Natural England Commissioned Report NECR135

Cereal invertebrates, extreme events and long-term trends in climate

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Foreword

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties.

Background

The effects of climate change on the natural environment have been the subject of many studies in recent decades. However, there has been little research to determine whether climate change is having an impact on invertebrate communities within arable dominated agricultural systems, and if they do, what factors (if any) may confer resilience on species populations.

This project was commissioned to investigate these issues and is one of a series of linked projects to develop the evidence base to inform climate change adaptation in the natural environment.

The results will be used by Natural England and others to inform the development and implementation of future agri-environment schemes and conservation practice. They will also be useful in developing large scale conservation initiatives, such as Nature Improvement Areas, especially within agricultural landscapes.

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Keywords - long-term monitoring, climate change, resilience, drought, pesticides, invertebrate populations, extremes

Further information
This report can be downloaded from the Natural England website: **www.naturalengland.org.uk**. For information on Natural England publications contact the Natural England Enquiry Service on 0845 600 3078 or e-mail **enquiries@naturalengland.org.uk**.

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Game & Wildlife
CONSERVATION TRUST

Cereal invertebrates, extreme events and long-term trends in climate

Final report

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Research need

The climate of the UK is changing (UKCP09) (Murphy et al. 2009), and the natural environment is responding to these changes. The effects of climate change on the natural environment have been the subject of many studies in recent decades and the impacts have recently been reviewed in the 'Climate Change Impacts Report Card for Terrestrial Biodiversity published by the Living with Environmental Change programme (Morecroft & Speakman 2013).

These impacts pose both threats and offer opportunities to conservation objectives. The national Climate Change Risk Assessment (Brown et al. 2012) provides an overview of the key risks to UK, including its natural environment and Natural England have reviewed the threats posed by climate change to its own objectives for the conservation of the natural environment (Natural England 2012).

In response to these threats various sets of principles have been developed to guide the adaptation of conservation strategies to climate change, both globally and within the UK. Heller and Zaveleta (2009) carried out a review of 113 papers which made recommendations about biodiversity conservation under climate change, published over a period of 22 years, from 1985 to 2007. Within the UK conservation community, the most widely quoted adaptation principles are those of Hopkins et al. (2007) produced for the UK Biodiversity Partnership and Smithers et al. (2008) produced for the England Biodiversity Strategy (EBS). These principles are based on robust ecological theory and evidence; however there is now a need to test their effectiveness in delivering increased resilience against climate change.

This is particularly important as the "perfect storm" (Beddington 2008) of population increase, increasing demand for food and climate change means that there is increasing pressure for space. Actions accordingly need to be prioritised, to maximise the impact and minimise the space required. Research is therefore required to determine habitat and landscape attributes that help promote adaptation in different circumstances and the most effective configuration of landscape attributes to deliver coherent and resilient ecological networks.

A number of common themes relating to ecological networks come out in many adaptation strategies (Heller and Zaveleta 2009) including increasing connectivity of habitat networks, buffering and enlarging patches of semi-natural habitats and protecting topographic and habitat heterogeneity. "The Making Space for Nature report" (Lawton et al 2010) also highlighted a series of principles for designing and managing ecological networks, ('bigger, better, more and joined) to ensure they are coherent and resilient in the face of environmental pressures including climate change. The effectiveness of the different elements of ecological networks, such as core protected areas and smaller patches of semi-natural habitat will be place and species specific; evidence is therefore needed to help identify they key attributes of network design for different situations, to enable prioritisation of actions.

Natural England has therefore initiated a series of linked research projects to develop the evidence base to inform climate change adaptation in the natural environment. This includes both work by our own staff and commissioning others to carry out targeted data analysis.

The main research projects in this area are as follows:

- Potential climate change refugia for wild species
- Risks and opportunities for species as a result of climate change
- Evaluation of the risks of favouring invasive species by increasing landscape connectivity
- The role of landscape and site scale characteristics in making species populations resilient to climate change and extreme events
- Costs, benefits and trade-offs in different approaches to establishing large conservation areas
- A spatially explicit model of climate change vulnerability of semi-natural habitats across England
- A review of climate change impacts on biodiversity in the UK (Climate Change Impact Report Card)
- Review of the Impacts of Drought on Biodiversity and Ecosystem Services
- Cereal invertebrates, extreme events and long-term trends in climate

Rationale for this project

Agricultural land occupies over 70% of England's land area; with arable land particularly cereal growing accounting for a large proportion. Invertebrate populations within arable systems provide key ecosystem services (Millennium Ecosystem Assessment 2005) such as pollination (Pimental et al 1997; Ricketts et al 2008), pest control (Altieri 1999, Gurr et al. 2003) and nutrient recycling (Losey & Vaughn 2006); represent a key link in the food chain supporting populations of farmland mammals (Hof & Bright 2010) and birds (Potts 1986, Brickle et al. 2000, Benton et al. 2002) and are of biodiversity interest in their own right (Pywell et al. 2004, Carvell et al. 2007).

Climate change will have diverse range of direct and indirect impacts on invertebrate populations (e.g. Robinet & Roques 2010; Thomson et al. 2010). For example the tolerance and responsiveness of different species, groups and guilds to direct climatic drivers such as temperature and drought will differ (Villapando et al. 2009). Population responses will also be mediated or moderated by trophic and tri-trophic interactions (e.g. Newman 2005, Robinet & Roques 2010) making changes to population size, community composition and ecosystem service provision difficult to predict.

In arable landscapes the management of the system have significant impacts on both the above and below ground biodiversity (Krebs et al. 1999, Tscharntke et al. 2005, Weibull et al 2003, Postma-Blaauw et al. 2010). It is therefore likely that the indirect impacts of changes to management as agriculture adapts to climate change, such as sowing date, cultivar and crop choice and changes to the control of pests and diseases are likely to be as important as direct impacts of climate change.

Direct impacts such as drought have been shown to have a negative impact on invertebrate abundance (Frampton et al 2000) under experimental conditions and the likelihood is that with the projected incremental changes to the climate and increased prevalence of extreme climatic events such impacts will increase.

Recent work focussed on semi-natural habitats has demonstrated how different elements of the landscape, such as the configuration and extent of semi-natural habitat can help moderate both the impact of climate change and the recovery from it in populations of butterflies (Oliver et al 2012). However there has been little research to determine whether climate change is having an impact on invertebrate communities within arable dominated agricultural systems, and if so what factors if any, may confer resilience on the system. This project was commissioned to investigate these issues.

Executive summary

A large part of the English countryside is covered by the cereal ecosystem that provides both human food resources and habitat for a specific suite of wildlife. Invertebrates play crucial roles in this ecosystem, ranging from pollinators and bio-control agents to food for mammals and birds. Little is known about potential impacts of climate change on many of these organisms, so this study examined the effect of past weather on a long-term dataset in a search for possible clues. Thus we examined changes through time in cereal invertebrate abundance in relation to trends in temperature and rainfall and also looked at the effects of extreme weather events on this abundance.

- The invertebrate data came from the GWCT's Sussex Study, a long-term project where invertebrates have been collected, identified and counted from 1970 to the present day on a wide area of farmland across the South Downs. (http://www.gwct.org.uk/research__surveys/wildlife_surveys_and_ngc/the_sussex_study/default.asp). We restricted ourselves to invertebrate groups that were widespread on the study area throughout the 41 years available to us, giving us 28 groups to work with.
- Weather was measured at local meteorological stations and summarised as average daily temperature from April to June and total monthly rainfall from April to June. Over the 41 years examined, the average daily temperature has increased, while there has been no long-term trend in rainfall. We identified four extreme cold/wet years (1972, 1986, 1991 and 1996) and six extreme hot/dry years (1976, 1984, 1989, 1995, 2007 and 2008).
- Annual abundance of 24 of the 28 invertebrate groups was related to annual average daily temperature or average monthly rainfall from April to June. In most cases abundance increased with temperature and declined with rainfall.
- Annual abundance of most invertebrate groups was negatively related to yearly intensity of pesticide use. Taking pesticide use together with weather, five invertebrate groups showed a significant negative relationship with pesticide use with no effect of weather, eight showed a significant relationship with temperature or rainfall but not pesticide use, and seven showed a significant relationship with pesticide use and at least one weather variable.
- Extreme weather events affected 11 of the 28 taxa examined. Average abundance increased in hot/dry years and decreased in cold/wet years for spiders, leaf-hoppers, adult bugs, thrips, braconid wasps, and mould beetles. The average abundance of plant-hoppers, rove beetle larvae, silken fungus beetles and fungus gnats increased in both hot/dry and cold/wet years relative to other years.
- The invertebrate groups that showed sensitivity to extreme weather events recovered quickly, on average in less than 1.5 years. This may reflect the ephemeral nature of the cereal ecosystem. Cereal crops are established, grow, senesce and are harvested within a year and invertebrates living in them must be able to respond to these changes quickly.
- At the field scale we found only one physical attribute of sampling location that influenced sensitivity to extreme weather events. For six invertebrate groups sensitivity to cold/wet events was reduced (translating into higher abundances) at locations with a westerly aspect. The other characteristics of sampling location that we examined (crop, land-cover, elevation, slope, patch density, field boundary density, and field size) did not significantly affect either sensitivity to or recovery from extreme weather events.

- We found no evidence to support the idea that locations with more extensive ecological networks have greater resilience to extreme weather events. Density of field boundaries (a potential indicator of connectivity of semi-natural habitat for some of these organisms in this arable environment) did not significantly relate to invertebrate sensitivity or resilience to extreme weather events. This is similar to other work on butterflies (Oliver et al. in press).
- Other researchers have found some mitigating effect of semi-natural habitat on the sensitivity of butterflies to drought and positive effects on their recovery after a drought when this semi-natural habitat was available as larger patches, but little effect of habitat on the sensitivity and recovery of birds following a drought event (Oliver et al. in press). Our results also show little evidence to suggest that resilience would be increased if the area of semi-natural habitat was higher.
- The long-term trends in some of the invertebrate abundances were related to trends in temperature and rainfall, indicating that climate change may be likely to affect them. However, the long-term increase in the intensification of cereal management, measured as the intensity of pesticide use, was as important in terms of explaining the long-term changes in abundance. For many of these species, minimising the effect of pesticide use may be the only realistic option to offset the impact of climate change.

Technical summary

1. In England, a third of land area is cropped and a fifth used to grow cereals (2.5 million hectares in 2010). A challenge for policy-makers is to maintain food production and environmental health in the face of climate change. Cereal fields are central to getting the balance right. Within them, invertebrates provide key ecosystem services such as pollination, nutrient recycling, wildlife food resources and the bio-control component of integrated pest management. This study investigated the sensitivity and resilience of cereal invertebrate species to extreme weather events, based on 41 years of monitoring data collected in Sussex by the Game & Wildlife Conservation Trust.

2. The Sussex Study database comprises over 100 invertebrate samples per year from 1970 to 2010, collected using a vacuum suction trap in the third week of June from cereal fields across 62 km^2 of the South Downs, Sussex. The samples are geo-referenced to digital maps of cropping, landscape and boundary features in each year and information on pesticides use is available from 1970 to 2005.

3. We selected 28 invertebrate groups based on frequency of occurrence (present in over 50% of fields annually) and statistical reliability (indices of change normally distributed). The taxa were: Araneae (spiders), Collembola (springtails), Aphididae (aphids), Cicadellidae (leaf-hoppers), Delphacidae (plant-hoppers), Heteroptera (bugs: all stages combined, adults and nymphs separately, ratio of adults to nymphs), Thysanoptera (thrips), Braconidae (braconid wasps), Chalcididae (chalcid wasps), Carabidae (ground beetles), *Tachyporus* (rove beetles: all stages combined, adults and larvae separately, ratio of adults to larvae), Lathridiidae (mould beetles: all combined, *Enicmus* only), Cryptophagidae (silken fungus beetles: all combined, *Atomaria* only), Cecidomyiidae (gall midges), Mycetophilidae (fungus gnats), Empididae (dance flies), Lonchopteridae (pointed-winged flies), Agromyzidae (leaf-miner flies), Opomyzidae (grass flies), and Drosophillidae (fruit flies).

4. Weather was described using average monthly temperature and total monthly rainfall in April, May and June of each year. No single station provided a full time series, so one was created using gridded climate data (in 5 X 5 km grids across the study area, 1970 to 2006) and data from two weather stations (Bognor Regis 1970 to 2010 and Herstmonceux 1977 to 2010), calibrated using the overlap period. Years with extreme weather events were defined as ones where the value of any weather variable lay in the extreme 5% of the yearly weather values for that variable. This identified four extreme cold/wet years (1972, 1986, 1991 and 1996) and six extreme hot/dry years (1976, 1984, 1989, 1995, 2007 and 2008).

5. All years covered by the study were grouped into three categories: hot/dry years, cold/wet years and non-extreme years. Sensitivity to extreme weather events was defined as when the average annual change in abundance differed significantly between the three groups, and was identified in 11 of the 28 taxa. Average abundance increased in hot/dry years and decreased in cold/wet years for Araneae, Cicadellidae, adult Heteroptera, Thysanoptera, Braconidae, *Enicmus* and Lathridiidae. For Delphacidae, *Tachyporus* larvae, Cryptophagidae and Mycetophilidae, average abundance increased in both hot/dry and cold/wet years relative to other years.

6. For sensitive invertebrate groups, recovery time was measured as the time taken for the average annual abundance to return to the long-term trend after an extreme weather event. It was longer

than a year for only four groups: Thysanoptera, Mycetophilidae, *Tachyporus* larvae and Cryptophagidae. The remaining seven sensitive groups reverted to the long-term trend within a year.

7. We examined the effect of land-cover, elevation, aspect, slope and pesticide use on the rate of recovery of sensitive invertebrate groups at the field scale. Only aspect had a significant effect across multiple groups, with Araneae, Cicadellidae, Thysanoptera, *Tachyporus* larvae, Cryptophagidae and Mycetophilidae showing greater resilience to cold/wet years when situated on west-facing slopes than on other slopes. This may reflect site-specific microclimate leading to warmer or drier conditions associated with warm westerly winds.

8. Annual abundance of 24 of the 28 invertebrate groups was correlated with annual average daily temperature or average monthly rainfall from April to June. In most cases abundance increased with temperature and dropped with rainfall.

9. We used spectral analysis to examine the relationship between long-term trends in weather metrics and long-term trends in invertebrate abundance. Spectral density analysis determined whether a time series had significant periodicities. Coherence and phase analysis compared two time series to identify any matching periodicities (coherence) and any lag effect (phase).

10. Average daily temperature from April to June had significant periodicity at long time periods (30-100 years) indicating that a long-term increase dominated this time series. Total rainfall from April to June showed 2-year periodicity with no long-term change. Fourteen invertebrate groups had significant periodicity at long time periods (Collembola, Heteroptera adults, Heteroptera nymphs, Heteroptera adult-nymph ratio, Braconidae, Chalcididae, Carabidae, *Tachyporus* adults, *Enicmus*, Lathridiidae, *Atomaria*, Cryptophagidae, Empididae, Opomyzidae). Two invertebrate taxa (Thysanoptera, Mycetophilidae) showed periodicity at medium time scales of 5 - 10 years and three taxa (Braconidae, Opomyzidae and Drosophillidae) showed short-term periodicity (2 - 3 years).

11. Sixteen groups showed significant coherence with temperature (Aphididae, Heteroptera, Heteroptera adults, Heteroptera nymphs, Thysanoptera, Braconidae, Chalcididae, Carabidae, *Tachyporus* adult, *Tachyporus* adult-larvae ratio, Lathridiidae, *Atomaria*, Cryptophagidae, Empididae, Opomyzidae and Drosophillidae), and nine with rainfall (Collembola, Delphacidae, Heteroptera adult-nymph ratio, Thysanoptera, *Tachyporus*, *Tachyporus* larvae, *Atomaria*, Lonchopteridae, Drosophilidae). The majority of significant coherences with temperature were long-term ones (10-100 years), or short-term (2-3 years). The majority of significant coherences with rainfall occurred at time frames of 5-7 years.

12. Annual abundance of most invertebrate groups was negatively correlated with yearly intensity of pesticide use. Taking pesticide use together with weather, five invertebrate groups showed a significant relationship with pesticide use but not with weather, eight showed a significant relationship with temperature or rainfall but not pesticide use, and seven showed a significant relationship with pesticide use and at least one weather variable.

13. In conclusion, amongst the 28 invertebrate groups examined, eleven proved sensitive to extreme weather events but showed a very quick recovery, usually within a year after the extreme event. This may reflect adaptations to the ephemeral nature of the cereal ecosystem, with its annual cropping rotation. The long-term trends in some of the invertebrate abundances were

related to trends in temperature and rainfall, indicating that climate change may be likely to affect them. However, the long-term increase in the intensification of cereal management, measured as the intensity of pesticide use, was perhaps more important in terms of explaining the long-term changes in abundance.

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Introduction

Global climate change is widely accepted as occurring (IPCC 2007), with a wide range of models predicting increased mean annual temperatures and changes in patterns of precipitation across Europe during the next 50 years (Bernstein et al. 2007; Murphy et al. 2009). In addition to shifts in mean values for a range of climate variables many models predict changes to patterns of weather events (Tank & Können 2003). This includes both increased frequency of extreme weather events (Mearns, Katz, & Schneider 1984; Easterling & Evans 2000; Peterson et al. 2012), as well as increased magnitude in the weather extremes experienced (Meehl et al. 2000).

There is a growing body of evidence demonstrating the ecological impacts of recent global climate change, across a range of biomes and from species to ecosystem levels (Walther et al. 2002; Parmesan & Yohe 2003; Rosenzweig et al. 2007; Mossman, Franco & Dolman, 2013; Morecroft & Speakman, 2013).The potential predicted impacts range from minor range shifts and changes in community assemblages (Walther et al. 2002) to extremes such as greatly increased extinction risks (Thomas et al. 2004). The effects of global climate change are well studied for a wide range of species, across invertebrates, animals and plants (Parmesan 2006). Much of the body of research focuses on the expansion or contraction of species ranges (Mair et al. 2012), increased risks from invasive species (Robinet & Roques 2010) and population changes of known pest species (Cannon 1998; Mossman, Franco & Dolman, 2013). There is relatively little work focusing on the impacts of climate change on species within areas of their natural range that are unlikely to change, so potential effects on populations in these areas remain poorly understood (Dormann et al. 2008; Forister et al. 2010).

Many of these studies also focus primarily on the impact of shifting means of climate variables and less focus is paid to the effect of increasing frequency of extreme weather events (Jentsch, Kreyling, & Beierkuhnlein 2007). The potential impacts of extreme disturbance events, such as extreme weather conditions, on an ecosystem can range from direct mortality to changes in population dynamics as systems are pushed beyond equilibrium (Scheffer & Carpenter 2003). As many climate models predict an increase in the number of extreme weather events per year in the future, understanding how vulnerable sensitive species are to extreme weather events could prove to be extremely important when developing models, as well as when planning and targeting conservation measures (Parmesan, Root, & Willig 2000). The resilience shown by species in response to extreme weather events is also an important area of study, as this coupled with estimates of sensitivity will help to identify species that are particularly vulnerable to the increases in the occurrence of extreme weather events. There is a need for further research to identify the sensitivity to climate change for invertebrate taxa and measure any potential factors conferring resilience to these changes. Developing a greater understanding of these factors will help to guide policy and conservation actions, helping to bridge the gap between ecological theory and practical land management (Morecroft et al. 2012).

There has been some work focusing on the influence of extreme weather events on invertebrate populations, both through experimental and observational studies. Summer droughts have been identified as a type of extreme weather event capable of causing a range of changes to butterflies, moth and carabid beetle communities (Morecroft et al. 2002). Morecroft et al. demonstrated a range of negative impacts on various taxa, particularly invertebrate species with limited mobility or poor dispersal capabilities. The study also suggested that the impacts on ecosystems from ‘one-off’ extreme weather events like droughts are readily reversed, though should the frequency of such events, increase population recovery may be limited. The effects of a drought on British farmland invertebrates, specifically arthropod species, has also been tested experimentally (Frampton, Brink, & Gould 2001), with results indicating a decline in the population of the studied arthropod species as a result of the simulated drought.

Extreme weather events can impact upon invertebrate populations as a result of direct responses in invertebrate physiology or life history strategies, or through indirect means such as changing land management practices in response to extreme weather events. Short-term exposure to high temperature (~32 °C) can be detrimental to many insect species (Zhou et al. 2011). The effects of short-term heat shock can range from reduced fecundity, reduced survival or shorter developmental cycles through to mortality of individual invertebrates. The effects of heat shock, although less severe, can still be seen at temperatures lower than 32 °C and this could begin to impact upon invertebrate populations in Northern Europe if extreme high temperature events increase as projected. It has been suggested that the effects of heat shock may potentially be mitigated by heat acclimatisation due to shifting temperature means, which may be the case under projected climate change scenarios (Barua & Heckathorn 2004). Any such adaptive response may develop too slowly to protect against extreme temperature events in the short term. Although it may seem logical that increasing mean temperatures may prove to be beneficial for many populations of invertebrates owing to their exothermic nature, there is a body of evidence highlighting potentially detrimental effects on invertebrate populations of exceeding their optimal temperature range or suffering the effects of desiccation as compared to their normal range (Harrington, Woiwod, & Sparks 1999; Bale et al. 2002).

