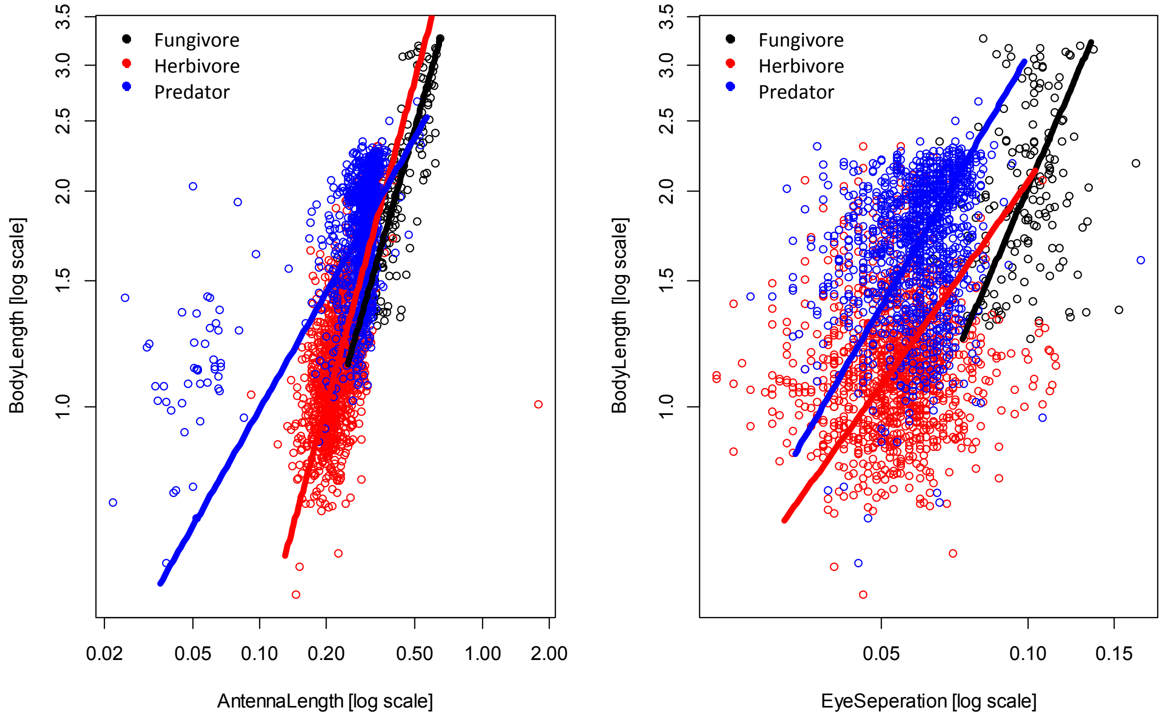

Figure 22: Morphological scaling of body length to antenna length (left) and body length to eye seperation (right) for the three identified thysanoptera feeding groups.