Under increasing temperatures, increases in populations of multivoltine species relative to univoltine species has been shown in a range of invertebrates, particularly moths and butterflies (Altermatt 2010). The number of generations per year produced by insect species is strongly dependent on local climatic conditions, with warmer temperatures allowing for extra generations to be produced in a single season. This could be as a result of a longer flight periods under climate warming, as demonstrated for a range of butterfly species (Roy & Sparks 2000), with similar trends expected across other taxa. Extreme weather events have also been associated with other changes directly impacting on invertebrates, including early emergence (Thomas, Singer, & Boughton 1996) and changes to host plant phenology (Ibáñez et al. 2010). Changes to invertebrate emergence dates can have detrimental effects on communities for example, if predators become asynchronous with the emergence of an important prey species, prey species emerge prior to their predators leading to predatory release or if the timing of emergence leads to interactions with predators, competitors or parasites not previously encountered on a frequent basis (Cannon 1998). Changes in timing of flowering and fruiting events have been identified (Menzel et al. 2006), which can lead to invertebrate species becoming asynchronous with host plants (Chuine 2010; Miller-Rushing et al. 2010). Slower plant growth rates may also mean they become unsuitable for supporting invertebrate development (Bale et al. 2002). These changes could be particularly relevant to a farmland ecosystem, as populations of important pollinator species may be those most affected.

Aside from the direct effects of changes in climate and weather patterns on invertebrate species, indirect effects that arise as a result of changes in agricultural practice in response to climate change have the potential to drastically influence invertebrate populations. A large body of scientific evidence exists demonstrating the impact of agricultural intensification on arable ecosystems, leading to declines in farmland birds and invertebrates, as well as changes in the composition of arable flora communities (Potts 1986; Chamberlain et al. 2000; Benton et al. 2002; Boatman et al. 2004; Donald et al. 2006; Potts, Ewald, & Aebischer 2010). As global food demand increases and ensuring food security becomes ever more difficult (Schmidhuber & Tubiello 2007; Chakraborty & Newton 2011), the challenges faced to maintain agricultural productivity may result in far-reaching consequences for many farmland ecosystems across Europe (Stoate et al. 2009; Olesen et al. 2011). The challenge to meet rising food and energy demands, whilst mitigating the impacts of climate change, may create a 'perfect storm' scenario (Beddington 2009); with potentially far-reaching ecological consequences. Evidence already exists that indicates changes in temperature and rainfall affect invertebrate abundance in an agricultural situation (Newman 2005; Musolin 2007; Stige et al. 2007; Villalpando, Williams, & Norby 2009; Robinet & Roques 2010). Climate change may also induce changes in agricultural management, which could lead to still greater intensification, changes in sowing date, choice of cultivar and ultimately the crop sown (Rosenzweig et al. 2007; Thomson, Macfadyen, & Hoffmann 2010; Olesen et al 2012).

In Northern Europe, climate change is expected to result in an increased length of growing season for cereal crops (Olesen & Bindi 2002; EEA 2012), which has been linked with a potential increase in outbreaks of invertebrate pest species and crop disease (Roos et al. 2010) leading to increases in pesticide applications to maintain cereal yields. Increasing pesticide applications will likely lead to declines in many invertebrate populations, as well as the associated impacts on higher trophic levels that use invertebrates as a food source, for instance birds and bats. Weed (arable flora) communities within arable fields have been identified as an important factor in maintaining biodiversity in an arable system and supporting invertebrate populations (Sotherton 1991; Marshall et al. 2003). Increasing herbicide applications may, therefore, lead to the removal of an important habitat used by invertebrate species and increase their sensitivity to extreme weather events. Restricting the use of herbicides at arable field edges has been demonstrated to have a positive influence on invertebrate numbers across a range of studies (Sotherton 1991; Frampton & Dorne 2007). The habitat surrounding arable fields affects the resilience of carabid beetle populations to pesticide applications (Lee, Menalled, & Landis 2001), with populations with suitable refuge habitat recovering more rapidly following insecticide application. Climate change has also been linked to potentially increasing application of pesticides, as ranges of pest species shift to areas outside the range of their natural enemies (Thomson, Macfadyen & Hoffmann 2010) , suggesting that increased frequency of extreme temperature events could lead to changes in management practices that could have serious consequences for non-target invertebrate species.

Understanding the ecological effects of the relationship between changing climate and agriculture practices is an area that has received little attention in the scientific literature but could prove to be one of the most influential factors for ecosystems across the globe. It is difficult to distinguish specific management practices from wider-scale land-use changes (Robinson & Sutherland 2002), as they often occur over the same time period, which makes the task of pinpointing exactly which management is harmful to farmland biodiversity difficult. Recently, attempts have been made to identify the role of individual management factors and landscape factor changes typically associated with agricultural intensification in driving biodiversity change in farmland ecosystems (Geiger et al. 2010). Although Geiger et al. (2010) included an invertebrate component in their biodiversity measure this formed only a small part of the analysis. With the wide array of invertebrate taxa that exist within arable ecosystems highly likely to show differing responses under climate change scenarios, a more focused approach is required to identify the specific factors important for different invertebrate taxa.

Landscape factors such as elevation, aspect and slope may play an important role in creating cooler microclimates (Bennie et al. 2008), with sites with these microclimates potentially acting as refugia for a range of taxa, both invertebrate and plants, against the effects of climate change (Ashcroft, Chisholm, & French 2009; Oliver et al. 2010; Oliver et al. in press).

In order fully to understand the effects of climate change on invertebrate species, the analysis of long-term data is required. Relatively few published studies examine a long-term (> 30 years) dataset, and many of those that do pool data from multiple sites to increase the time span of the available data (but see Oliver et al. 2013 for information on butterflies and birds). The Sussex Study dataset used in this study provides a continuous 40-year time series collected at a single landscape-scale study site for a wide range of invertebrate taxa. Data collected on management practices, including cropping, pesticide use and conservation options, on a field-by-field basis allow us to examine how different management practices may influence the response of invertebrate species to increased frequency of extreme weather events under a climate-change scenario, with the results of this project helping to guide policy makers in the design of mitigation measures on farmland, assisting the cereal ecosystem to adapt to a changing climate (Benton et al. 2002; Newton 2004; Ewald et al. 2010).

Natural England is trying to establish what evidence exists, based on the scientific literature and the analysis of data that have already been collected, for climate effects on invertebrates within an agricultural system. If evidence is found to suggest that there is an effect, then Natural England would like to determine if there is any habitat-based or agricultural management technique (pesticide use, cropping patterns) which may mitigate the damaging effects of climate. Climate effects, in this case, could be measured as either correlations between trends in invertebrate abundance and trends in measured aspects of weather or relationships between invertebrate abundance and extreme weather events. It is also possible to determine the resilience of invertebrate abundance to extreme events other than identifiable weather-related effects, by identifying significant short-term changes in long-term trends in abundance (i.e. sensitivity to some unmeasured effect) and then examining the abundance trends following this event in order to the time to recovery (for definitions of resilience, sensitivity and recovery time see Box 1). Specifically we have used the Sussex Study invertebrate dataset to answer two questions:

1. Do the overall trends in the annual abundance of invertebrate families in cereals over forty years correlate with weather?

2. Are major changes in the annual abundance of invertebrates families in cereals associated with extreme climatic factors such as droughts?

These two questions were used to determine the sensitivity of individual invertebrate taxa to climate. We then determined if there are habitat and management characteristics that predict greater resilience in the invertebrate taxa identified as sensitive to extreme weather events on a field by field basis. For all sensitive taxa identified a series of regression models were used to test for relationships between recovery time at the field scale and landscape diversity configuration variables held within the Sussex study GIS database (Figure 1) such as cropping (Figure 2), pesticide use (Figure 3), boundaries – area, interconnectedness, surrounding semi-natural habitat – area, patches interconnectedness, agri-environmental options, field shape, altitude and aspect.

Box 1. Definitions as per Oliver et al. 2013

Resilience: The amount of disturbance a system can absorb and still remain in the same state or domain of attraction (Holling, 1973); or, alternatively, the ability of a system to return to a pre-disturbed state (Pimm, 1984).

Sensitivity: the extent of perturbation of species populations from a long term trajectory after an extreme climatic event (for example, a drought year, an exceptionally cold winter etc.)

Recovery time: the rate of recovery of species populations after an extreme climatic event

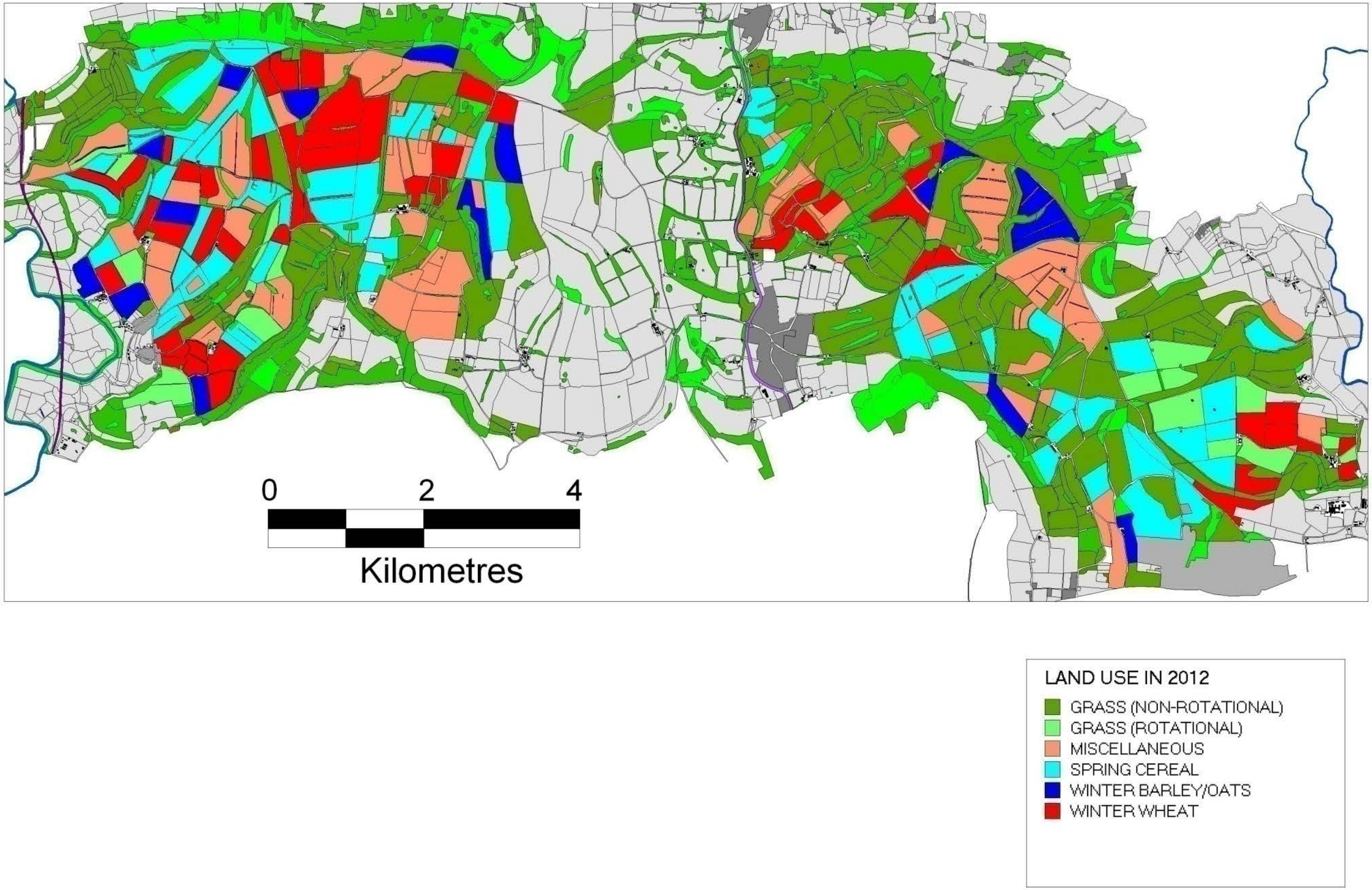

Figure 1. Cropping on the Sussex Study area in 2012. Information exists on cropping, as well as field boundaries and surrounding semi-natural habitat, from 1970 to 2012, within the Sussex Study GIS database.

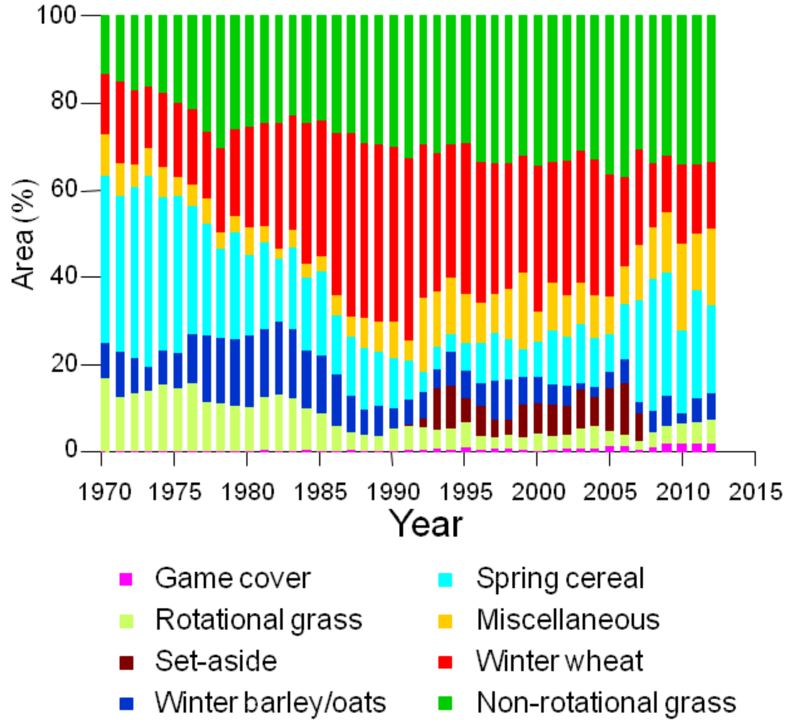

Figure 2. Changes in cropping through time on the Sussex Study area. Game cover includes wild bird cover crops. The main difference in cereal farming has been the increase in winter wheat from the 1980s through to 2005, with a recent increase in spring cereals, with a decline in winter wheat farming. Set-aside was an important component of the area until it was lost in 2008 and there was an early shift from rotational grass to non-rotational grass in the mid to late 1980s coinciding with the Environmentally Sensitive Area scheme.

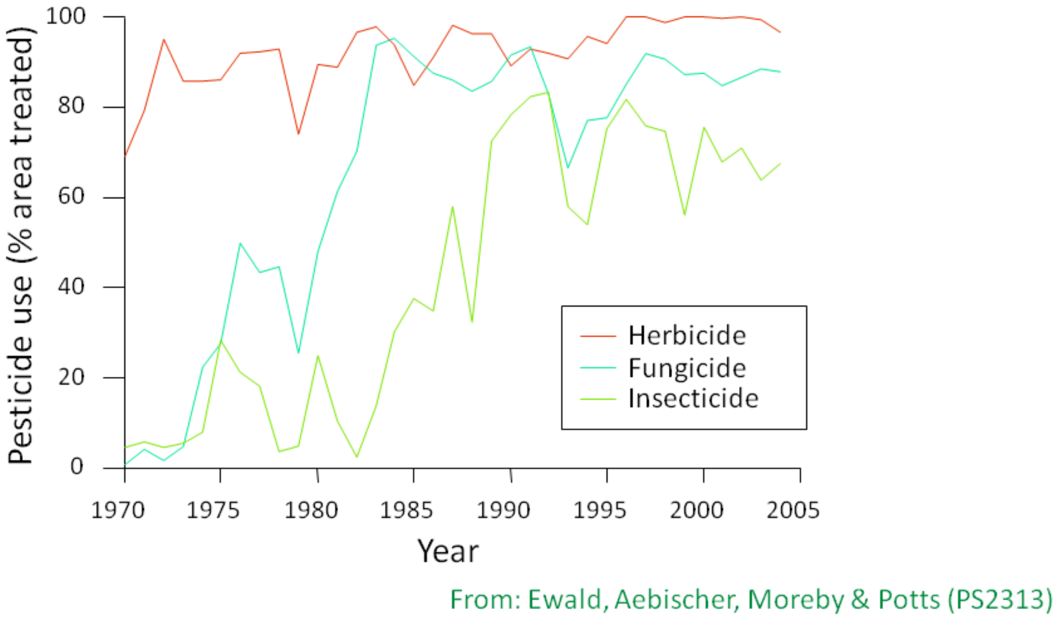

Figure 3. Trends in pesticide use (% area treated). Herbicide use was common at the beginning of the study, with fungicide and insecticide use increasing in the late 1970s and late 1980s respectively. Use has stabilised recently, with 100% of crops treated with herbicides, nearly 90% treated with fungicides and two thirds with insecticides.

Materials and methods

Data collation

Invertebrates

The Sussex Study dataset contains information on the abundance of cereal invertebrates from 1970 to 2011, sampled in mid-June using a Dietrick vacuum suction trap (D-Vac, Dietrick 1961). Although there are over 500 individual taxa (from species to Class) recorded in the dataset, most analysis undertaken on this dataset has been restricted to the long-term trends at the genus, family and class level to ensure identification consistency over time. This results in 74 taxa that were considered for analysis. Time allowed for the analysis of approximately twenty taxa.

We used two methods to ensure that the taxa selected gave us the greatest possibility of finding out if extreme weather events had an effect on changes in invertebrate abundance. Firstly we restricted the analysis to those taxa that occurred, on average over the 42 years of data (or the total number of years where these taxa were identified), in an average of 50% of the fields that were sampled (Figure 4). Secondly, as we would calculate changes in invertebrate abundance from annual indices we only included taxa where these changes in indices were distributed normally and did not suffer significantly from kurtosis or skewness. In order to obtain these annual indices, the invertebrate data were analysed using a generalised linear model with a Poisson error distribution and logarithmic link function, with field and year as factors. Fields with only one year's data were omitted. For most invertebrate taxa, the data spanned the period from 1970 to 2011, but for several taxa the start year had to be moved forward to 1971 or 1972. The year coefficients were exponentiated to give an index of invertebrate abundance on the arithmetic scale. All index values were relative to the start year, which had a value of 1. Once these indices had been calculated the difference between successive years was computed and the distribution of these differences was compared to a normal distribution (Shapiro-Wilk test, W statistic) and values of kurtosis (a measure of whether the data are peaked or flat relative to a normal distribution, values outside the interval -3 to +3 indicating non-normality) and skewness (a measure of symmetry, values outside the interval -1 to +1 indicate significant skewness), were calculated. Taxa where the differences were not normally distributed were excluded from further analysis (Figure 5).

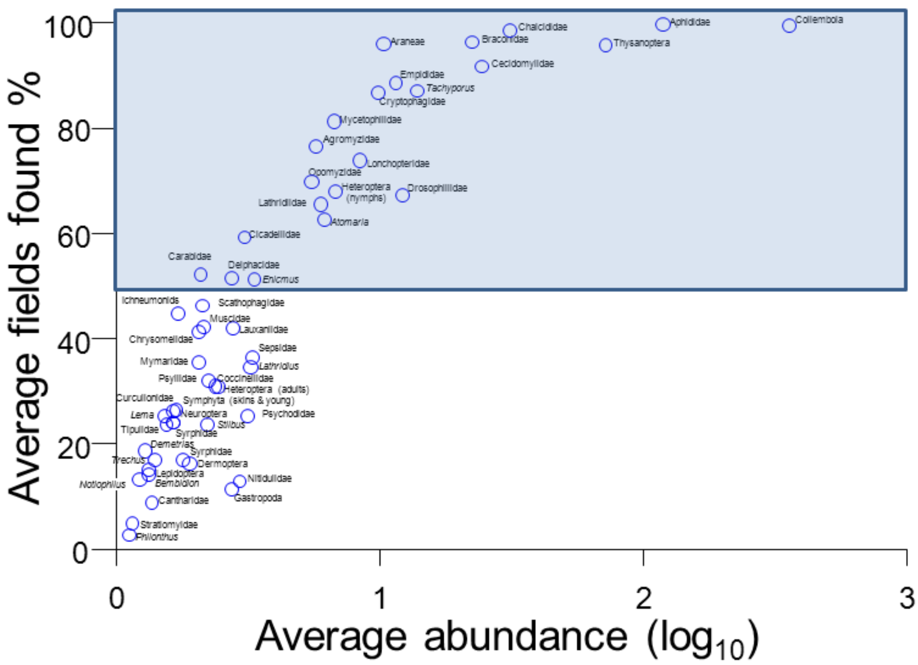

Figure 4. The average percentage of fields where each taxon was found over the 42 years of the survey compared to average abundance (log transformed).

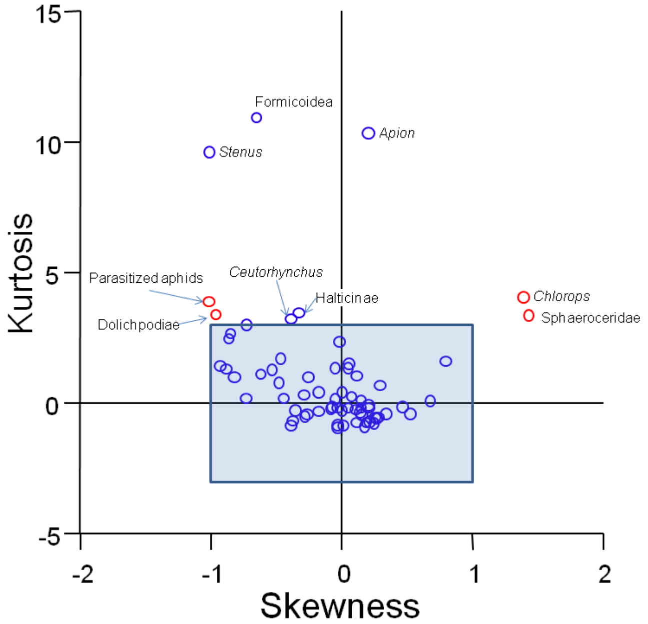

Figure 5. The kurtosis and skewness of changes in annual abundance indices of all 76 taxa examined. Those taxa where these values indicated significant departures from that of a normal distribution are outside the shaded box. Points in red indicate taxa where the annual differences in abundance indices failed the Shapiro-Wilk test.

Weather events

The type of weather events that are commonly associated with changes in invertebrate abundance in published work examining the effects of climate change are either droughts (low precipitation) or temperature anomalies. Consequently, we used two weather variables in the analysis: monthly mean temperature and total monthly precipitation. The months of April, May, June, as well as an average of the three were selected, as this was considered to be the time period of the greatest importance to invertebrate development prior to our invertebrate sampling in mid-June. This meant a total of eight weather variables would be used to identify extreme weather events.

Data for each of the weather variables were identified from the UK 5x5km gridded climate dataset provided by the MetOffice (Perry and Hollis, 2005). A total of eight 5x5km grid squares contained at least some part of the Sussex Study Area, so an average value was calculated for each of the weather variables across these eight grid squares. Unfortunately, the published MetOffice gridded dataset only runs until 2006, leaving us with four years of missing data for our invertebrate data time series. To complete the time series, two alternate sources of weather data for the study area were identified; Bognor Regis weather station (Latitude: 50.78; Longitude: -0.676) with data available from 1970 to 2010 and Herstmonceux weather station (Latitude: 50.9; Longitude: 0.317) with data available from 1977 to 2010.

Principal Component Analysis (PCA) was used to calculate the first principal component score between Bognor Regis and Herstmonceux weather data for each of the eight weather variables. The first principal component score was then compared against the original weather data for each of the three weather data sources to produce a correlation matrix.

Simple linear regression with the first principal component score as the explanatory variable and the corresponding gridded weather data as the response variable was used to model the relationship between the two variables. From this model an equation for the line of best fit could be found, and solving this equation by substitution of first principal component scores for the years with missing gridded data generated estimates for each weather variable in each missing year. This approach allowed us to utilize the gridded dataset without the need to shorten the invertebrate time series.

Years with extreme weather events were then identified for each weather variable. An extreme weather event was where the climatic variable deviated from the mean by more than 2.02 standard deviations. This considers that an extreme weather event will happen once every twenty years, and in either direction about the mean. All variables were tested for normality before the mean and standard deviation were calculated, to ensure that the data are suitable for identifying extreme events when using this procedure.

Invertebrate events

The changes in annual invertebrate indices were used to identify extreme events from the invertebrate data series, in addition to the extreme weather events. For a given taxon/age group, extreme event years were identified as such if inter-annual change deviated by at least 2.02 standard deviations from the mean change, as this considers an extreme event will happen once in twenty years. Where such events differed from those already identified in the climatic data, they may not be weather-related, but they may still be used to calculate recovery times and hence resilience.

Habitat composition

The Sussex Study dataset includes a GIS database of land use from 1970 to the present day. In addition to geographical location of all invertebrate sampling locations, it contains annual data on cropping, field boundaries, land ownership, agri-environment habitats and semi-natural habitats (trees, downland). Habitat variables were those recorded in the second year of the change measurement, so in the analysis looking at sensitivity, the habitat variables were from the event year, in the resilience analysis, the habitat variables were from the year following an event year. A buffer of 100-m radius around each of the invertebrate sampling locations was used to extract habitat composition data (proportions) for each of the sampled locations for each relevant year. Extracted habitat data were combined into seven categories for analysis of the composition of the habitat surrounding the sampling location. These were:

- Winter cereal - consisting of winter wheat, winter barley and winter oats.
- Spring cereal - consisting of spring barley and spring cereal.
- Miscellaneous crops - consisting of oil-seed rape (both winter- and spring-sown), linseed, maize, peas and game cover.
- Grass crops - consisted of grass fields, including both under-sown and direct-sown grasses, as well as downland, rough pasture, water meadows, grass pens, paddocks and permanent set-aside.
- Field boundaries - consisting of grassy strip habitat at edges of fields, strip lynchets, beetle banks, verges, thin banks and grass strips.
- Trees, scrub & hedges - woodland, scrubland, hedges and overgrown verges.
- Urban/built environment: consisting of roads, tracks, building sites and car parks.

Landscape variables

Around each of the invertebrate sample site locations a 100-m buffer was used to calculate the number of patches of habitat in its vicinity and the length of field boundaries around the site. These resulted in two variables describing the sampling location:

- Patch density - the number of individual habitat patches within 100-m of the sampling location divided by the area (ha) of the buffer; this variable was transformed to natural logarithms.
- Field boundary density -the density of field boundaries (m/ha).

Other descriptive variables concerning the sampling location, extracted from the GIS database, were:

- Crop - a factor describing the crop in which the sample was taken (spring cereal, winter wheat, winter barley/oats).
- Field area - the area of the field in which the sample was taken (ha), transformed to natural logarithms.

Additionally the GIS database includes a Land-form Panorama Digital Terrain Model and the elevation, aspect and slope of the sampling location were extracted from this. Aspect is a circular variable and was categorised into north (315° - 45°), east (45° - 135°), south (135° - 225°) and west (225° - 315°).

Pesticide use

Field-by-field information on pesticide use from 1970 to 2004 was collected retrospectively in 1996 and 2005 (Ewald & Aebischer, 1999; 2000; Game Conservancy Trust, 2007). Pesticide data were available for approximately half the field-years in the Sussex Study dataset, and included the number and type of herbicide, foliar fungicide and insecticide applications made per year. The yearly intensity of pesticide use (herbicides, foliar fungicides and insecticides) was measured as percentage spray area, which takes into account the number of times a field is treated with a pesticide (*i.e.* if a field is treated twice then its spray area would be twice the area of the field). Spray area is transformed to percentage spray area by dividing it by cropped area and multiplying by 100. Further details on the long-term trends in use, including changes in herbicide specificity and active ingredients applied can be found in Ewald & Aebischer (1999, 2000) and the Game Conservancy Trust report to DEFRA (2007).

Analysis – sensitivity and recovery

To investigate the factors influencing sensitivity to extreme weather events, we considered change in abundance between the year preceding an event and the event year at the scale of individual sample locations.

Invertebrate long-term trends

For display of the long-term changes in the abundance indices, 95% confidence limits around the index values were obtained by bootstrapping at the field level. For each of the 199 bootstrap runs, fields were selected at random with replacement and a new set of indices obtained as described above. For each year, the 95% confidence limits were taken as the lower and upper 95th percentiles of the distribution of all 200 index values. To obtain the long-term trends in invertebrate abundance, a generalised additive model (GAM) was fitted to the abundance indices with one degree of freedom per decade or part-decade. The 95% confidence limits were obtained by fitting GAMS to each bootstrap sample and selecting the lower and upper 95th percentiles of the 200 values that resulted.

Sensitivity to weather events

Analysis of variance was used to compare the average annual change in indices between the hot/dry event years, the cold/wet ones and the remaining years (including the years identified as long-term trend extremes). The nature of the differences was explained using polynomial contrasts (linear and quadratic). When significant differences were found between the three types of events, they were compared using least significant difference tests (LSD). If changes in the indices of invertebrate abundance for a given taxon indicated that either hot/dry or cold/wet events led to significant differences, the invertebrate taxon was considered to be sensitive to extreme weather events.

Recovery from extreme weather events

We defined the recovery time of a taxon as the number of years taken for the annual index to return to the underlying smoothed long-term trend after an extreme weather event. The long-term trend was estimated for each taxon using a smoothing spline, calculated by fitting a GAM to the abundance index with 1 degree of freedom per decade (or part decade). Any years in which an extreme weather event was identified were excluded from the model, to limit the influence that extreme weather events may have had on the overall trend. Any years in which invertebrate trend-derived extreme events were identified for a taxon were also excluded from the model.

The annual index was deemed to have returned to the long term trend following an extreme weather event when the annual abundance index value lay within the 95% confidence intervals of the smoothing spline fitted to the data. The number of years from an event until the annual index returned to the long-term trend line was then counted. If the annual abundance index was within the 95% confidence interval of the smoothed long-term trend line in the same year as the weather event occurred, a recovery time of zero years was recorded; equivalent to saying the index had not deviated from the long-term trend as a result of the weather event.

Event years were only included in the analysis of recovery time if no other extreme weather event occurred in the three years following, to remove any influence of other events on observed recovery times.

Analysis -resilience

To investigate the factors influencing resilience, we considered the change in abundance between the event year and the year following the event. In both cases the factors examined as potential influences on the magnitude of change described landscape, habitat and pesticide use.

Compositional analysis

In order to determine whether habitat composition had a significant effect on the recovery of taxa to an extreme weather event, for each taxon sample locations were divided into those where the change in abundance of a taxon was higher than the average and those where the abundance change was lower than the average. Changes in abundance were considered from the year preceding an extreme weather event to the event year, and from the event year to the year following. Compositional analysis was used to compare the habitat compositions between the two groups (Aitchison, 1986, Aebischer *et al.*, 1993). This analysis was carried out in Genstat Release 15.0 for Windows.

Linear mixed modelling analysis

We used linear mixed modelling to examine the influence of the habitat and landscape variables on the change in abundance of the taxa (ln-transformed) shown to be sensitive to extreme weather events at the level of sampling location. We restricted the extreme weather events to exclude any occurring in consecutive years to limit compounding effects. Individual sampling location, the location within a field where the invertebrate sample was taken, was entered as a random effect and all measured habitat variables were entered as fixed effects. Year was also entered as a categorical fixed effect to avoid confounding temporal effect with habitat and landscape ones. Generalised linear modelling was first undertaken without the variables for pesticide use, as their inclusion reduced sample sizes by half. After this initial analysis, information on the number of pesticide applications in a field in the year corresponding to the other habitat variables (year of the event in the case of sensitivity and year following an event in the case of resilience) were included in the model as fixed terms.

Residuals from the models were checked for normality and heteroscedasticity. Relationships between explanatory habitat variables were evaluated using correlations; only the number of patches and the density of field boundaries were shown to be significantly ($P < 0.05$) positively correlated.

This analysis was carried out in Genstat Release 15.0 for Windows.

Invertebrate abundance and weather correlation

To test for a correlation between overall invertebrate abundance trends and weather, the annual abundance index was compared to each of the 8 weather variables identified previously. To void issues of linearity, Spearman's rank correlation was used to calculate the correlation coefficients between each taxon and each of the weather variables.

Analysis – time series

Correlation analysis

We investigated further the correlations between weather and the change in indices of abundance for each sensitive taxa. We also correlated changes in the indices of taxon abundance with changes in pesticide use – one measure of agricultural intensification that may be confounded with changes in weather variables. We used principal component analysis to combine the trends in herbicide, fungicide and insecticide use into one variable (Pesticide PC1) to represent the annual variation in pesticide use intensity. Correlations between the indices of invertebrate abundance and pesticide use were examined as were correlations between the trends in weather variables and pesticide use. Spearman Rank correlations were undertaken in all cases to avoid issues of non-linearity and the analysis was carried out in Genstat Release 15.0 for Windows.

Spectral and coherence analysis

Significant correlations identified between the yearly indices of the abundance of invertebrate taxa and measured temperature and precipitation variables led to an analysis that compared the long-term trends in indices of taxon abundance to trends in weather.

Standardized (zero mean, unit variance) series of abundance indices and their five-year running means for each taxon, as well as for temperature, rainfall and Pesticide PC1, were calculated to allow visual comparison between the trends. Spectral density and coherence analysis were used to compare the patterns in the long-term trends of weather (both temperature and rainfall) and invertebrate abundance, applying methods previously used to compare long-term trends in weather and four marine trophic levels (Aebischer, et al. 1990).

The spectrum of a time series is a means of identifying the measure of recurring cyclical patterns in the data over time, by decomposing the variation into its frequency components. A strong cyclical pattern recurring every 5 years, for instance, would show as a peak at a frequency of 0.2. Coherence analysis compares two time series across the frequency domain to identify the frequencies at which matching cyclical patterns occur in both sets of data (detected by peaks in coherence at those frequencies) and the phasing (degree of synchronicity) of any such matches. For example, two time series, both with a four year cycle but where the cyclical peaks and troughs of the second series that lag behind the cyclical peaks and troughs of the first series by one year, will exhibit a peak in coherence at 0.25 and a phase of $-\frac{\pi}{2}$ radians equal to -90°, i.e. one quarter of the cycle length (Figure 6).

Spectra were calculated according to Barrowdale and Erickson (1980), and coherences were calculated according to Strand (1977), both with a filter length of 4. Estimating the spectral density allowed the identification of periodicity in the long-term trends and coherence analysis determined where the periodicities of two time series overlap. Significance was determined by comparison to results calculated from 1000 randomly generated time-series for both spectral densities and coherence of trends in invertebrate indices with trends in weather.

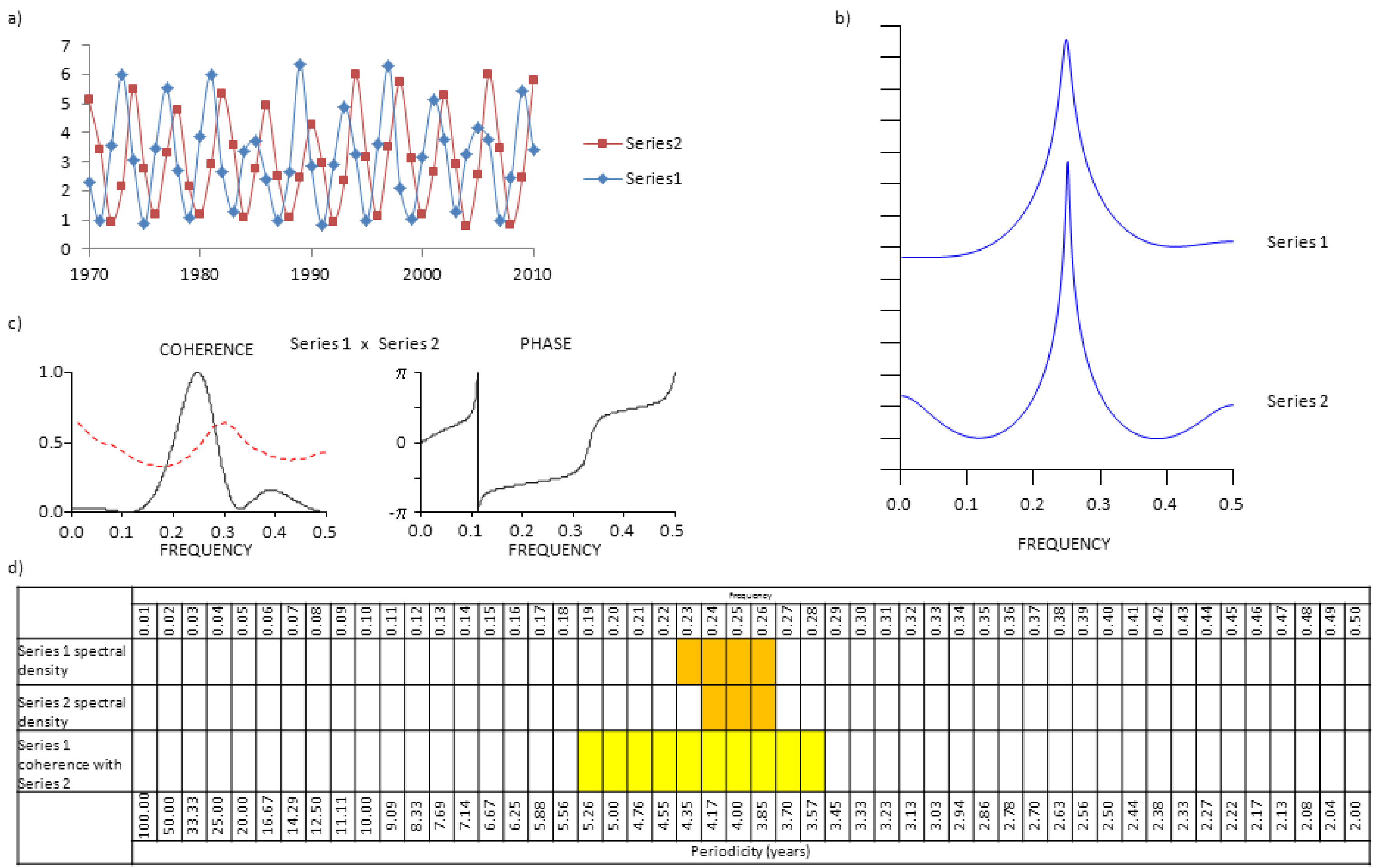

Figure 6. Illustrated example of spectral and coherence analysis to aid with interpretation of results. (a) Two time series, each demonstrating a four year cycle with a one year lag between the series. (b) The spectral density of both series 1 and series 2, showing an almost identical peak at a frequency of 0.25 (equivalent to a period of 4 years). (c) .Coherence and phase spectra for series 1 paired with series 2. The red dotted line is the coherence level to exceed for significance at P < 0.05. (d) Orange rectangles are where spectral densities are significant different from those of a random time series. Yellow rectangles are where spectral frequencies (and periodicity in years) of the two time series were significantly similar.

Multiple regression

The effect of both weather and pesticide use on the changes observed in the indices of invertebrate abundance were examined using multiple linear regression. Average monthly mean temperature (April – June) and average total monthly precipitation were used to represent the trend in weather and Pesticide PC1 represented the trend in pesticide use. This analysis was carried out in Genstat Release 15.0 for Windows.

Results

Invertebrate taxa selected for analysis

The invertebrate taxa that were selected for analysis, fulfilling both criteria (occurring in > 50% of field on average-- Figure 4, and changes in indices being normally distributed and not suffering significantly from kurtosis or skewness- Figure 5), are listed below. In total, 28 individual taxa/age groups were included in this analysis:

Araneae (spiders); Collembola (springtails); Aphididae (aphids); Cicadellidae (leafhoppers); Delphacidae (planthoppers); Heteroptera (bugs), including all stages combined, adults and young separately and a ratio of adults to nymphs (A/Y); Thysanoptera (thrips); Braconidae (braconid wasps); Chalcididae (chalcid wasps); Carabidae (ground beetles); *Tachyporus* (Rove Beetles) , including all stages combined, adults and young; *Enicmus* and Lathridiidae (both a genus of and the family of mould beetles); *Atomaria* and Cryptophagidae (both a genus of and the family of silken fungus beetles); Cecidomyiidae (gall midges); Mycetophilidae (fungus gnats); Empididae (dance flies); Lonchopteridae (spear-winged flies); Agromyzidae (leaf-miner flies); Opomyzidae (grass flies); and Drosophillidae (fruit flies).

Weather

The first principal component of the Bognor Regis and Herstmonceux weather data was significantly positively correlated with each of the eight weather variables for the gridded dataset, in each case explaining at least 95% of the variation. In all instances, the correlation between the first principal component score and the gridded weather dataset was stronger than those between the weather variables from either of the weather station datasets and the gridded dataset. This indicated that the first principal component score could reliably be used to produce an estimate for the values of each weather variable in all four years missing from the gridded dataset. The relationship between the first principal component score and gridded weather data was then modelled using linear regression, and the first principal component scores for the missing years substituted into the equation of the line of best fit. The long term trends in both weather variables can be seen in Appendix 1 Figures 1-2.

When tested for normality, all of the temperature variables were found to be normally distributed, as were the four precipitation variables after a square root transformation.

A total of 12 extreme weather events were identified: 4 low precipitation events, 1 high precipitation event, 4 high temperature events and 3 low temperature events (Appendix 2). Some overlap in years amongst these 12 extreme weather events left a total of 10 event years for use in the analysis. The extreme events were grouped into two categories to simplify the analysis and produce results that are easier to interpret. These two categories were: cold and wet (low mean monthly temperature and high monthly precipitation) and hot and dry (high mean monthly temperature and low monthly precipitation). The years identified in each category are as follows:

Cold/Wet	Hot/Dry
	1976
1972	1984
1986	1989
1991	1995
1996	2007
	2008

Sensitivity and recovery

Invertebrate taxa extreme events

Overall 40 extreme events in the long-term invertebrate trends were identified (Appendix 3), of which 12 (30%) coincided with extreme weather events. All extreme events (weather and invertebrate trend) are summarised in Table 1.

Table 1. Extreme weather events (hot/dry shaded pink, cold/west shaded grey) and extreme events in the long-term trends of invertebrates (increases as +, decreases as -). Years where data were not available are shaded in black.