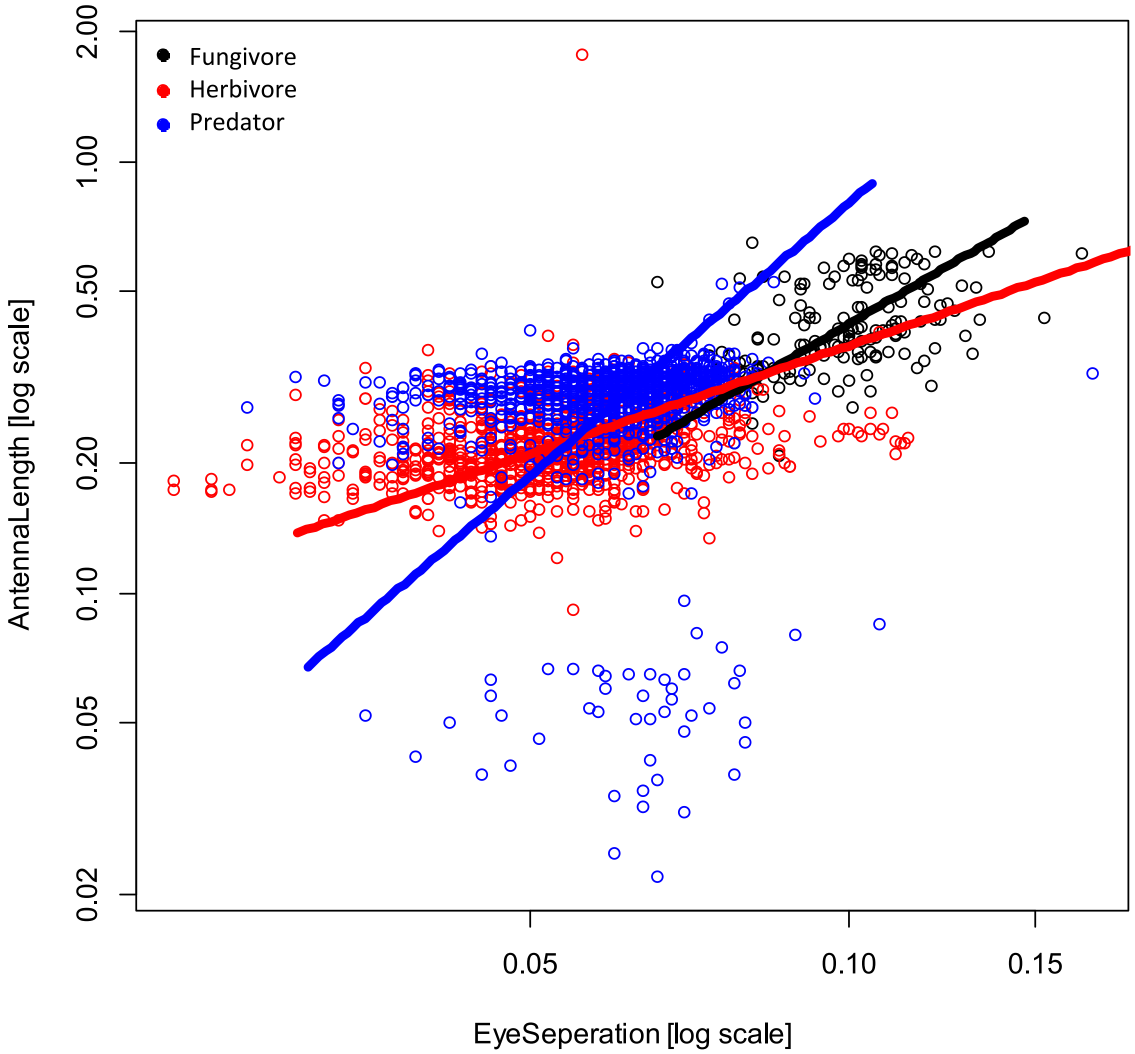

Figure 23: Morphological scaling of antenna length to eye seperation for the three identified thysanoptera feeding groups.

Antenna length to eye separation scaling is shown in Figure 23. Slope for all feeding groups are different. Predators have the steepest slope of 2.1, meaning eye separation remains proportionately narrow as antenna length increases and fungivores have a similar but less severe scaling (slope: 1.44). Herbivores have a slope of 0.83 meaning as eye separation increases, antenna length is proportionately shorter.