	Araneae	Collembola	Aphididae	Cicadellidae	Delphacidae	Heteroptera	Heteroptera (adults)	Heteroptera (nymphs)	Heteroptera A/Y	Thysanoptera	Braconidae	Chalcididae	Carabidae	*Tachyporus*	*Tachyporus* (adults)	*Tachyporus* (young)	*Tachyporus* A/Y	*Enicmus*	Lathridiidae	*Atomaria*	Cryptophagidae	Cecidomyiidae	Mycetophilidae	Empididae	Lonchopteridae	Agromyzidae	Opomyzidae	Drosophilidae	
1970																													
1971																													
1972																													Low June temp
1973																	-												
1974																													
1975																													
1976				+															+		+			-		-			Low average rainfall High June temp
1977				-	-	-		-			-	-																+	
1978	+							+			+	+													+	+			
1979																										-			
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1984	+																												Low April rain
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2007													+																High April temp High average temp
2008																													High May temp
2009																													
2010																								-					
2011									+																				

Sensitivity to extreme weather events

Eleven (39%) of the 28 taxa examined were sensitive to extreme weather events (Table 2). The taxa found to be sensitive were: Araneae, Cicadellidae, Delphacidae, adult Heteroptera, Thysanoptera, Braconidae, young *Tachyporus*, *Enicmus*, Lathridiidae, Cryptophagidae and Mycetophilidae. For seven taxa (Araneae, Cicadellidae, adult Heteroptera, Thysanoptera, Braconidae, *Enicmus*, Lathridiidae) there was a significant linear component, with the hot/dry events resulting in an increase in the abundance index, which was usually higher than the rest of the years, where the change in the abundance index was significantly higher than was the case for the cold/wet years. The remaining four taxa (Delphacidae, young *Tachyporus*, Cryptophagidae and Mycetophilidae) showed a relationship where the average change in the abundance indices in either type of event year was higher than that in the remainder of the years. Not all of the taxa/age groups that showed sensitivity to extreme events showed significant correlations with either temperature or precipitation. This was the case for Araneae and Braconidae where their abundance was not significantly correlated with either temperature or precipitation.

Recovery from extreme weather events

Resilience was calculated for all taxa/age groups originally selected, regardless of the results from the sensitivity analysis. Only 5 of the 10 extreme weather event years were suitable for use in the calculation of recovery time based on the criteria of no other extreme event in the following three years. The distribution of event types was two hot/dry and three cold/wet.

The number of years taken for the annual index to return to the long-term trend following an event year was counted for these five events years across all taxa. The mean recovery time in years (± standard error) was then calculated for each taxon for both extreme weather event types (Table 3). The frequency with which each recovery time was observed was also recorded for both extreme weather event types (Appendix 4).

Table 2. Comparisons between yearly changes in invertebrate abundance (controlling for field to field variation) in hot/dry, cold/wet and the remaining years of the survey, significant results indicate sensitivity to weather events. Results are from analysis of variance weighting by the reciprocal of the variance.

Taxa	Comparison	Linear comparison	Quadratic comparison	Hot/dry	Remainder	Cold/wet
Araneae	**$F_{2,38}$ = 4.30, P = 0.021**	**$F_{1,38}$ = 6.45, P = 0.015**	**$F_{1,38}$ = 2.15, P = 0.151**	**0.549 ± 0.221[a]**	**-0.141 ± 0.096[b]**	**-0.225 ± 0.290[b]**
Collembola	$F_{2,36}$ = 1.18, P = 0.320	$F_{1,36}$ = 2.00, P = 0.166	$F_{1,36}$ = 0.36, P = 0.554	0.327 ± 0.256	-0.083 ± 0.118	-0.196 ± 0.354
Aphididae	$F_{2,38}$ = 1.06, P = 0.356	$F_{1,38}$ = 1.51, P = 0.227	$F_{1,38}$ = 0.62, P = 0.437	0.191 ± 0.347	-0.028 ± 0.196	-0.919 ± 0.679
Cicadellidae	**$F_{2,37}$ = 3.52, P = 0.040**	**$F_{1,37}$ = 6.30, P = 0.017**	$F_{1,37}$ = 0.75, P = 0.393	**0.761 ± 0.318[a]**	**-0.078 ± 0.143[b]**	**-0.409 ± 0.401[c]**
Delphacidae	**$F_{2,37}$ = 4.38, P = 0.020**	$F_{1,37}$ = 3.22, P = 0.081	**$F_{1,37}$ = 5.54, P = 0.024**	**0.906 ± 0.377[a]**	**-0.282 ± 0.190[b]**	**0.640 ± 0.719[a]**
Heteroptera	$F_{2,38}$ = 1.01, P = 0.372	$F_{1,38}$ = 2.03, P = 0.163	$F_{1,38}$ = 0.01, P = 0.972	0.288 ± 0.256	0.003 ± 0.110	-0.267 ± 0.300
Heteroptera adults	**$F_{2,38}$ = 3.27, P = 0.049**	**$F_{1,38}$ = 5.61, P = 0.023**	$F_{1,38}$ = 0.93, P = 0.340	**0.884 ± 0.369[a]**	**-0.105 ± 0.158[b]**	**-0.365 ± 0.577[b]**
Heteroptera nymphs	$F_{2,38}$ = 0.56, P = 0.578	$F_{1,38}$ = 1.03, P = 0.317	$F_{1,38}$ = 0.08, P = 0.774	0.179 ± 0.286	0.031 ± 0.118	-0.257 ± 0.311
Heteroptera A/Y	$F_{2,38}$ = 1.39, P = 0.261	$F_{1,38}$ = 0.21, P = 0.653	$F_{1,38}$ = 2.58, P = 0.117	0.254 ± 0.209	-0.075 ± 0.092	0.209 ± 0.261
Thysanoptera	**$F_{2,36}$ = 2.54, P = 0.093**	**$F_{1,36}$ = 4.44, P = 0.042**	$F_{1,36}$ = 0.65, P = 0.427	**0.622 ± 0.306[a]**	**-0.112 ± 0.141[b]**	**-0.306 ± 0.528[b]**
Braconidae	**$F_{2,37}$ = 4.22, P = 0.022**	**$F_{1,37}$ = 5.04, P = 0.031**	$F_{1,37}$ = 3.39, P = 0.074	**0.321 ± 0.268[a]**	**0.130 ± 0.163[a]**	**-1.238 ± 0.480[b]**
Chalcididae	$F_{2,37}$ = 0.97, P = 0.389	$F_{1,37}$ = 0.63, P = 0.433	$F_{1,37}$ = 1.31, P = 0.260	0.018 ± 0.220	0.027 ± 0.102	-0.516 ± 0.378
Carabidae	$F_{2,38}$ = 0.72, P = 0.495	$F_{1,38}$ = 0.04, P = 0.842	$F_{1,38}$ = 1.39, P = 0.245	0.186 ± 0.238	-0.072 ± 0.101	0.153 ± 0.264
Tachyporus	$F_{2,38}$ = 2.17, P = 0.128	$F_{1,38}$ = 0.39, P = 0.535	$F_{1,38}$ = 3.95, P = 0.054	0.517 ± 0.360	-0.219 ± 0.129	0.152 ± 0.337
Tachyporus adult	$F_{2,38}$ = 0.49, P = 0.618	$F_{1,38}$ = 0.27, P = 0.604	$F_{1,38}$ = 0.70, P = 0.408	0.188 ± 0.318	-0.146 ± 0.115	-0.089 ± 0.251
***Tachyporus* young**	$F_{2,38}$ = 2.37, P = 0.108	$F_{1,38}$ = 0.28, P = 0.600	**$F_{1,38}$ = 4.45, P = 0.042**	**0.548 ± 0.379[a]**	**-0.234 ± 0.136[b]**	**0.238 ± 0.368[a]**
Tachyporus A/Y	$F_{2,38}$ = 0.46, P = 0.636	$F_{1,38}$ = 0.39, P = 0.535	$F_{1,38}$ = 0.52, P = 0.474	0.018 ± 0.311	-0.039 ± 0.136	0.271 ± 0.294
Enicmus	**$F_{2,38}$ = 8.50, P = 0.001**	**$F_{1,38}$ = 8.53, P = 0.006**	**$F_{1,38}$ = 8.46, P = 0.006**	**1.400 ± 0.368[a]**	**-0.247 ± 0.155[b]**	**-0.073 ± 0.399[ab]**
Lathridiidae	**$F_{2,38}$ = 11.16, P < 0.001**	**$F_{1,38}$ = 11.79, P = 0.001**	**$F_{1,38}$ = 10.53, P = 0.002**	**1.360 ± 0.320[a]**	**-0.282 ± 0.136[b]**	**-0.083 ± 0.381[ab]**
Atomaria	$F_{2,38}$ = 2.38, P = 0.106	$F_{1,38}$ = 3.12, P = 0.086	$F_{1,38}$ = 1.64, P = 0.208	0.527 ± 0.311	-0.163 ± 0.111	-0.260 ± 0.261
Cryptophagidae	**$F_{2,38}$ = 7.23, P = 0.002**	$F_{1,38}$ = 1.84, P = 0.183	**$F_{1,38}$ = 12.61, P = 0.001**	**0.836 ± 0.280[a]**	**-0.247 ± 0.110[c]**	**0.234 ± 0.260[b]**
Cecidomyiidae	$F_{2,37}$ = 2.39, P = 0.105	$F_{1,37}$ = 3.75, P = 0.061	$F_{1,37}$ = 1.04, P = 0.315	0.570 ± 0.313	-0.174 ± 0.148	-0.248 ± 0.497
Mycetophilidae	**$F_{2,37}$ = 5.18, P = 0.010**	$F_{1,37}$ = 0.01, P = 0.951	**$F_{1,37}$ = 10.36, P = 0.003**	**0.562 ± 0.334[a]**	**-0.276 ± 0.142[b]**	**0.730 ± 0.369[a]**
Empididae	$F_{2,37}$ = 0.72, P = 0.494	$F_{1,37}$ = 1.27, P = 0.268	$F_{1,37}$ = 0.17, P = 0.683	-0.309 ± 0.274	0.006 ± 0.104	0.133 ± 0.300
Lonchopteridae	$F_{2,37}$ = 1.35, P = 0.271	$F_{1,37}$ = 2.61, P = 0.115	$F_{1,37}$ = 0.10, P = 0.757	-0.527 ± 0.387	-0.189 ± 0.169	0.347 ± 0.380
Agromyzidae	$F_{2,36}$ = 0.89, P = 0.418	$F_{1,36}$ = 0.15, P = 0.699	$F_{1,36}$ = 1.64, P = 0.209	-0.423 ± 0.438	0.091 ± 0.202	-0.629 ± 0.760
Opomyzidae	$F_{2,37}$ = 0.80, P = 0.457	$F_{1,37}$ = 1.35, P = 0.253	$F_{1,37}$ = 0.25, P = 0.621	0.186 ± 0.293	-0.005 ± 0.138	-0.499 ± 0.456
Drosophillidae	$F_{2,37}$ = 2.56, P = 0.091	$F_{1,37}$ = 2.05, P = 0.161	$F_{1,37}$ = 3.08, P = 0.088	-1.300 ± 0.501	-0.049 ± 0.234	-0.319 ± 0.531

Means with the same letter are not significantly different (P < 0.05).

Table 3. Average number of years ± standard error taken to recover following an extreme weather event and for trend events, where the number of years varies from 1 to 3, the mean and range where appropriate. Taxa identified as being sensitive to extreme weather events are shown in bold.

Taxa	Hot/dry	Cold/wet	Trend Events
Araneae	**0.5 ± 0.5**	**0.33 ± 0.33**	**1**
Collembola	1 ± 1	0 ± 0	1
Aphididae	0.5 ± 0.5	0.33 ± 0.33	
Cicadellidae	**0.5 ± 0.5**	**0.33 ± 0.33**	**1**
Delphacidae	**1 ± 1**	**0.33 ± 0.33**	**2**
Heteroptera	0.5 ± 0.5	0.33 ± 0.33	2.5 (1-4)
Heteroptera adults	**1 ± 1**	**0.67 ± 0.33**	**1**
Heteroptera nymphs	0.5 ± 0.5	0.67 ± 0.67	0.5 (0-1)
Heteroptera A/Y	0 ± 0	0 ± 0	
Thysanoptera	**0.5 ± 0.5**	**1.5 ± 0.5**	
Braconidae	**0.5 ± 0.5**	**0.67 ± 0.67**	0.5 (0-1)
Chalcididae	0 ± 0	0.33 ± 0.33	1 (1-1)
Carabidae	0.5 ± 0.5	0.67 ± 0.33	1
Tachyporus	1 ± 0	1.33 ± 0.33	
Tachyporus adult	0.5 ± 0.5	0.33 ± 0.33	
***Tachyporus* young**	**1 ± 0**	**1.33 ± 0.33**	
Tachyporus A/Y	1 ± 0	0.67 ± 0.33	
Enicmus	**1 ± 1**	**0 ± 0**	
Lathridiidae	**1 ± 1**	**0 ± 0**	**1**
Atomaria	0 ± 0	0 ± 0	0.66 (0-1)
Cryptophagidae	**1 ± 1**	**1 ± 0.58**	
Cecidomyiidae	1.5 ± 0.5	0.67 ± 0.33	
Mycetophilidae	**1.5 ± 0.5**	**0.33 ± 0.33**	
Empididae	1 ± 1	1 ± 0	1
Lonchopteridae	1 ± 1	0.67 ± 0.33	0.5 (0-1)
Agromyzidae	1 ± 1	0 ± 0	1 (1-1)
Opomyzidae	0 ± 0	0.33 ± 0.33	
Drosophillidae	0.5 ± 0.5	0.33 ± 0.33	1

Of all the taxa displaying sensitivity to extreme weather events, the recovery time of Thysanoptera to cold/wet events is the longest, although data is missing for the 1972 extreme event. For this taxon, in all cold/wet events identified from the gridded weather data used in this analysis, the time taken for the annual index to return to the long term trend was at least a year. This results in the joint longest mean time to recovery from an extreme weather event of all taxa across both weather event types. The recovery time following hot/dry years takes on average less than a year for Thysanoptera, suggesting that they are particularly vulnerable to cold/wet events.

Tachyporus young and Cryptophagidae were the only other taxa identified as sensitive to extreme events that demonstrated a mean recovery time of at least a year in response to cold/wet weather events. For *Tachyporus* young recovery time was never less than a year in any of the cold/wet events. Cryptophagidae showed greater variability in recovery time, with a different time in the range 0-2 years recorded for each cold/wet event. Both *Tachyporus* young and Cryptophagidae also showed a mean recovery time of at least a year for hot/dry events as well as for cold/wet events. They were the only sensitive taxa with a mean recovery time of at least a year in both event types.

Mycetophilidae displayed the longest mean recovery time in response to hot/dry type extreme events, with recovery taking at least a year in both events included in the analysis. Delphacidae, Lathridiidae, *Enicmus* and Heteroptera adults all showed a mean recovery time of a year in response to hot/dry events, with all of these taxa showing the same pattern of recovery within the same year to one event but a recovery time of 2 years in response to the other. This high level of variability would suggest a need to examine more hot/dry events years to determine a more reliable mean recovery time for these taxa.

Araneae, Cicadellidae and Braconidae showed high resilience to both types of extreme events, with recovery times of less than a year on average for each event type.

Resilience

Two approaches were used to examine the effect of land use, habitat and landscape on changes in the abundance of invertebrate taxa sensitive to extreme weather events, compositional analysis of land use around sampling locations and linear mixed modelling using habitat and landscape variables to explain variation in changes in invertebrate abundance.

Compositional analysis

Only one significant difference in habitat composition was found when comparing sampling locations where the change in invertebrates was higher than the average versus where the change was lower than the average, in both the year of an extreme weather event and in the year following an extreme event (Table 4a). This was for *Tachyporus* young when considering abundance in the year after a hot event relative to that in the hot-event year (resilience). Higher abundances were associated with higher proportions of grass habitat at the expense of winter cereal and miscellaneous crop habitat (Table 4b). The lack of a clear-cut pattern in land use, coupled with a number of significant differences that is lower than what could be expected through chance when testing at $P < 0.05$ (5% of 44 = 2.2) meant that these variables were not included in further analyses of the effects of habitat and landscape.

There was again only one significant difference in habitat composition across all locations where the change in invertebrates was higher than the average versus where the change was lower than the average, in both the year of an extreme weather event and in the year following an extreme event, for three taxa not deemed sensitive to extreme events. This was for Lonchopteridae in a year following a hot/dry event year (Appendix 5).

Table 4a. Analysis of habitat compositions in 100 m buffers surrounding invertebrate sampling locations in the Sussex study. Sampling locations were divided into those samples that showed an invertebrate abundance change greater than the mean value and those that showed change less than the mean value, and the compositions were compared. Significant results indicate where the habitat compositions varied between the two groups (* indicates significance at the P < 0.05 level).

Event Type	Taxa	WIlk's Lambda	d.f	P
Pre Hot (year of a hot/dry event-relative to the year before)	Araneae	0.995	6,204	0.980
	Cicadellidae	0.988	6,204	0.873
	Delphacidae	0.986	6,204	0.807
	Heteroptera adults	0.974	6,204	0.476
	Thysanoptera	0.953	6,204	0.126
	Braconidae	0.942	6,204	0.056
	Tachyporus young	0.994	6,204	0.969
	Enicmus	0.986	6,204	0.821
	Lathridiidae	0.983	6,204	0.743
	Cryptophagidae	0.954	6,204	0.135
	Mycetophilidae	0.981	6,204	0.676
Pre Cold (year of a cold/wet event-relative to the year before)	Araneae	0.990	6,203	0.911
	Cicadellidae	0.963	6,203	0.266
	Delphacidae	0.989	6,203	0.886
	Heteroptera adults	0.986	6,203	0.818
	Thysanoptera	0.959	6,203	0.198
	Braconidae	0.971	6,203	0.422
	Tachyporus young	0.967	6,203	0.327
	Enicmus	0.971	6,203	0.411
	Lathridiidae	0.969	6,203	0.367
	Cryptophagidae	0.980	6,203	0.645
	Mycetophilidae	0.981	6,203	0.689
Post Hot (year after hot/dry event-relative to the event year)	Araneae	0.933	6,174	0.058
	Cicadellidae	0.943	6,174	0.112
	Delphacidae	0.956	6,174	0.250
	Heteroptera Adults	0.961	6,174	0.325
	Thysanoptera	0.954	6,174	0.223
	Braconidae	0.955	6,174	0.228
	Tachyporus young	0.929*	6,174	0.045
	Enicmus	0.983	6,174	0.802
	Lathridiidae	0.976	6,174	0.631
	Cryptophagidae	0.971	6,174	0.511
	Mycetophilidae	0.975	6,174	0.607
Post Cold (year after cold/wet event- relative to the event year)	Araneae	0.953	6,230	0.084
	Cicadellidae	0.992	6,230	0.926
	Delphacidae	0.975	6,230	0.450
	Heteroptera adults	0.988	6,230	0.829
	Thysanoptera	0.976	6,230	0.457
	Braconidae	0.972	6,230	0.348
	Tachyporus young	0.969	6,230	0.288
	Enicmus	0.995	6,230	0.978
	Lathridiidae	0.993	6,230	0.948
	Cryptophagidae	0.984	6,230	0.712
	Mycetophilidae	0.956	6,230	0.111

Table 4b. Only one taxon showed significant differences in their habitat compositions. For *Tachyporus* young, comparing the year of a hot event to the year following the hot event, at sites where numbers increased there was relatively more grass habitat and less winter cereal and miscellaneous, while the opposite was true for sites where numbers went down. Means with the same rank (a, b or c) are not significantly different at the P < 0.05 level.

Braconidae increasing group vs. declining group		
Rank	**Habitat type**	**Ranks Differ**
7 (highest)	Grass	a
6	Trees + Hedge	a b
5	Field Boundaries	a b
4	Urban	a b
3	Spring Cereal	a b c
2	Miscellaneous	b c
1 (lowest)	Winter Cereal	c

Linear mixed modelling

In general, there were few overall patterns in the effect of habitat and landscape on either the sensitivity or resilience of invertebrate taxa that had previously been shown to be sensitive to extreme changes in weather (Tables 5 -8, results from analysis of non-sensitive taxa are shown in Appendix 6, Tables 1 - 4). The one exception to this was the effect of aspect on the sensitivity of taxa to cold, wet years, where changes in the abundance of six of the eleven taxa examined (Araneae, Cicadellidae, Thysanoptera, *Tachyporus* young, Cryptophagidae and Mycetophilidae) showed a significant effect of aspect (Table 6). Examining this in more detail showed that an increase in abundance was mainly associated with west-facing slopes and a decrease in abundance with east-facing slopes (Table 10 and Appendix 8, Figure 1). The large variation in the samples from north facing slopes was due to small sample size within the study area and made it unlikely to find a significant difference with north facing slopes vs. other slopes. In the case of Cicadellidae, abundance in samples on north facing slopes declined significantly more than those in on samples on other slopes. In the other taxa with significant differences, west facing slopes showed significant increases in abundance compared to east and south facing slopes, while increases in abundance in samples from west facing slopes were not significantly different to changes in abundance on north facing slopes which were, in turn, not significantly different to declines on south and east facing slopes. This effect was still obvious in the models that incorporated pesticide use but where the sample size was reduced by 40% for Cicadellidae, Heteroptera adults and Thysanoptera. Mean abundances for each aspect group for non-sensitive taxa are given in Appendix 7, where changes in abundances were significantly associated with aspect in six of the eighteen taxa/age groups (Aphididae, *Tachyporus*, *Tachyporus* AY, Empididae, Lonchopteridae and Agromyzidae). Here the pattern was similar for *Tachyporus*, Agromyzidae and, to a certain degree, Lonchopteridae, with the reciprocal seen for *Tachyporus* AY. A different pattern was seen in the changes in abundance of Aphididae and Empididae, where samples on north facing slopes show increases in abundance compared to all other slopes (Appendix 8, Figure 2).

Table 5. Sensitivity to hot, dry events from generalised linear modelling of changes in invertebrate abundance in the event year relative to the pre-event year for those taxa shown to be sensitive to extreme weather events on a field-by-field basis. Wald statistics (for models including all effects) excluding (a) and including the number of pesticide applications in the event year (b). Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

	Degrees of freedom	Araneae	Cicadellidae	Delphacidae	Heteroptera adults	Thysanoptera	Braconidae	*Tachyporus* young	*Enicmus*	Lathridiidae	Cryptophagidae	Mycetophilidae
a. Overall: Sample size = 211 pairs of fields.												
Year	3	**8.70***	4.33	1.56	3.85	1.47	1.48	3.47	**10.19***	4.45	**14.38****	0.82
Crop	2	1.94	1.78	0.24	0.58	2.52	2.86	2.19	0.01	0.05	0.61	2.68
Aspect	3	2.13	4.66	1.79	0.38	3.10	0.92	2.95	0.62	0.40	1.53	1.92
Field boundary density	1	0.03	0.51	0.04	0.99	0.98	0.01	0.30	0.04	1.50	0.32	0.01
Slope	1	1.31	0.20	2.12	1.99	0.20	0.10	0.22	0.01	0.60	0.23	0.95
Elevation	1	2.46	0.12	1.52	0.66	0.03	0.01	0.12	0.30	0.32	0.04	0.05
Patch density (log)	1	1.61	0.01	0.05	1.54	0.14	0.35	0.39	0.22	1.30	0.01	0.01
Field area (log)	1	0.57	1.05	1.15	0.38	1.33	2.27	0.26	**3.95***	2.49	3.27	0.01
b. Including pesticide applications: Sample size = 110 pairs of fields.												
Year	3	7.26	5.75	0.28	3.14	2.19	1.51	3.94	**12.60****	**9.33***	**8.77***	0.69
Crop	2	0.93	2.20	2.01	0.10	1.08	0.95	0.05	2.26	1.80	0.45	0.84
Aspect	3	0.72	**9.91***	2.49	0.65	3.55	0.32	1.74	0.70	1.02	1.90	1.45
Field boundary density	1	0.64	1.58	0.22	0.61	0.15	0.20	0.01	0.27	0.08	0.12	0.14
Slope	1	1.12	0.08	0.05	0.28	0.14	0.08	**4.85***	1.90	**4.86***	1.04	1.64
Elevation	1	0.01	0.53	0.08	0.07	0.41	0.04	**5.65***	1.06	0.93	**4.99***	0.11
Patch density (log)	1	1.79	0.04	0.02	0.48	0.07	0.12	0.21	0.34	1.03	0.35	0.07
Field area (log)	1	1.41	2.09	0.45	1.23	0.27	0.92	0.40	**4.50***	**4.39***	1.98	0.33
Herbicide	1	0.75	0.01	0.52	0.01	3.70	**4.17***	0.50	0.19	1.23	1.76	2.27
Fungicide	1	0.64	0.33	0.81	0.72	0.01	**4.35***	2.20	**6.17***	**10.49****	0.11	0.19
Insecticide	1	0.34	0.42	0.88	0.25	0.45	3.35	0.01	3.53	**5.76***	0.20	0.26

Table 6. Sensitivity to cold, wet events from generalised linear modelling of changes in invertebrate abundance in the event year relative to the pre-event year for those taxa shown to be sensitive to extreme weather events on a field-by-field basis. Wald statistics (for models including all effects) excluding (a) and including the number of pesticide applications in the event year (b). Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

	Degrees of freedom	Araneae	Cicadellidae	Delphacidae	Heteroptera adults	Thysanoptera	Braconidae	*Tachyporus* young	*Enicmus*	Lathridiidae	Cryptophagidae	Mycetophilidae
a. Overall: Sample size = 210 pairs of fields.												
Year	3	**14.46****	**9.50***	1.48	**12.58****	2.40	1.58	0.36	3.29	2.08	2.47	**11.26***
Crop	2	2.88	0.41	1.01	0.51	2.11	0.83	0.06	0.28	2.22	1.44	2.09
Aspect	3	**8.79***	**10.50***	2.70	5.32	**12.21****	3.22	**11.22***	6.51	3.68	**9.35***	**11.75***
Field boundary density	1	0.43	2.43	0.01	1.37	1.22	0.33	0.42	0.34	0.48	0.88	2.48
Slope	1	0.37	0.28	0.01	0.02	3.61	0.35	0.22	1.82	1.29	1.39	1.64
Elevation	1	0.50	0.60	0.01	0.18	0.48	3.28	0.39	3.70	3.23	**4.22***	1.44
Patch density (log)	1	0.02	0.14	0.01	1.25	2.93	0.69	0.93	0.18	1.12	0.27	1.57
Field area (log)	1	0.83	0.58	0.01	1.19	0.13	0.26	0.70	3.65	0.55	0.24	**5.19***
b. Including pesticide applications: Sample size = 126 pairs of fields.												
Year	3	1.92	3.94	0.78	1.07	1.17	1.29	3.03	4.74	1.93	2.42	**10.59***
Crop	2	2.30	0.13	2.14	1.06	0.50	1.96	0.96	0.61	1.83	1.11	**9.23***
Aspect	3	5.93	**10.05***	5.29	6.30	**10.63***	2.05	4.34	5.45	4.66	**10.32***	4.78
Field boundary density	1	0.14	1.21	1.18	0.01	0.32	1.52	0.06	0.09	1.49	0.15	0.17
Slope	1	3.50	2.28	2.91	0.01	0.31	3.04	0.01	2.43	0.20	0.46	0.10
Elevation	1	0.02	0.26	2.60	3.69	0.02	0.72	0.96	1.03	2.74	1.85	1.30
Patch density (log)	1	0.14	1.05	1.29	0.06	3.73	1.04	1.34	0.56	3.25	0.01	2.56
Field area (log)	1	0.99	2.69	0.99	0.14	0.01	3.56	0.17	3.12	0.07	0.05	**7.36****
Herbicide	1	0.01	0.01	0.01	2.95	0.81	0.05	0.12	0.22	1.30	1.83	0.60
Fungicide	1	0.29	0.31	2.13	0.01	0.48	0.24	1.18	0.08	0.59	0.01	**4.16***
Insecticide	1	1.13	0.83	**4.14***	2.07	3.27	1.19	0.01	0.63	1.12	0.01	0.98

Table 7. Resilience to hot, dry events from generalised linear modelling of changes in invertebrate abundance in the post-event year relative to the event year for taxa shown to be sensitive to extreme weather events on a field-by-field basis. Wald statistics (for models including all effects) excluding (a) and including the number of pesticide applications in the year following the event year. Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

a. Overall: Sample size = 181 pairs of fields.

	Degrees of freedom	Araneae	Cicadellidae	Delphacidae	Heteroptera adults	Thysanoptera	Braconidae	*Tachyporus* young	*Enicmus*	Lathridiidae	Cryptophagidae	Mycetophilidae
Year	3	0.89	**10.51***	0.58	4.53	2.53	**11.05***	5.57	2.14	2.65	3.34	0.64
Crop	2	0.50	0.03	2.75	2.72	2.20	0.10	**7.35***	3.93	1.71	4.77	0.82
Aspect	3	3.49	2.22	4.51	3.89	2.41	1.51	0.70	2.46	2.77	4.37	3.69
Field boundary density	1	1.35	0.08	0.47	0.01	0.38	0.05	0.47	0.12	0.05	1.68	0.59
Slope	1	1.35	0.43	0.69	0.20	0.38	0.20	0.18	0.03	0.90	0.02	0.20
Elevation	1	0.22	0.04	0.11	2.17	0.49	0.65	2.44	**14.60*****	**8.58****	3.70	0.30
Patch density (log)	1	2.51	**4.96***	0.01	0.53	0.72	0.49	0.08	0.15	2.02	**4.51***	1.45
Field area (log)	1	0.03	3.83	2.19	2.24	0.29	0.29	1.54	0.88	1.88	2.67	2.16

b. Including pesticide applications: Sample size = 92 pairs of fields.

	Degrees of freedom	Araneae	Cicadellidae	Delphacidae	Heteroptera adults	Thysanoptera	Braconidae	*Tachyporus* young	*Enicmus*	Lathridiidae	Cryptophagidae	Mycetophilidae
Year	3	-	**8.56***	0.46	3.41	1.64	2.90	2.07	0.05	2.76	0.44	2.39
Crop	2	-	0.21	1.98	1.14	0.39	2.70	**9.98***	0.40	1.41	4.30	2.34
Aspect	3	-	**11.15***	2.34	2.63	4.34	2.25	4.68	2.81	5.57	6.54	**15.01****
Field boundary density	1	-	0.22	0.03	0.14	1.74	0.15	1.26	0.17	0.56	1.25	0.04
Slope	1	-	2.17	0.05	0.01	0.63	0.01	0.18	0.13	0.08	0.08	2.44
Elevation	1	-	2.05	0.18	0.13	0.37	1.98	0.93	**12.35*****	**6.58***	0.50	1.57
Patch density (log)	1	-	**5.91***	0.46	0.42	0.68	0.70	0.55	0.03	0.66	2.82	0.24
Field area (log)	1	-	1.17	1.54	0.74	0.39	1.85	0.34	**5.19***	**5.14***	1.85	0.07
Herbicide	1	-	0.24	0.17	0.19	0.09	0.06	0.37	0.69	0.01	0.01	0.78
Fungicide	1	-	0.77	0.52	2.10	0.98	**5.60***	0.07	0.15	0.45	0.30	**5.16***
Insecticide	1	-	2.32	1.46	0.47	0.08	**9.68****	0.17	0.08	0.22	0.35	1.71

Table 8. Resilience to cold, wet events from generalised linear modelling of changes in invertebrate abundance in the post-event year relative to the event year for taxa shown to be sensitive to extreme weather events on a field-by-field basis. Wald statistics (for models including all effects) excluding (a) and including the number of pesticide applications in the year following the event year. Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

	Degrees of freedom	Araneae	Cicadellidae	Delphacidae	Heteroptera adults	Thysanoptera	Braconidae	*Tachyporus* young	*Enicmus*	Lathridiidae	Cryptophagidae	Mycetophilidae
a. Overall: Sample size = 210 pairs of fields.												
Year	3	1.48	4.04	2.16	2.54	2.41	5.03	4.32	1.69	3.83	1.89	2.25
Crop	2	2.00	2.65	2.70	0.48	0.03	2.23	3.08	1.72	1.43	4.65	0.28
Aspect	3	7.42	1.85	**8.86***	2.06	0.92	1.19	2.29	4.60	2.55	2.43	5.65
Field boundary density	1	0.44	0.01	0.18	1.03	0.01	0.01	0.01	0.64	1.05	0.84	2.19
Slope	1	0.74	0.03	2.61	0.24	2.13	0.19	0.73	0.02	0.03	0.74	2.89
Elevation	1	0.04	0.08	0.02	0.01	3.48	0.01	0.06	1.97	0.21	0.13	1.60
Patch density (log)	1	0.05	2.31	0.01	2.19	0.26	0.47	1.90	3.39	**5.18***	1.36	1.79
Field area (log)	1	0.14	1.31	0.23	**5.03***	0.46	1.77	0.09	1.41	0.28	**4.41***	1.34
b. Including pesticide applications: Sample size = 92 pairs of fields.												
Year	3	3.52	5.33	2.15	3.43	2.61	3.71	2.41	3.39	6.24	2.84	2.38
Crop	2	2.68	4.50	0.35	4.59	2.58	0.07	0.74	0.92	0.48	0.21	0.29
Aspect	3	7.74	1.50	6.39	2.10	2.50	1.04	1.21	4.06	7.02	3.49	3.55
Field boundary density	1	0.01	1.23	0.01	0.01	0.04	1.74	0.56	0.77	3.00	**4.00***	1.76
Slope	1	1.80	0.19	1.39	0.02	3.56	0.69	0.29	0.01	0.03	0.16	0.23
Elevation	1	0.45	0.12	0.61	2.26	**5.00***	0.01	0.36	0.28	0.24	0.01	0.22
Patch density (log)	1	0.01	**5.13***	0.23	0.93	0.04	0.01	3.48	2.04	**4.02***	2.73	0.95
Field area (log)	1	0.01	2.08	0.70	**9.22****	0.25	1.32	0.62	0.98	0.04	0.02	**4.50***
Herbicide	1	0.04	0.10	0.08	**4.54***	0.20	1.99	1.13	0.53	0.10	0.25	0.09
Fungicide	1	3.04	2.17	0.11	0.15	3.55	0.11	1.53	**4.95***	3.50	1.99	0.54
Insecticide	1	0.02	**7.37****	1.23	0.01	**4.19***	0.01	0.01	1.62	2.12	0.06	0.99

Table 9a. Mean change (± 1 SE) in abundance of invertebrates in relation to aspect of sampling location following a significant result for aspect within a mixed model (Table 4a). Means are adjusted for other factors in the model, and ones that are not different (P< 0.05) are labelled with the same letter.

Aspect	Araneae	Cicadellidae	Thysanoptera	*Tachyporus* (young)	Cryptophagidae	Mycetophilidae
North	-0.254 ± 0.376 ab	-1.038 ± 0.346 a	-0.633 ± 0.56 ab	0.982 ± 0.578 bc	0.349 ± 0.448 ab	0.57 ± 0.418 bc
East	-0.235 ± 0.223 a	-0.151 ± 0.206 b	-0.827 ± 0.323 a	-0.599 ± 0.339 a	-0.258 ± 0.259 ab	-0.385 ± 0.244 a
South	-0.013 ± 0.125 a	0.006 ± 0.115 b	0.122 ± 0.18 b	-0.083 ± 0.19 ab	-0.377 ± 0.145 a	-0.19 ± 0.137 ab
West	0.464 ± 0.166 b	0.165 ± 0.154 b	0.439 ± 0.234 b	0.546 ± 0.249 c	0.254 ± 0.189 b	0.392 ± 0.179 c

Table 9b. Mean change (± 1 SE) in abundance of invertebrates in relation to aspect of sampling location following a non-significant result for aspect within a mixed model (Table 7a). Means are adjusted for other factors in the model.

Aspect	Delphacidae	Heteroptera adults	Braconidae	*Enicmus*	Lathridiidae
North	-0.224 ± 0.367	0.09 ± 0.302	-0.521 ± 0.515	0.449 ± 0.341	0.643 ± 0.437
East	-0.282 ± 0.217	-0.218 ± 0.176	-0.079 ± 0.298	0.247 ± 0.188	0.14 ± 0.253
South	0.042 ± 0.122	0.118 ± 0.098	-0.34 ± 0.167	-0.133 ± 0.094	-0.127 ± 0.141
West	0.104 ± 0.162	0.273 ± 0.128	0.083 ± 0.217	0.077 ± 0.131	0.064 ± 0.183

Time series analysis

Long-term trends in invertebrate indices

For each of the taxa investigated long-term trends in the indices of abundance, the long-term trends in indices minus event years (used to determine recovery time) and a comparison of the two spline curves for these trends are shown in Appendix 9.

Invertebrate abundance and weather correlation

Of the 28 taxa/age groups identified to use in the analysis, 19 showed a significant correlation between their annual index of abundance and at least one measure of temperature for the April-May-June period (Table 10). Seventeen showed a significant correlation between their annual index of abundance and at least one measure of precipitation for the April-May-June period. There was some pattern with positive correlations between temperature and the abundance of Homoptera (Aphididae and Delphacidae), Heteroptera (though more for nymphs than for adults) Chalcididae and two families of Diptera (Empididae and Opomyzidae). The opposite was true of all Coleopteran taxa tested, with at least one measure of temperature significantly negatively correlated with the abundance of all Coleopteran families and genera tested. The abundance of Drosophillidae were also negatively correlated with two measures of temperature. The average of the three month's temperature was correlated with sixteen of the taxa tested, with May temperatures correlating with fifteen taxa. Precipitation showed more positive correlations with invertebrate abundance, with only Aphididae, Cicadellidae, Heteroptera (again more for nymphs than for adults), Thysanoptera, Lathridiidae and Cryptophagidae showing negative correlations with precipitation (the latter two only with precipitation in the earlier months). Positive correlations were found between precipitation and Collembola, several Coleoptera taxa (*Tachyporus* particularly the young age group, *Enicmus*, *Atomaria* and Cryptophagidae as a whole) as well as five of the seven Diptera taxa tested. Comparing the results of temperature and precipitation, in general if the abundance of a taxon increased with temperature, they declined with increased precipitation and vice versa.

Table 10. Spearman's correlation coefficients and associated significance for correlation between each weather variable and annual abundance index for each of the 28 selected taxa. * indicates significance at the 0.05 level, ** indicates significance at the 0.01 level and *** indicates significance at the 0.001 level.

	Years	Mean monthly temperature				Total monthly precipitation			
		April	May	June	AMJ	April	May	June	AMJ
Araneae	40	0.089	0.286	0.095	0.177	-0.251	0.057	0.035	-0.097
Collembola	38	0.009	-0.153	-0.190	-0.222	0.130	**0.495****	0.280	**0.508*****
Aphididae	40	0.060	**0.391***	0.259	**0.433****	-0.147	**-0.384***	-0.179	**-0.353***
Cicadellidae	39	0.287	0.105	0.286	0.268	**-0.427 ****	-0.175	0.063	-0.230
Delphacidae	39	0.314	0.294	**0.321***	**0.361***	-0.218	0.062	0.143	0.004
Heteroptera	40	**0.431****	**0.423****	0.238	**0.474****	-0.038	**-0.425****	-0.213	**-0.348***
Heteroptera (adults)	40	**0.403****	**0.502*****	**0.397***	**0.550*****	-0.175	-0.286	0.006	-0.236
Heteroptera (nymphs)	40	**0.428****	**0.356***	0.198	**0.426****	-0.029	**-0.429****	-0.214	**-0.353***
Heteroptera AY	40	**-0.389***	-0.229	-0.130	**-0.315***	-0.032	0.122	0.188	0.146
Thysanoptera	38	0.160	0.275	0.274	0.306	**-0.366***	-0.196	-0.176	**-0.413****
Braconidae	39	-0.013	0.167	0.037	0.144	-0.192	-0.254	-0.076	-0.286
Chalcididae	39	**0.424****	**0.543*****	**0.455****	**0.584*****	0.121	-0.021	-0.239	-0.160
Carabidae	40	**-0.317***	**-0.377***	**-0.372***	**-0.449****	-0.160	0.077	0.108	0.020
Tachyporus	40	-0.006	-0.140	**-0.445 ****	-0.265	-0.107	0.120	**0.501*****	**0.346***
***Tachyporus* (adults)**	40	**-0.497*****	**-0.605*****	**-0.526*****	**-0.713*****	-0.115	0.159	0.276	0.181
***Tachyporus* (young)**	40	0.062	-0.078	**-0.430****	-0.206	-0.092	0.116	**0.508*****	**0.359***
***Tachyporus* AY**	40	**-0.464****	**-0.362***	-0.223	**-0.462****	0.049	-0.087	-0.273	-0.242
Enicmus	40	**-0.417****	**-0.508*****	**-0.440****	**-0.564*****	-0.311	0.054	**0.334***	0.134
Lathridiidae	40	**-0.465****	**-0.483****	**-0.454****	**-0.570*****	**-0.364 ***	-0.040	0.298	0.008
Atomaria	40	**-0.551*****	**-0.506*****	**-0.547*****	**-0.657*****	-0.209	0.084	**0.332***	0.183
Cryptophagidae	40	**-0.440****	**-0.500*****	**-0.460****	**-0.580*****	**-0.360***	-0.028	**0.406****	0.098
Cecidomyiidae	39	0.219	-0.153	0.026	-0.032	0.127	**0.592*****	0.013	**0.318***
Mycetophilidae	39	0.052	-0.225	-0.111	-0.164	0.206	**0.445****	0.161	**0.450****
Empididae	39	0.248	**0.321***	-0.046	0.258	**0.339***	-0.117	0.097	0.142
Lonchopteridae	39	0.038	-0.190	-0.134	-0.153	0.296	**0.553*****	0.056	**0.505*****
Agromyzidae	38	0.124	0.064	0.005	0.044	0.206	0.298	-0.011	0.250
Opomyzidae	39	0.196	**0.412****	0.197	**0.387***	-0.136	-0.243	-0.034	-0.210
Drosophillidae	39	-0.178	**-0.338 ***	-0.186	**-0.362***	0.185	**0.586*****	0.068	**0.465****

Correlation analysis with average temperature and rainfall

Of the 28 taxa/age groups examined for correlations with average monthly temperature and average total rainfall, only four taxa showed no significant correlations with at least one of the weather variables: Araneae, Braconidae, Empididae and Agromyzidae (Table 11). In the remaining 24 taxa/groups, positive correlation with temperature with the long-term changes in taxon abundance was often combined with a negative correlation with rainfall and vice versa.

Significant correlations between measures of the intensity of pesticide use and indices of invertebrate abundance were found for 14 taxa/age groups in the case of herbicide and for 15 taxa/age groups, in the cases of fungicide and insecticide use. Although the majority of these were negative, as may be expected, there were several that were positive, most notably for Heteroptera nymphs, Chalcids and Empids (Table 11). Pesticide use has increased throughout the time of the Sussex Study, with big increases noted in the late- 1980s to early 1990s (Figure 8). Temperature was significantly positively correlated with increases in pesticide use, reflecting the increase in both temperature and pesticide use throughout the time of the Sussex Study (Figures 7, 8 and 9).Graphs for each correlation are shown in Appendix 10.