Leg Morphology

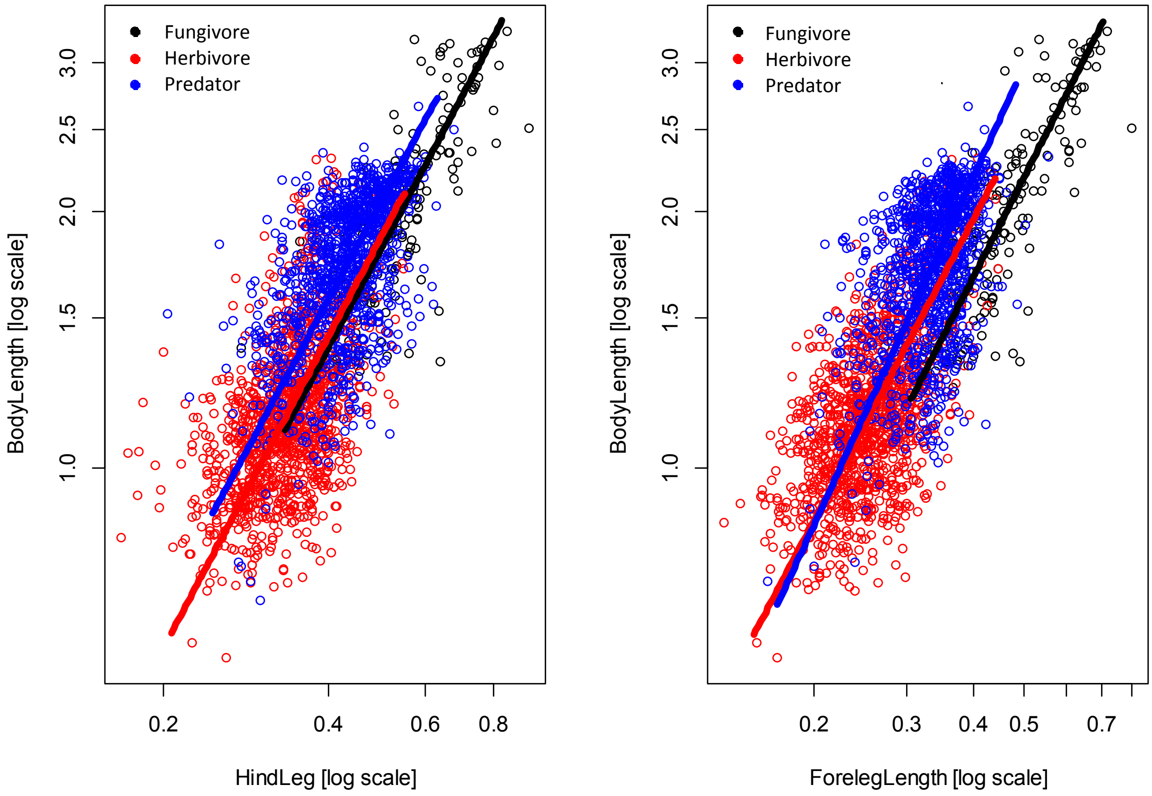

Figure 24: Morphological scaling of body length to hind leg length (left) and body length to foreleg length (right) for the three identified thysanoptera feeding groups.

Figure 24 shows leg scaling to body size in Thysanoptera. All feeding groups, including the wingless fungivores, had the same scaling of hind leg to body length of around 1.2, this means that as body size increases, hind leg gets proportionately smaller.

Fungivores and herbivores had similar foreleg to body size scaling (slope of about 1.2) and predators had a steeper slope of 1.36. This means predator foreleg length is proportionately smaller than herbivores and fungivores at larger body sizes.