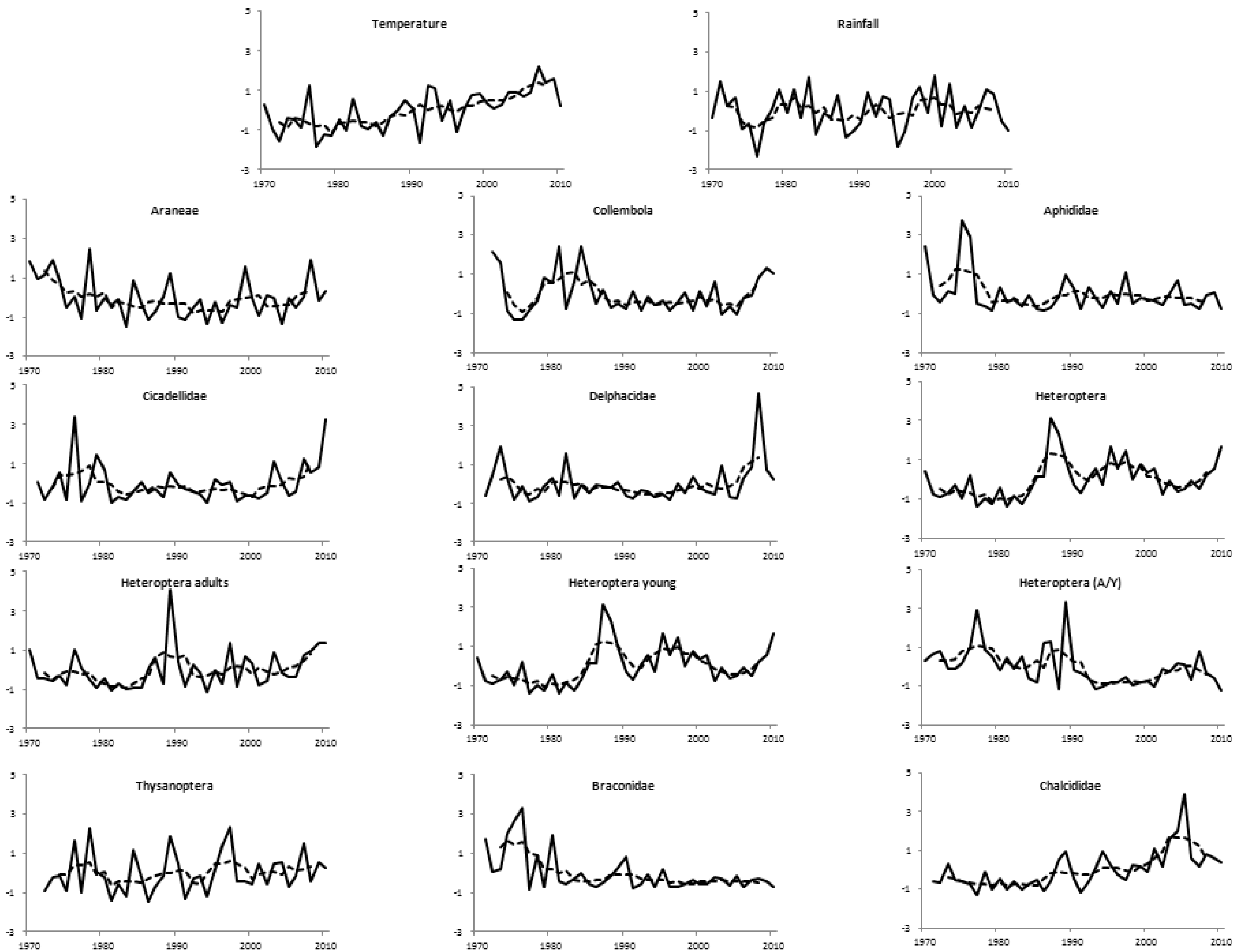


Figure 7. Standardized (zero mean, unit variance) time series and five-year running means (dotted line) for annual measurements of in temperature, rainfall and invertebrate abundance.

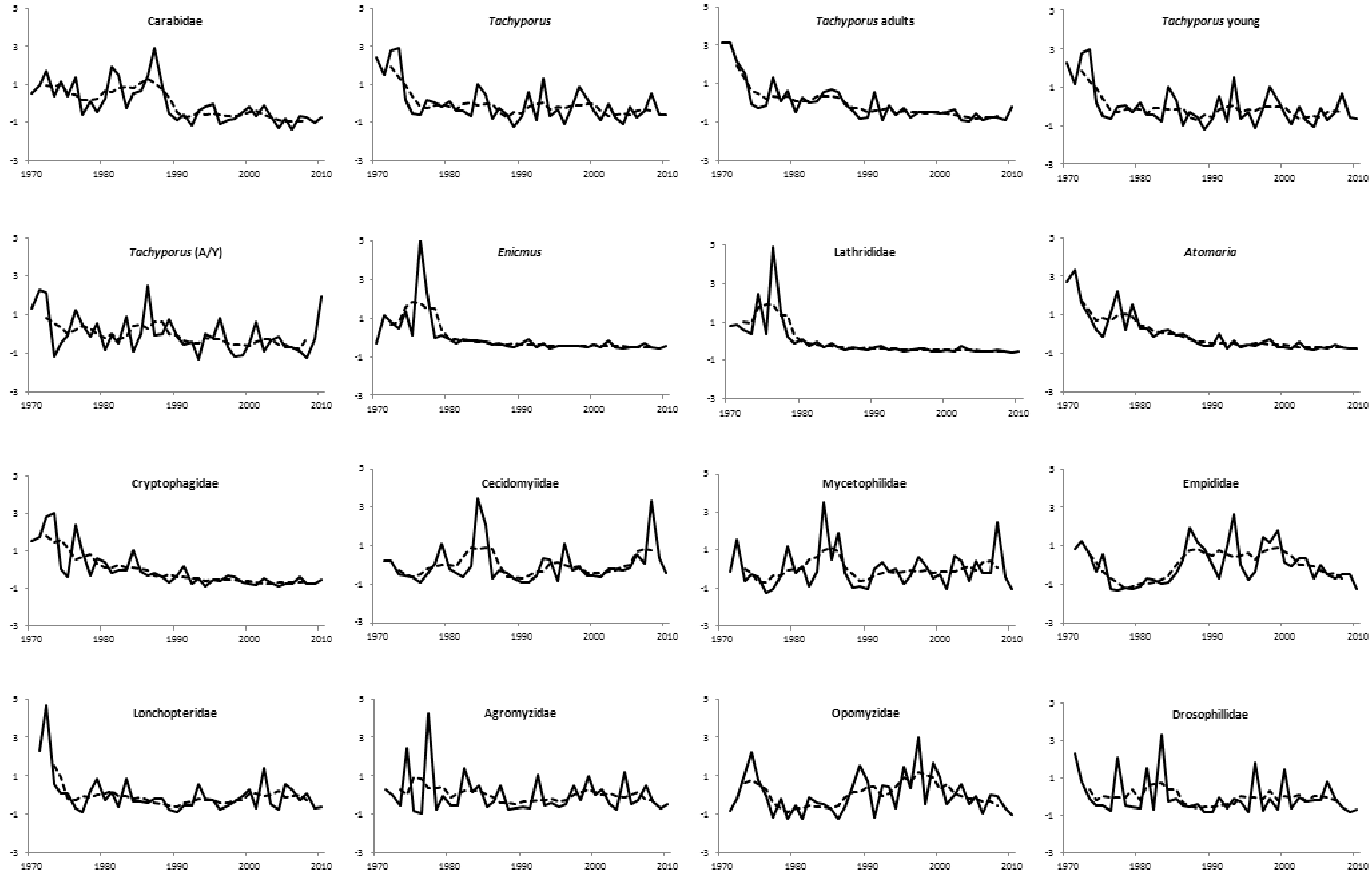
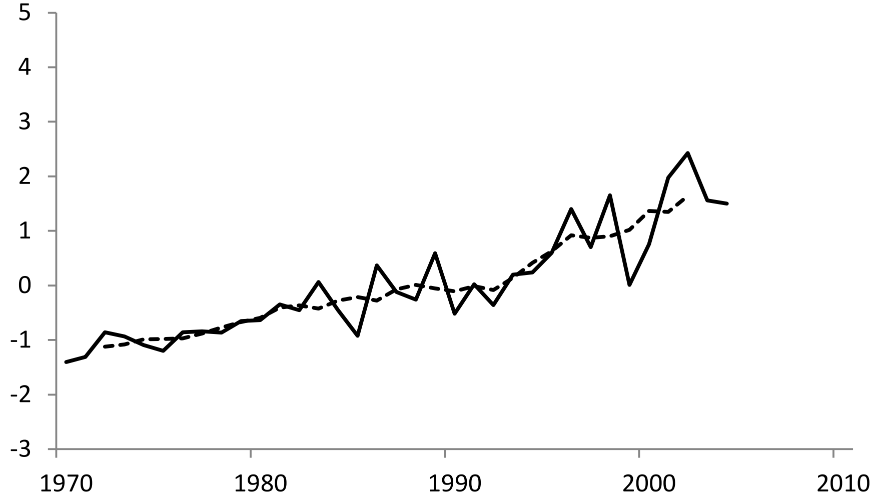
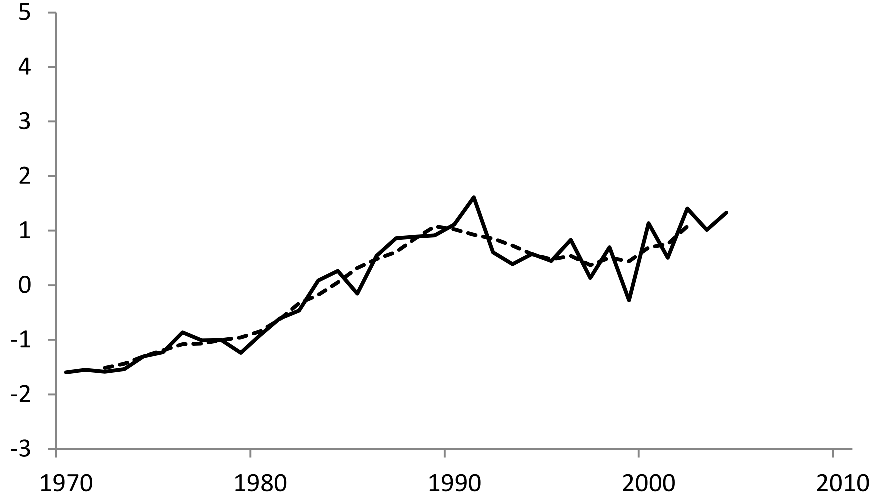


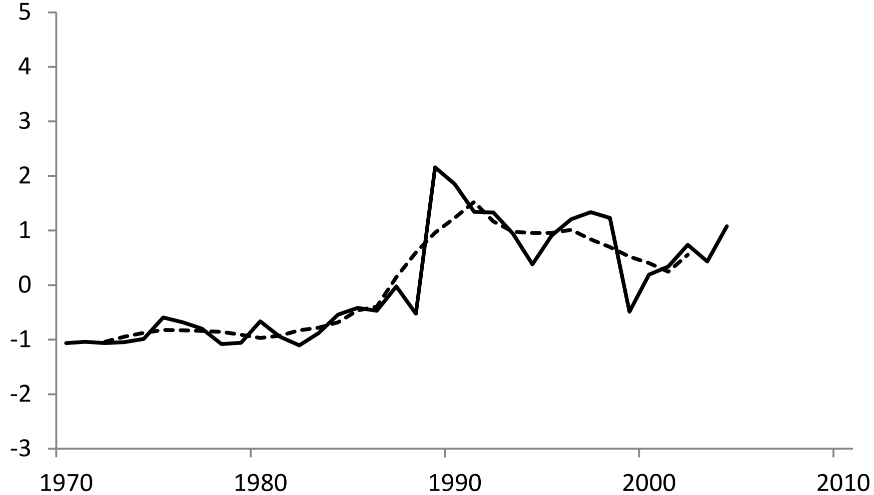
Figure 7 (continued).



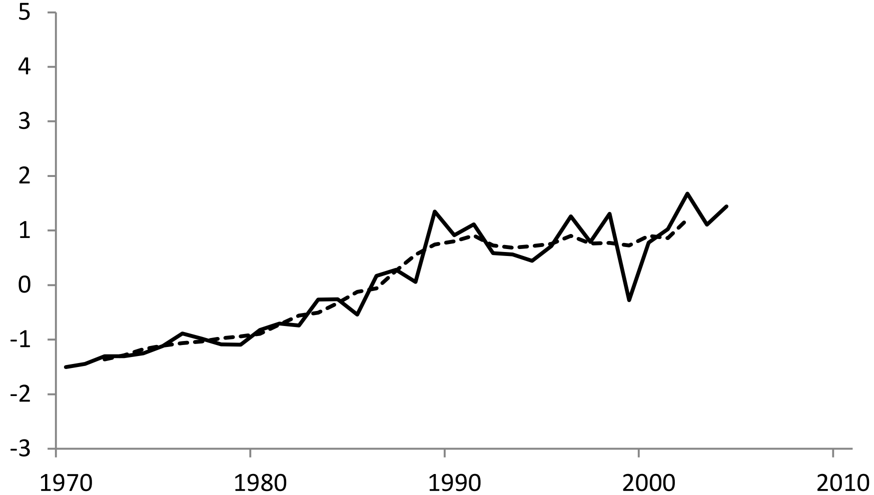
a) Herbicide use



b) Fungicide use

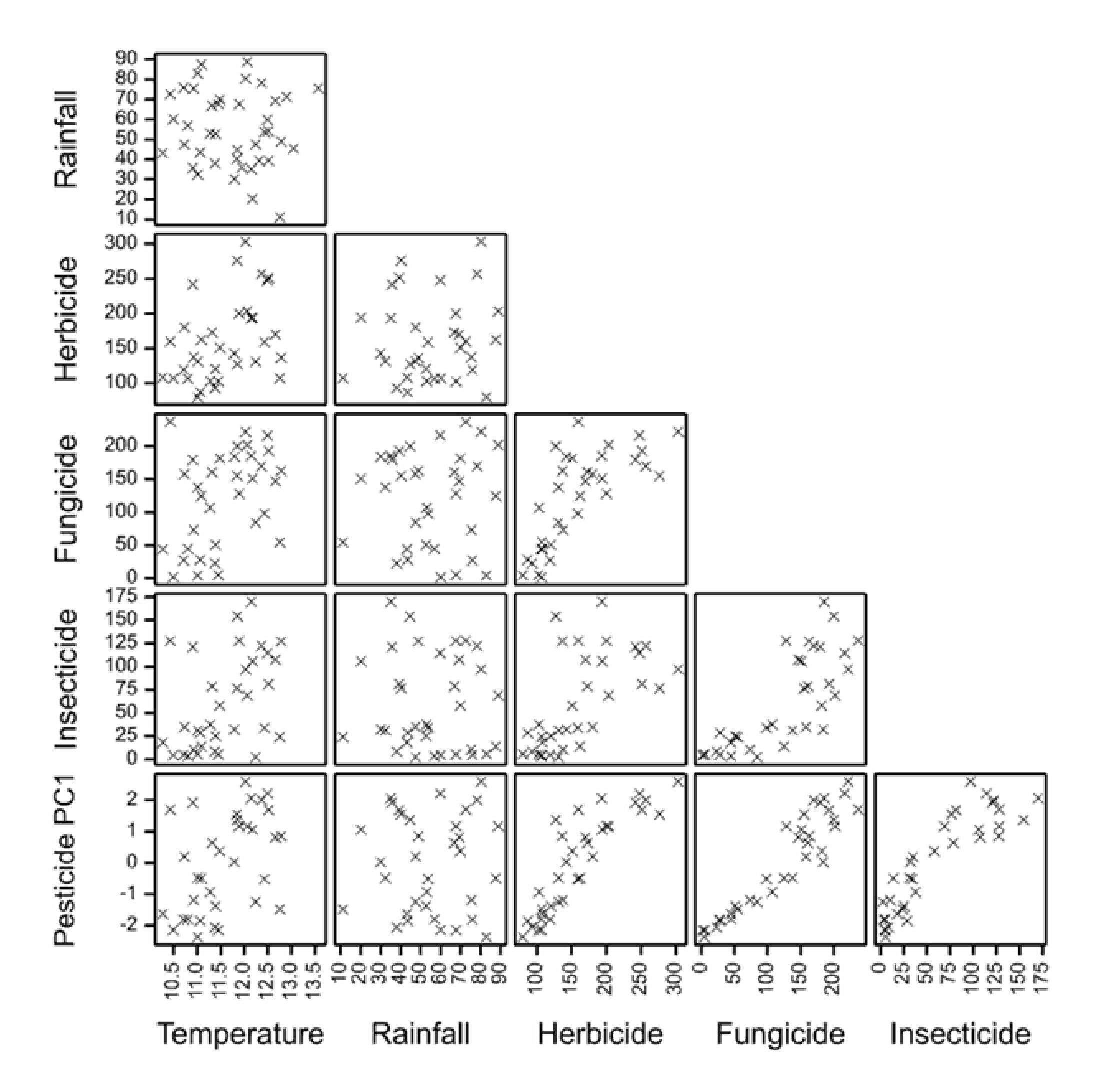


c) Insecticide use



d) Pesticide PC1

Figure 8. Standardised (zero mean, unit variance) time series and five- year running means for percentage spray area of (a) herbicide, (b) fungicide and (c) insecticide and (d) Pesticide PC1.



Rainfall	-0.154				
Herbicide	0.406*	0.085			
Fungicide	0.385*	0.004	0.77***		
Insecticide	0.430*	-0.084	0.673***	0.806***	
Pesticide PC1	0.438**	-0.014	0.892***	0.921***	0.885***
	Temperature	Rainfall	Herbicide	Fungicide	Insecticide

Figure 9. Spearman rank correlation analysis between the weather and pesticide use variables in Sussex. Temperature shows a significant positive correlation with all measures of pesticide use, while rainfall is not significantly correlated with any of the pesticide measures. Significant results indicated as*P < 0.05, ** P < 0.01, and*** P < 0.001.

Table 11. Spearman's correlation coefficients and associated significance for correlation between weather, pesticide use and annual abundance index for each of the 28 selected taxa. Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

	Years	Temperature	Rainfall	Years	Herbicide	Fungicide	Insecticide	Pesticide PC1
Araneae	38	0.225	-0.097	32	**-0.347***	**-0.361***	**-0.371***	**-0.376***
Collembola	36	-0.161	**0.508 *****	30	0.014	-0.045	-0.170	-0.051
Aphididae	38	**0.374***	**-0.353 ***	32	-0.111	-0.074	0.179	0.002
Cicadellidae	37	**0.317***	-0.230	31	-0.112	0.016	0.126	0.042
Delphacidae	37	**0.411****	0.004	31	-0.117	-0.237	-0.241	-0.242
Heteroptera	38	**0.462****	**-0.348 ***	32	**0.44****	**0.463****	**0.587*****	**0.475****
Heteroptera (adults)	38	**0.574*****	-0.236	32	0.122	0.175	0.317	0.184
Heteroptera (nymphs)	38	**0.403****	**-0.353 ***	32	**0.457****	**0.451****	**0.572*****	**0.476****
Heteroptera AY	38	-0.286	0.146	32	**-0.403***	**-0.344***	**-0.425***	**-0.395***
Thysanoptera	36	0.312	**-0.413 ****	30	0.058	-0.003	0.186	0.161
Braconidae	37	0.141	-0.286	31	**-0.417***	-0.306	-0.249	-0.342
Chalcididae	37	**0.596*****	-0.160	31	**0.486****	**0.383***	**0.372***	**0.465****
Carabidae	38	**-0.448****	0.020	32	**-0.522****	**-0.486****	**-0.685*****	**-0.643*****
Tachyporus	38	-0.242	**0.346 ***	32	**-0.457****	**-0.495****	**-0.376***	**-0.485****
Tachyporus (adults)	38	**-0.716*****	0.181	32	**-0.61*****	**-0.646*****	**-0.682*****	**-0.702*****
Tachyporus (young)	38	-0.182	**0.359 ***	32	**-0.422***	**-0.44****	-0.326	**-0.435***
Tachyporus AY	38	**-0.481****	-0.242	32	-0.163	-0.175	-0.220	-0.204
Enicmus	38	**-0.561*****	0.134	32	**-0.739*****	**-0.684*****	**-0.693*****	**-0.743*****
Lathridiidae	38	**-0.576*****	0.008	32	**-0.786*****	**-0.666*****	**-0.642*****	**-0.721*****
Atomaria	38	**-0.661*****	0.183	32	**-0.715*****	**-0.743*****	**-0.72*****	**-0.772*****
Cryptophagidae	38	**-0.576*****	0.098	32	**-0.715*****	**-0.653*****	**-0.634*****	**-0.701*****
Cecidomyiidae	37	0.012	**0.318 ***	31	0.038	-0.135	-0.174	-0.066
Mycetophilidae	37	-0.145	**0.450 ****	31	0.116	-0.001	0.015	0.034
Empididae	37	0.213	0.142	31	0.269	0.263	**0.398***	0.266
Lonchopteridae	37	-0.134	**0.505 *****	31	-0.216	**-0.352***	**-0.490****	**-0.430***
Agromyzidae	37	0.019	0.250	31	0.104	-0.114	-0.131	-0.039
Opomyzidae	37	**0.377***	-0.210	31	0.058	0.041	0.236	0.104
Drosophillidae	37	**-0.342***	**0.465 ****	31	0.072	0.030	-0.167	-0.022

Spectral and coherence analysis.