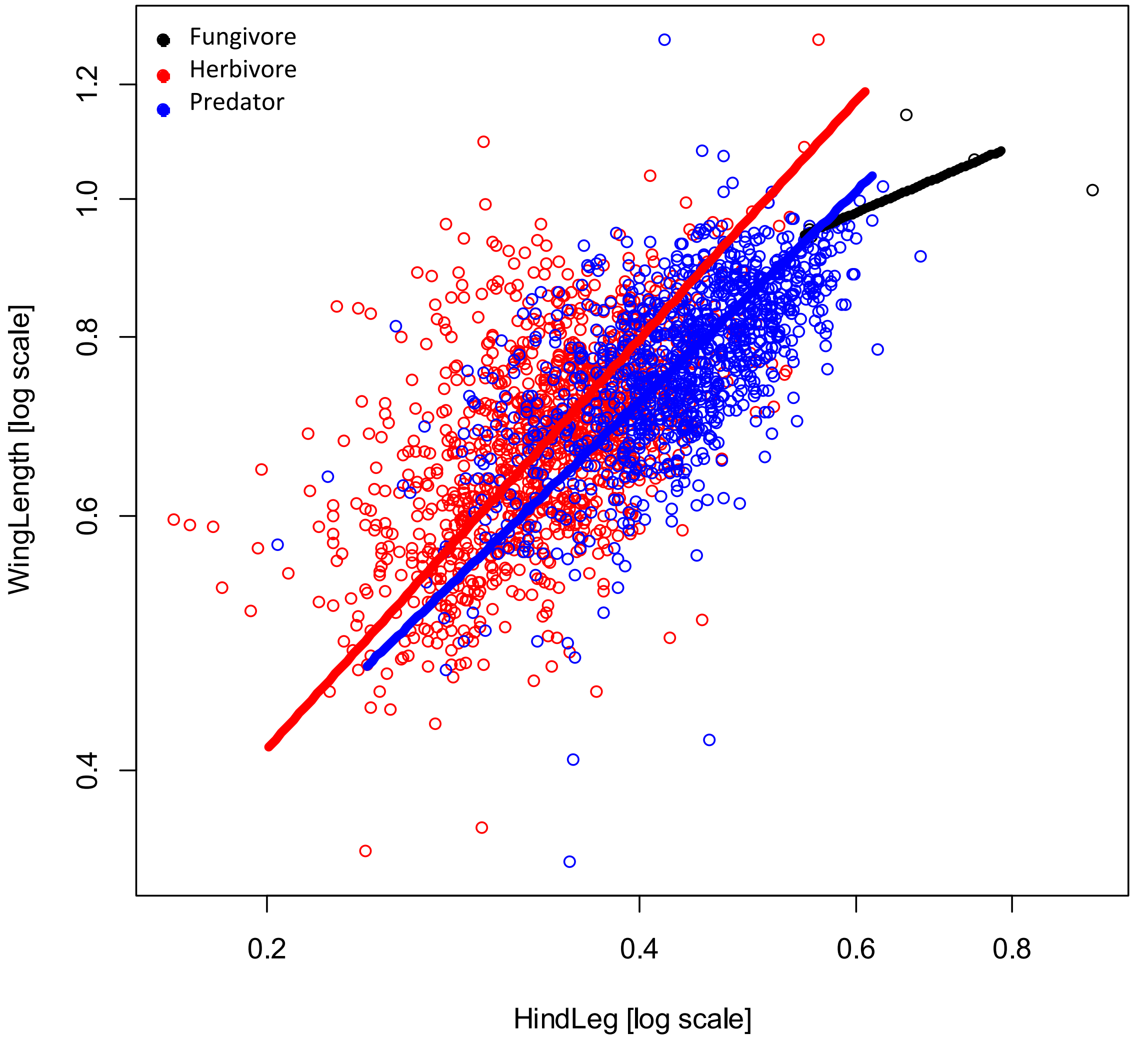

Figure 25: Morphological scaling of wing length to hind leg length for the three identified thysanoptera feeding groups.

Figure 25 again shows that fungivores are mostly wingless, but it also shows differences in wing length to hind leg length scaling in herbivores and predators. Herbivores have an almost linear scaling (slope: 0.95) and predators have a slope (0.83) that means predator wing length gets proportionately shorter as hind leg length increases.

A4.2. Allometry supplementary discussion

Sensory receptor morphology

The scaling of antenna with body size was skewed by the smaller predators found with very short antennae. Eye separation is often considered to be important for predators (Silva and Brandão 2010), although in *Themeda* dwelling thysanoptera eye separation range was similarly spread out among predators and herbivores, but mostly wide for fungivorous thrips (despite the narrower heads).

Leg Morphology

Leg scaling was similar across all groups. Predator wing length gets proportionately shorter as hind leg length increases. Thrips predators often chase ground dwelling prey or eat fairly immobile prey such as eggs (Mound 2005) so wing length would be an unnecessary use of resources when running is the optimal hunting mode.

A.5. Supplementary data for the chapter 4 transplant experiment

Table 2: Soil characteristics for each site

	Cool temperate	**Warm dry**	**Hot dry**
Total Nitrogen (%)	0.182	0.098	0.071
Total Carbon (%)	2.123	1.808	1.025
Available P (ug/g)	10.43	10.16	3.41
Available S (ug/g)	13.18	9.23	8.41
pH	5.62	6.51	7.59
K (cmol+/kg)	0.03	0.06	0.18
Mg (cmol+/kg)	0.95	1.37	7.19
Na (cmol+/kg)	3.73	4.05	6.08

A.6. References

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