Although significant correlations were found between measures of weather and indices of abundance, it is clear from an examination of the standardized time-series (Figure 7) that the relationship for many of the taxa examined will not be straightforward. Spectral density curves were similar for some weather variables and some taxa but not all, with most spectral densities varying from a random time series at frequencies relating to long time scales – 20-100 years (Table 12; Appendix 11, Figure 1). Significant periodicity at long time scales was identified for temperature and fourteen of the taxa/age groups examined (Collembola, Heteroptera adults, Heteroptera young, Heteroptera AY; Braconidae, Chalcididae, Carabidae, *Tachyporus* adults, *Enicmus*, Lathridiidae, *Atomaria*, Cryptophagidae, Empididae and Opomyzidae). Significant shorter periodicity was identified for rainfall and only two taxa (Braconidae and Drosophillidae). Three taxa show periodicity at medium frequencies: Thysanoptera, Mycetophilidae and Agromyzidae. The general pattern, when examining the results of the coherence analysis between temperature and changes in invertebrate indices is of significant similarities at two time scales (Table 13a; Appendix 11, Figure 2). These are at long time scales from around 10 to 100 years, reflecting some of the long-term changes seen in invertebrate abundance over the whole of the time of the Sussex Study, and shorter time scales, centring around 2 years. The ten taxa/age groups with coherence with temperature at long time scale were: Cicadellidae, Braconidae, Chalcididae, Carabidae, *Tachyporus* adults, *Tachyporus* AY, Lathridiidae, *Atomaria*, Cryptophagidae and Empididae. There were twelve taxa/age groups that's showed coherence with temperature at shorter time scales (Aphididae, Cicadellidae, Heteroptera, Heteroptera adults, Heteroptera nymphs, Thysanoptera, Braconidae, Carabidae, Lathridiidae, *Atomaria*, Opomyzidae and Drosophillidae) Interestingly these short-term scale events are not confined to taxa shown to be sensitive to extreme weather events, although the time scales involved reflect the recovery rates identified in earlier work, which showed very quick recovery times across all taxa to an extreme event. The similarities at long-time scales raise the question of whether the observed increase in temperature is behind some of the more long-term changes seen in the indices of abundance in the invertebrate taxa/age groups examined here.

The results of the comparison between rainfall and changes in invertebrate indices (Table 13b; Appendix 11, Figure 3) produced fewer significant similarities, with the general trend of most significant coherences being at a timescale of between 5-10 years , as was the case for Delphacidae, Thysanoptera, *Tachyporus*, *Tachyporus* young, *Atomaria* and Lonchopteridae. Coherence between rainfall and Collembola and Drosophillidae were significant at shorter timescales (2 years), while Heteroptera AY showed significant coherence with rainfall at long time scales.

Table 12. Results from spectral analysis for trends in insect abundance indices and trends in temperature and rainfall. Taxa with significant correlations are in bold. Orange rectangles are where spectral densities are significant different from those of a random time series.

	Frequency																																																
	0.01	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.09	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35	0.36	0.37	0.38	0.39	0.40	0.41	0.42	0.43	0.44	0.45	0.46	0.47	0.48	0.49	0.50
Temperature	■	■	■	■																																														
Rainfall																																															■	■	■	■
Araneae																																																		
Collembola				■	■	■	■	■	■	■																																								
Aphididae																																																		
Cicadellidae																																																		
Delphacidae																																																		
Heteroptera																																																		
Heteroptera (adults)	■	■	■	■	■	■	■	■	■	■	■																																							
Heteroptera (nymphs)	■	■	■	■	■	■	■	■	■	■	■																																							
Heteroptera AY	■	■	■	■	■	■	■																																											
Thysanoptera																■	■	■	■																															
Braconidae	■	■	■	■																																													■	■
Chalcididae	■	■	■	■	■	■																																												
Carabidae	■	■	■	■	■	■	■																																											
Tachyporus																																																		
Tachyporus (adults)	■	■	■	■	■	■	■																																											
***Tachyporus* (young)**																																																		
Tachyporus AY																																																		
Enicmus	■	■	■	■	■	■	■																																											
Lathridiidae	■	■	■	■	■	■																																												
Atomaria	■	■	■	■	■	■																																												
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Empididae	■	■	■	■	■	■	■																																											
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Opomyzidae				■	■	■	■																																											
Drosophillidae																																												■	■	■	■	■	■	■
	100.00	50.00	33.33	25.00	20.00	16.67	14.29	12.50	11.11	10.00	9.09	8.33	7.69	7.14	6.67	6.25	5.88	5.56	5.26	5.00	4.76	4.55	4.35	4.17	4.00	3.85	3.70	3.57	3.45	3.33	3.23	3.13	3.03	2.94	2.86	2.78	2.70	2.63	2.56	2.50	2.44	2.38	2.33	2.27	2.22	2.17	2.13	2.08	2.04	2.00
	Periodicity (years)																																																	

Table 13. Results from coherence analysis for trends in insect abundance indices and trends in weather (temperature). Taxa with significant correlations are shown in bold. Yellow rectangles are where spectral frequencies of taxa (and periodicity in years) were significantly similar to weather variable frequencies.

a) Temperature versus taxa spectral frequencies

	Frequency																																																	
	0.01	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.09	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35	0.36	0.37	0.38	0.39	0.40	0.41	0.42	0.43	0.44	0.45	0.46	0.47	0.48	0.49	0.50
Araneae																																																		
Collembola																																																		
Aphididae																																																		
Cicadellidae																																																		
Delphacidae																																																		
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Braconidae																																																		
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	100.00	50.00	33.33	25.00	20.00	16.67	14.29	12.50	11.11	10.00	9.09	8.33	7.69	7.14	6.67	6.25	5.88	5.56	5.26	5.00	4.76	4.55	4.35	4.17	4.00	3.85	3.70	3.57	3.45	3.33	3.23	3.13	3.03	2.94	2.86	2.78	2.70	2.63	2.56	2.50	2.44	2.38	2.33	2.27	2.22	2.17	2.13	2.08	2.04	2.00
	Periodicity (years)																																																	

Table 13 (continued).

b) Rainfall versus taxa spectral frequencies

	Frequency																																																	
	0.01	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.09	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35	0.36	0.37	0.38	0.39	0.40	0.41	0.42	0.43	0.44	0.45	0.46	0.47	0.48	0.49	0.50
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Collembola																																																		
Aphididae																																																		
Cicadellidae																																																		
Delphacidae																																																		
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Heteroptera (adults)																																																		
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	100.00	50.00	33.33	25.00	20.00	16.67	14.29	12.50	11.11	10.00	9.09	8.33	7.69	7.14	6.67	6.25	5.88	5.56	5.26	5.00	4.76	4.55	4.35	4.17	4.00	3.85	3.70	3.57	3.45	3.33	3.23	3.13	3.03	2.94	2.86	2.78	2.70	2.63	2.56	2.50	2.44	2.38	2.33	2.27	2.22	2.17	2.13	2.08	2.04	2.00
	Periodicity (years)																																																	

Multiple regression

Trends in the indices of invertebrate abundance were compared to trends in temperature, rainfall and pesticide use (Pesticide PC1) using multiple regression (Table 14). There was no overall pattern, but there were patterns when considering the results in terms of higher taxonomy – so, for example considering the Homoptera (Aphididae, Cicadellidae, Delphacidae) and Heteroptera together, indicates that changes in their long-term trends more closely reflected the long-term trends in weather than those in pesticide use. Conversely, considering all the Coleoptera (Carabidae, *Tachyporus*, *Enicmus*, Lathridiidae, *Atomaria* and Cryptophagidae) the over-riding finding is that increase in pesticide use negatively affected their long-term trends, with a few instances of weather (either temperature or rainfall) having had an effect. Changes in the abundance indices of Araneae were negatively related to measures of pesticides, while Collembola abundance was positively related to increases in rainfall. The long-term trends in Braconidae and Chalcididae revealed an effect of both weather and pesticide use, but the effects were not similar. Braconidae were negatively affected by increases in rainfall and pesticide use, while Chalcididae were positively affected by increases in temperature and pesticide use. The spectral densities of these two taxa were unique amongst the taxa examined (Appendix 11, Figure 1) and this may reflect their parasitoid life histories, where effects of weather or pesticides on their hosts may affect them as well as the direct effects of weather and pesticides on them directly. Little effect of pesticide use was found for the Dipteran taxa examined, but increases in Empididae and Opomyzidae and decreases in Drosophillidae were associated with increasing long-term trends in temperature, with increased changes in the abundance index of Lonchopteridae associated with increases in rainfall. Dipterans, as a group, are highly mobile and can recolonize a cereal field quickly after pesticide applications, so have not been considered to be especially susceptible to pesticide use.

Table 14. Multiple regression of abundance indices against temperature, rainfall and first principal component of pesticide use for each of the 28 taxa examined. Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

Taxa/age groups	Test statistics	Regression coefficients		
		Temperature	Rainfall	Pesticide use principal component (Pesticide PC1)
Araneae	**$F_{3,30}$ = 3.60***	0.105	0.002	**-0.090****
Collembola	**$F_{3,28}$ = 3.76***	-0.076	**0.076***	-0.027
Aphididae	**$F_{3,30}$ = 4.59****	**0.146***	**-0.076***	-0.053
Cicadellidae	**$F_{3,29}$ = 4.06***	0.219	**-0.183***	-0.082
Delphacidae	**$F_{3,29}$ = 3.60***	**1.676***	0.165	**-0.912****
Heteroptera	**$F_{3,30}$ = 4.06***	0.159	-0.095	0.106
Heteroptera (adults)	**$F_{3,30}$ = 3.07***	0.179	-0.076	0.047
Heteroptera (nymphs)	**$F_{3,30}$ = 3.22***	0.152	-0.103	0.126
Heteroptera AY	$F_{3,30}$ = 1.65	-0.186	-0.046	-0.031
Thysanoptera	$F_{3,28}$ = 2.87	0.224	-0.370	0.104
Braconidae	**$F_{3,29}$ = 7.76*****	0.141	**-0.111***	**-0.135****
Chalcididae	**$F_{3,29}$ = 6.64*****	**0.506***	-0.032	**0.204***
Carabidae	**$F_{3,30}$ = 4.64****	-0.021	-0.017	**-0.174****
Tachyporus	**$F_{3,30}$ = 4.68****	0.014	**0.062***	**-0.083****
Tachyporus (adults)	**$F_{3,30}$ = 13.66*****	**-0.097***	0.030	**-0.071*****
Tachyporus (young)	**$F_{3,30}$ = 3.89***	0.032	**0.067***	**-0.085***
Tachyporus AY	**$F_{3,30}$ = 2.97***	**-0.203***	-0.057	-0.007
Enicmus	**$F_{3,30}$ = 6.76*****	0.499	-0.887*	**-1.255****
Lathridiidae	**$F_{3,30}$ = 8.85*****	0.163	**-0.214****	**-0.289*****
Atomaria	**$F_{3,30}$ = 12.94*****	-0.078	0.019	**-0.105*****
Cryptophagidae	**$F_{3,30}$ = 7.45*****	-0.030	-0.015	**-0.164*****
Cecidomyiidae	$F_{3,29}$ = 0.88	-0.279	-0.009	0.007
Mycetophilidae	$F_{3,29}$ = 1.58	-0.374	0.081	0.040
Empididae	**$F_{3,29}$ = 3.20***	**0.262***	0.096	0.020
Lonchopteridae	**$F_{3,29}$ = 3.52***	-0.022	**0.082***	-0.072
Agromyzidae	$F_{3,29}$ = 0.47	-0.007	0.012	-0.110
Opomyzidae	**$F_{3,29}$ =3.02***	**1.016***	-0.136	-0.089
Drosophillidae	**$F_{3,29}$ = 3.40***	**-0.169***	0.060	0.0151

Discussion

Effects of habitat, landscape and management on sensitivity and resilience to weather events

The only consistent trend to emerge from the analysis of habitat and landscape features on the sensitivity to and resilience to extreme weather events was an effect of aspect on invertebrate sensitivity to extreme cold and wet weather events. The general pattern was that during such events, invertebrate abundance increased from the preceding year on west-facing slopes whereas it tended to decrease from the preceding year on other slopes, especially east-facing ones.

Aspect has been highlighted as a potentially key landscape component in influencing climatic conditions at a small, localised scale (Oliver et al. 2010). It is thought that these microclimates provide microrefugia from weather events, and their influence on abundance and distribution has been reported for a range of species (at a range of scales), from invertebrates such as Lepidoptera (Weiss et al. 1993) and Coleoptera (Dennis, Thomas & Sotherton 1994), to bird species (Calladine & Bray 2012). Explanations for the influence of aspect on local climatic conditions range from differing levels of exposure to solar radiation across differing aspects (Bennie et al. 2008) to differences in available soil moisture (Western et al. 1999), warmer winter daytime temperature (Dennis, Thomas & Sotherton 1994) and increased exposure to warm dry NW winds (Ashcroft, Chisholm & French 2009). As the effect of aspect in our study was apparent only during cold and wet event years, some interplay between temperature, moisture and wind on a microclimate level leading to conditions more suitable for invertebrates on those west-facing slopes is likely to be occurring. It is difficult to pinpoint exactly what this combination of conditions might be since we have no measurements of either temperature or humidity at this micro scale. These localised conditions may help to mitigate the effects of extreme weather events experienced across the study area, allowing invertebrate taxa at those sample locations to avoid the declines in abundance seen at other locations. Extrapolating our results to other localities should be done with caution; thermal microclimate effects have been shown to be sensitive to local conditions, making predictions on the effects of climate on species difficult (Bennie et al. 2010). One other consideration may have been sampling efficiency, but the sampling method used (D-Vac) dictated that sampling was only undertaken in warm, dry conditions. More frequent sampling of cereal fields on the Sussex Study Area would help to produce more comprehensive measures of invertebrate abundance, although to do so would need a vastly increased level of resources than the current monitoring practice requires. Alternative sampling methods, such as pitfalls, sweep and vortex, have been considered, but sampling efficiency would still vary between cereal types and for different invertebrate taxa. Employing all of these methods would again increase the level of resources required.

Density of field boundaries, which is a potential indicator of connectivity of semi-natural habitat, did not significantly relate to invertebrate sensitivity or resilience to extreme weather events. For some members of the groups examined, for example Araneae or the Dipterans, this is perhaps not surprising as they may readily move throughout a field (Holland et al. 1999). However other taxa, in particular Carabidae, have shown associations with field boundaries in within-field spatial sampling (Holland et al. 1999; Thomas, Holland & Brown 2002). It may be that some of the recent habitat management on the Sussex study area will provide better quality field boundaries and it might be worth revisiting this analysis in succeeding years, as this develops further.

The lack of any other clear-cut associations between landscape/habitat and either sensitivity or resilience supports results from our analysis of recovery time. This showed that the sensitive invertebrate taxa and age groups recovered quite quickly, usually within a year and a half after an extreme event. The cereal invertebrate taxa that we examined exhibit great variability in their abundance (as shown in the standardised time series in Figure 7). This variability may reflect the annual perturbation cycle of their cereal ecosystem habitat, where crops are harvested, ground is ploughed and a new habitat sown within months, which probably favours species with an ability to cope in a highly variable environment. Farming intensification, with the associated increase in pesticide use, will have increased the selection for taxa that are able to recolonize fields after pesticide treatment (but see Ewald & Aebischer 1999 and Game Conservancy Trust 2007 for evidence of a "carry-over" effect of pesticide use on some invertebrate groups).

Long-term trends in invertebrate abundance, climate and pesticide use

The measures of weather that we considered had significant positive and negative correlations with invertebrate taxa over the duration of the study. This may indicate that long-term changes in weather – consistent with climate change - has been altering invertebrate abundance; any change in weather will also have been confounded with other changes taking place in the Sussex Study area, for instance increases in pesticide use.

Our comparisons of time-series of invertebrate taxa with the time-series in temperature showed coherence between them at two time periods, one of a relatively short time frame (~2 years) and the other acting over long time scales (10+ years). The shorter time frame may represent the impact of direct weather events that, owing to the quick recovery of cereal ecosystem invertebrates, have had little long-term effect on the community. In general, the taxa found to have short-term coherences with weather differed from those found to be sensitive to extreme weather events; only five of the eleven taxa showed both sensitivity to extreme weather events and coherence with trends in temperature over a short time frame. The long time-scale coherence may represent an effect of long-term changes in weather, particularly temperature and seems to corroborate the correlations between temperature and changes in abundance across the taxa examined.

Our multivariate analysis of the long-term trends in invertebrate abundance in relation to weather and pesticide use (taken as an index of farming intensification) suggest that the long-term trends in some higher level-taxa in Sussex (Araneae and Coleopterans for example) are driven by farming intensification. Others (Collembola, Aphididae, Cicadellidae, Thysanoptera, Lonchopteridae, Opomyzidae and Drosophillidae) appear to be related to changes in weather over the long term. One driving force behind changes in some groups may be a response to changing food resources, which was not considered in this analysis. It is possible for instance that Heteroptera and Chalcididae were responding to increases in broad-leaved weeds (Potts et al. 2010; Potts 2012).

Lastly, in order to better manage changes in invertebrate long-term trends in abundance and distribution in response to climate change the interaction with other factors (habitat and management practices) needs to considered (WallisDeVries, Baxter & Van Vliet 2011).

Data on pesticide use in the Sussex study area, our measure of farming intensification, is available from 1970 to 2004 (Ewald & Aebischer 1999; 2000; Game Conservancy Trust 2007), and it is perhaps worth considering the picture that this paints of arable pesticide use on the study area. All measures of pesticide use increased, including both area sprayed and the number of times crops were sprayed. Most of this increase took place by the 1990s in the case of fungicide and insecticide use, and while the use of herbicides was widespread at the beginning of the study in 1970, the number of applications increased through 2004. The pesticide use in Sussex was compared to figures for the UK, adjusting for cropping. Herbicide and fungicide use in Sussex from 1970 to 2004 matched that across the UK, whereas the intensity of their use was lower than nationally. Insecticide use and intensity was higher than nationally during the 1990s, but recent years (2002, 2004) agreed with national figures. The efficacy of the cocktail of herbicides used increased over the time of the study, fungicide use included more multi-site specific compounds and the use of pyrethroids and non-systemic organophosphates increased, while systemic organophosphate insecticide use decreased. Work is on-going to update information on pesticide use on a field-by-field basis from 2005 to the present day.

Comparison of our results to published results

The most studied taxa that we have considered are the Aphididae. Glasshouse and some field-based experiments indicate that aphid responses to the effects of climate change (increased temperature, higher CO_2) have been varied and are species-specific (Newman et al. 2003; Awmack, Woodcock & Harrington 1997; Auad et al. 2012). The interaction of temperature and CO_2 may result in little change in abundance (Hoover & Newman 2004) , while models that have taken these experimental results and applied them on a regional basis have found the same (Newman 2005; Newman 2006). Monitoring across Europe suggests an increase in the number of species recorded and earlier spring flights (Hulle et al. 2010), but no change in abundance. Our results for Sussex indicate a positive relationship with temperature, but the long-term trend in aphid abundance in Sussex indicates no increase. Other research has emphasized the importance of the effects of parasitoids and predators on regulating the abundance of aphids (Duffield & Aebischer 1994; Legrand et al. 2004) and that may be part of what is taking place in Sussex where there has been no long-term increase in the abundance of Aphididae as a group. If this regulation of abundance were absent, pest pressure from aphids may increase if temperature rises occur as projected under climate change models.
In line with our results, other researchers have noted the negative effect of agricultural intensification on the diversity of spiders in arable landscapes (Dormann et al. 2008), with the effect of reducing pesticides theorised to have a greater effect on spider abundance where precipitation was highest (Amano et al. 2011). Our results for the long-term trends in Collembola (positive correlation with rainfall) reflect the results in other studies that examined the effect of drought (and irrigation) on the abundance of this taxon (Frampton, van den Brink & Gould 2000a; Frampton, van den Brink & Gould 2000b). For parasitoid taxa (Braconidae and to some extent Chalcididae) the expectation from modelling work is that increases in temperature will decrease reproductive success (Denis et al. 2011), though this may be offset through adaptation (Denis et al. 2012). Results from a comparison of parasitoid infections in Lepidopteran caterpillars from Brazil to Canada indicated that areas with higher precipitation variability had lower levels of Hymenopteran parasitoid infection, hypothesized to result from the inability of these parasitoids to find their hosts in a more variable environment (Stireman et al. 2005). In northerly UK moorland habitats, declines have been recorded in species of Carabidae, perhaps indicating a negative effect of climate change especially on species adapted to northerly climes (Morecroft et al. 2009; Brooks et al. 2012). However, in arable systems, others have noted that declines in Carabidae abundance in an agricultural setting are related to agricultural intensity (Geiger et al. 2010) while some have found no effect on species

richness of Carabids (or Heteroptera) of either climate, land-use intensity or landscape variables (Dormann et al. 2008).

We note that most other datasets cover shorter time periods and often begin between the mid-1980s to the 1990s, significantly after many of the changes that we have observed in the Sussex Study dataset in connections with the advent of fungicide and insecticide use (Ewald & Aebischer 1999; Ewald & Aebischer 2000). The first hot, dry extreme event identified here (1976) is correlated with the first indications of large scale insecticide use within the Sussex study area. Aphicides were applied to winter wheat crops in the summer of 1976 in response to large scale aphid outbreaks (Ewald & Aebischer 1999). Our results indicate that the increasing pesticide use that has accompanied the long-term increase in temperature on the Sussex Study area (Ewald & Aebischer, 1999; 2000; Game Conservancy Trust, 2007) has had more of an effect on long-term changes in invertebrate abundance for some of the taxa we investigated (particularly Araneae and Coleoptera such as Carabidae and Staphylinidae – i.e. *Tachyporus*). Changes in the abundance of farmland birds across the UK have been linked more closely to increases in agricultural intensification than climate change (Eglington & Pearce-Higgins 2012). Both of these findings may indicate that the main driver of change in an agricultural ecosystem is the anthropogenic management undertaken in this system.

Implications for cereal crop management

Our results suggest that there is little habitat manipulation that can (or even should) be done to offset short-term responses by cereal invertebrates to extreme weather events. Methods to mitigate the effect of farming intensification are well known and many are currently funded in England through Environmental Stewardship (beetle banks, conservation headlands). There may be some advantage in targeting the location of these to east-facing slopes in order to counteract the effects of a cold, wet summer or to create west-facing slopes by orienting beetle banks, in particular, in a north-south direction. However, earlier work on beetle bank location showed that those running east to west had higher winter densities of *Tachyporus hypnorum* (Dennis et al. 1994). As several of the long-term effects of climate change may lead to increases in some taxa (Rosenzweig et al. 2001; Shaw et al. 2008; Chakraborty & Newton 2011; Finlay & Luck 2011; Kristensen, Schelde & Olesen 2011), several of which contain cereal pests (Aphididae, Thysanoptera and Opomyzidae), this may lead to an increased use of insecticide, which will have a detrimental effect on other taxa. This appears to be the most likely long-term negative effect of climate change on cereal invertebrates from our results here and in other analyses of the effects of pesticide use carried out within the GWCT (Potts 1986; Aebischer 1990; Aebischer 1991; Sotherton 1991; Ewald & Aebischer 1999). It is also supported by other researchers (Benton et al. 2002; Geiger et al. 2010). The utilisation of conservation headlands (Sotherton 1991) together with beetle banks (Collins et al. 2002), as part of an agri-environmental package for the conservation of farmland birds, will also reap benefits for the conservation of cereal invertebrates (Winspear et al. 2010).

Considerations

One note of caution regarding our results is the taxonomic level to which invertebrates are identified within the Sussex Study dataset. Some researchers have found that changes in weather, particularly increases in temperature, have led to changes in abundance at the species level but that there was no overall change in abundance measured at higher taxonomic levels (e.g. Collembola – Bokhurst et al. 2012; Braconidae - Fernandez-Triana et al. 2011). Some studies have even revealed changes within species reflected in DNA-level changes over time (*Drosophila* - Umina et al. 2005). This could be the case here, though our analyses at the genus/family level for *Enicmus*/Lathridiidae and *Atomaria/C*ryptophagidae showed similar patterns and would seem to offer some reassurance that such effects may be small in the present study.

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Appendix 1

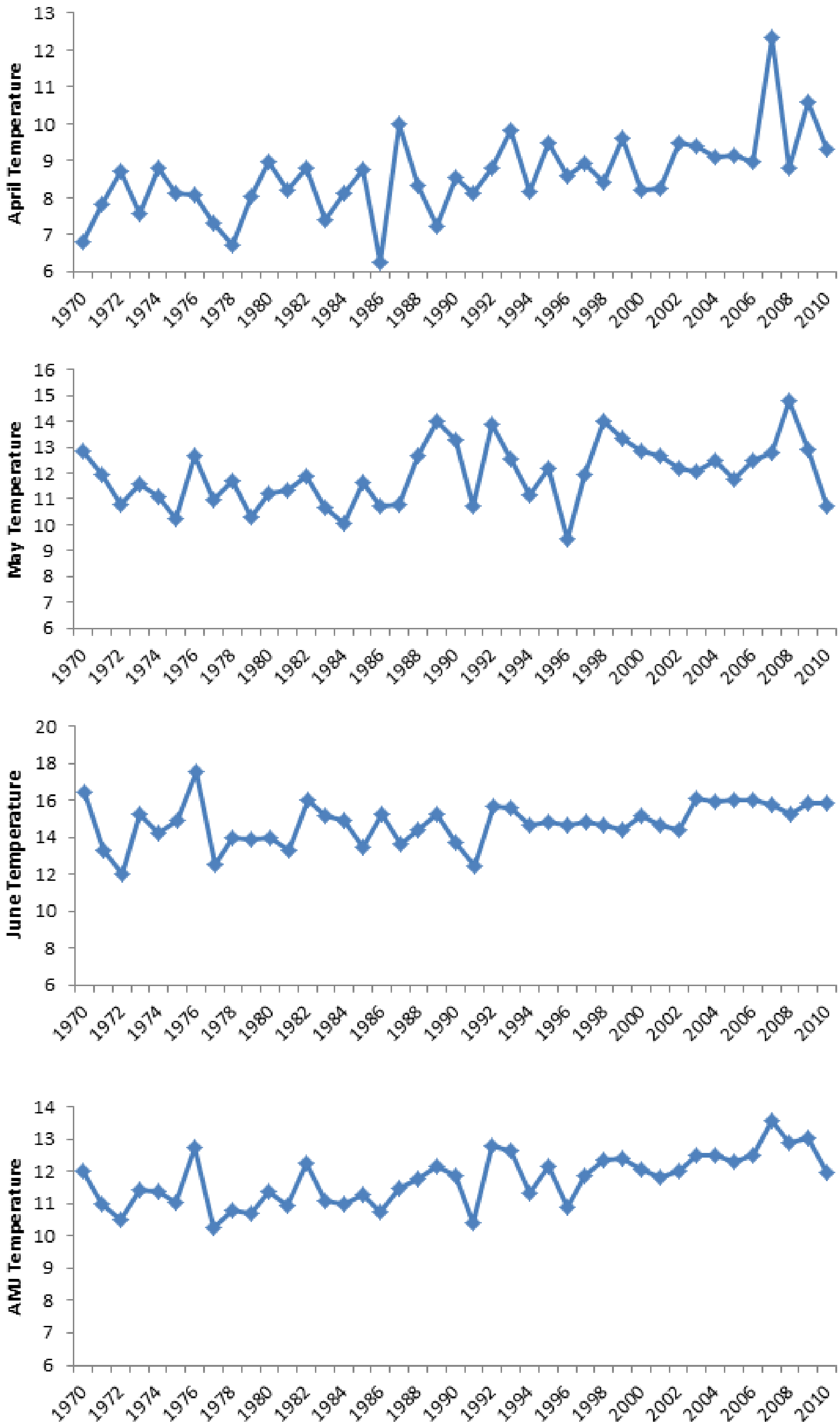


Figure 1. Average monthly temperature for (A.) April, (B.) May, (C.) June and (D.) the average of April, May and June.

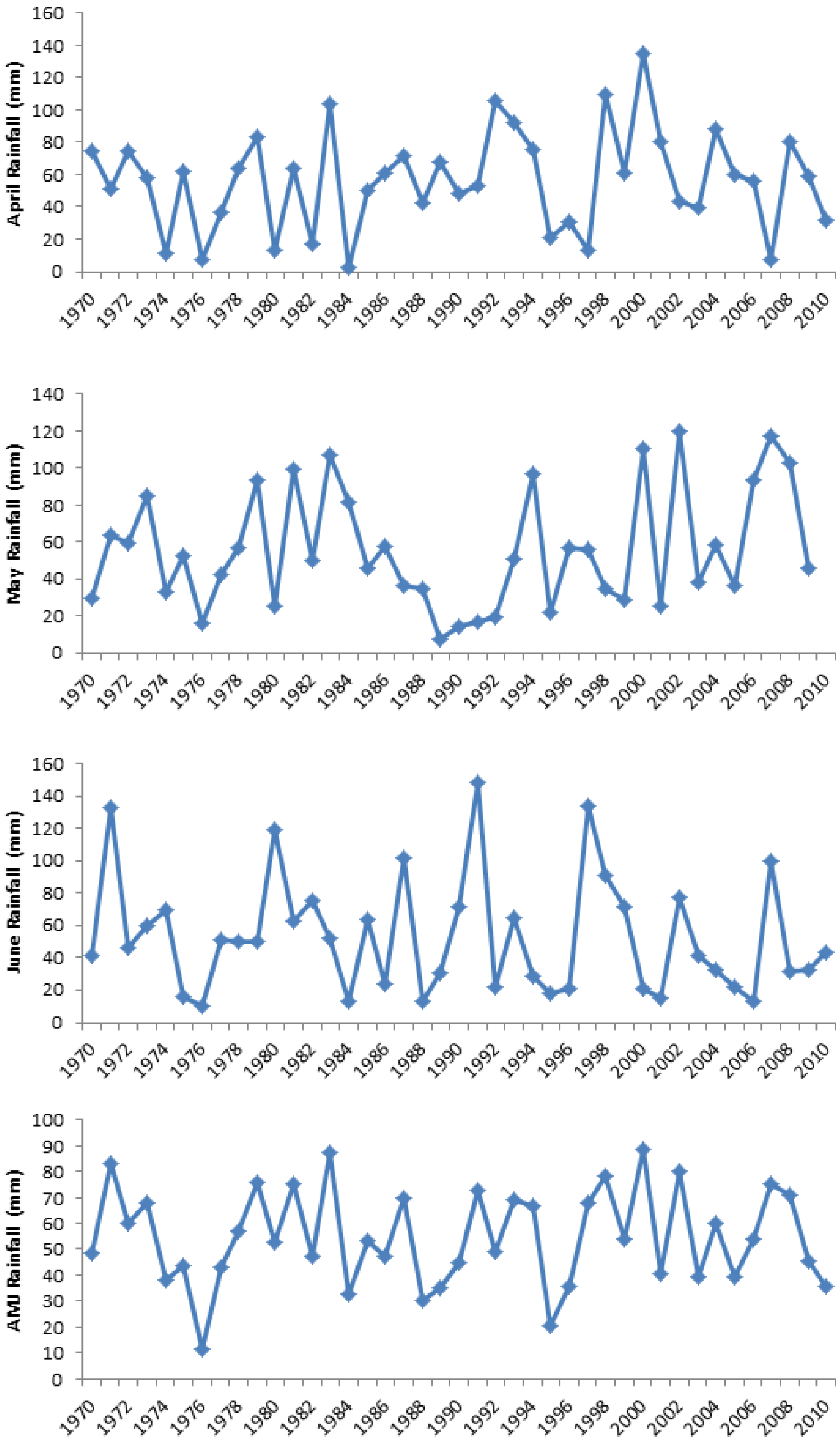


Figure 2. Total monthly rainfall for (A.) April, (B.) May, (C.) June and (D.) the average of April, May and June.

Appendix 2

Table 1. Weather data used to identify extreme weather events. Extreme events are indicated using shaded cells: low values are shaded in blue, high in pink.

	Mean Monthly Rainfall (mm)				Mean Monthly Temperature (°C)			
Year	**April**	**May**	**June**	**AMJ**	**April**	**May**	**June**	**AMJ**
1970	74.37	29.25	41.80	48.47	6.77	12.84	16.40	12.00
1971	51.54	63.84	133.42	82.93	7.81	11.96	13.26	11.01
1972	74.38	59.20	46.48	60.02	8.72	10.78	11.97	10.49
1973	58.04	84.74	60.40	67.73	7.54	11.54	15.25	11.44
1974	11.60	33.13	69.48	38.07	8.78	11.09	14.26	11.38
1975	61.74	52.21	16.34	43.43	8.09	10.21	14.89	11.06
1976	7.33	15.82	10.23	11.13	8.06	12.64	17.55	12.75
1977	36.57	41.81	51.05	43.14	7.29	10.96	12.56	10.27
1978	63.43	56.95	50.23	56.87	6.72	11.68	14.01	10.80
1979	83.80	93.67	50.03	75.83	8.02	10.27	13.84	10.71
1980	13.31	25.27	119.72	52.77	8.98	11.19	13.99	11.39
1981	64.13	99.19	62.72	75.35	8.18	11.32	13.27	10.92
1982	17.09	50.22	75.11	47.47	8.78	11.89	16.05	12.24
1983	103.66	106.90	52.12	87.56	7.40	10.68	15.19	11.09
1984	2.30	81.52	13.51	32.44	8.09	10.04	14.91	11.01
1985	50.34	45.23	63.61	53.06	8.74	11.61	13.48	11.28
1986	60.94	57.69	23.81	47.48	6.22	10.74	15.22	10.73
1987	71.80	36.00	101.95	69.92	10.00	10.78	13.65	11.48
1988	42.56	34.89	12.75	30.07	8.32	12.66	14.38	11.79
1989	67.91	6.99	30.54	35.15	7.20	14.01	15.22	12.15
1990	48.52	14.27	71.35	44.72	8.54	13.27	13.74	11.85
1991	52.73	16.40	148.53	72.55	8.11	10.73	12.45	10.43
1992	105.91	18.90	21.98	48.93	8.79	13.89	15.66	12.78
1993	91.84	51.03	65.16	69.35	9.81	12.54	15.63	12.66
1994	75.17	96.65	28.90	66.91	8.13	11.16	14.65	11.31
1995	20.66	21.68	18.49	20.28	9.49	12.21	14.82	12.17
1996	30.41	56.28	20.48	35.73	8.60	9.43	14.69	10.91
1997	13.64	55.73	133.58	67.65	8.92	11.96	14.80	11.89
1998	109.22	34.59	90.92	78.24	8.40	14.01	14.68	12.36
1999	60.88	28.51	71.69	53.69	9.59	13.32	14.37	12.43
2000	135.03	110.29	21.12	88.81	8.21	12.84	15.13	12.06
2001	80.64	25.31	14.85	40.27	8.24	12.67	14.62	11.85
2002	43.49	119.66	77.79	80.31	9.47	12.20	14.40	12.02
2003	39.40	37.74	40.97	39.37	9.39	12.03	16.12	12.51
2004	88.46	58.59	32.25	59.77	9.11	12.47	15.90	12.49
2005	60.07	36.22	21.65	39.32	9.15	11.76	16.02	12.31
2006	55.75	93.76	12.99	54.17	8.98	12.49	16.06	12.51
2007	7.50	116.83	99.73	75.48	12.34	12.80	15.77	13.57
2008	80.61	102.80	33.14	71.22	8.78	14.78	15.29	12.90
2009	59.13	45.71	32.50	45.45	10.57	12.91	15.81	13.04
2010	31.50	*	43.29	35.93	9.29	10.75	15.83	11.95

* Missing data

Appendix 3

Indices of changes in abundance for the 28 taxa/age groups chosen for analysis. Low extreme events identified from the long-term trends are shaded in blue, high events in blue.

	Araneae	Collembola	Aphididae	Cicadellidae	Delphacidae	Heteroptera	Heteroptera (adults)	Heteroptera (nymphs)	Heteroptera AY	Thysanoptera	Braconidae	Chalcididae	Carabidae	*Tachyporus*	*Tachyporus* (adults)	*Tachyporus* (young)	*Tachyporus* AY	*Enicmus*	Lathridiidae	*Atomaria*	Cryptophagidae	Cecidomyiidae	Mycetophilidae	Empididae	Lonchopteridae	Agromyzidae	Opomyzidae	Drosophilidae
1971	-0.25		-1.40			-0.91	-1.07	-0.87	0.15				0.18	-0.30	0	-0.35	0.28	1.75	0.08	0.16	0.09							
1972	0.06		-0.48	-0.96	1.64	-0.19	-0.04	-0.21	0.03		-0.99	-0.07	0.29	0.38	-0.26	0.49	-0.03	-0.18	-0.21	-0.55	0.33	0	0.86	0.16	0.54		0.68	-0.65
1973	0.20	-0.15	0.73	0.78	0.76	0.28	-0.14	0.37	-0.35	0.61	0.15	0.78	-0.54	0.03	-0.22	0.05	-2.17	-0.31	-0.22	-0.32	0.05	-0.82	-1.32	-0.29	-1.34	-0.24	0.68	-0.75
1974	-0.29	-1.46	-0.13	0.49	-0.86	0.37	0.38	0.35	-0.02	0.04	0.96	-0.63	0.33	-1.06	-0.99	-1.06	0.96	0.63	1.14	-0.55	-1.36	-0.14	0.38	-0.57	-0.38	-0.68	0.36	-0.59
1975	-0.60	-1.12	1.62	-1.33	-2.74	-0.80	-0.90	-0.78	0.16	-0.65	0.19	-0.10	-0.34	-0.61	-0.19	-0.67	0.32	-1.02	-1.15	-0.44	-0.49	-0.08	-0.18	0.55	0.02	1.86	-0.48	-0.14
1976	0.31	-0.06	-0.20	2.22	2.28	1.14	1.79	1.00	0.31	1.40	0.17	-0.15	0.43	-0.15	0.16	-0.20	0.63	2.06	1.74	1.09	1.68	-0.94	-1.99	-2.18	-1.33	-2.62	-0.45	-1.33
1977	-0.68	1.19	-2.20	-2.28	-3.49	-2.19	-0.54	-3.69	0.47	-1.45	-4.3	-1.63	-1.12	0.77	0.95	0.73	-0.33	-0.65	-0.97	0.46	-0.53	1.17	0.9	-0.53	-1.66	-0.86	-1.5	3.41
1978	1.39	0.53	-0.41	1.04	2.11	1.11	-0.62	2.65	-0.53	1.61	3.44	2.27	0.57	-0.08	-0.75	0.05	-0.32	-1.58	-0.90	-1.11	-1.01	0.65	1.19	0.77	3.08	3.89	1.38	-1.97
1979	-1.09	0.65	-0.83	0.70	1.43	-0.61	-1.05	-0.52	-0.12	-0.79	-2.17	-1.16	-0.42	-0.21	0.40	-0.31	0.37	0.2	-0.48	0.86	0.79	0.66	0.91	-0.28	0.47	-2.91	-1.61	-0.29
1980	0.32	-0.14	2.35	-0.32	0.43	1.23	1.15	1.24	-0.29	-0.19	2.64	0.82	0.47	0.24	-1.10	0.41	-0.98	-0.4	0.25	-0.79	-0.15	-0.92	-0.79	0.55	-0.99	1.26	1.29	-0.09
1981	-0.16	0.65	-0.98	-1.70	-1.40	-1.85	-1.90	-1.85	0.27	-1.56	-1.82	-0.74	0.68	-0.41	0.86	-0.56	0.65	-0.48	-0.74	0.03	-0.51	-0.24	0.23	0.72	0.49	-0.73	-1.13	2.12
1982	0.14	-1.56	0.25	0.58	2.11	1.46	1.35	1.47	-0.26	1.34	-0.24	0.65	-0.13	-0.02	-0.23	0.03	-0.33	0.55	0.52	-0.51	0.14	-0.34	-1.16	-0.08	-1.18	0.1	1.53	-2.53
1983	-1.05	0.94	-0.70	-0.21	-2.97	-0.89	-0.76	-1.13	0.29	-0.76	0.49	-0.64	-0.89	-0.42	0.10	-0.56	0.79	-0.2	-0.72	0.34	0.04	0.76	0.99	-0.43	1.66	1.54	-0.25	3.11
1984	1.44	0.61	0.99	0.59	1.86	1.06	0.06	1.35	-0.54	1.64	0.37	0.45	0.51	1.34	0.35	1.54	-1.26	0.07	0.61	0.09	0.73	1.47	1.34	0.22	-1.08	-0.72	-0.09	-1.87
1985	-0.48	-0.57	-1.81	0.42	-0.68	0.65	0.17	0.66	-0.16	-0.65	-0.96	0.23	0.05	-0.30	0.09	-0.35	0.84	-0.32	-0.64	-0.35	-0.84	-0.36	-0.94	0.58	-0.01	0.26	-0.25	0.14
1986	-0.56	-0.72	-0.47	-0.52	0.69	-0.01	1.55	-0.11	0.93	-1.68	-0.48	-0.94	0.32	-1.30	-0.09	-1.76	0.93	-0.48	-0.41	0.11	-0.27	-2.01	0.55	0.53	-0.16	-1.24	-1.04	-0.55
1987	0.33	0.48	0.97	0.25	-0.07	1.03	0.35	1.08	0.01	1.26	0.66	0.87	0.39	0.82	-0.46	1.28	-0.98	0.42	0.5	-0.29	0.19	0.61	-1.04	0.66	0.38	0.43	1.17	-0.19

Appendix 3 (continued).

1988	0.37	-0.66	1.25	-0.53	-0.14	-0.20	-1.32	-0.15	-1.26	0.47	0.65	0.81	-0.60	-0.38	-0.47	-0.36	0.04	-0.75	-0.38	-0.65	-0.28	-0.15	-0.99	-0.25	0.03	0.83	0.81	0.30
1989	0.43	0.17	0.90	1.07	0.40	-0.42	2.42	-0.84	1.74	0.79	0.45	0.21	-0.89	-2.07	-1.12	-2.31	0.4	-0.95	-0.1	-0.52	-0.52	-0.61	0.11	-0.15	-1.62	-1.59	0.42	-2.15
1990	-1.04	-0.27	-0.45	-0.40	-1.19	-0.67	-1.22	-0.47	-1.04	-0.49	0.36	-0.89	-0.48	1.93	0.37	2.24	-0.46	1.62	0.5	0.12	0.63	-0.70	-0.37	-0.46	-0.78	0.09	-0.32	0.45
1991	-0.09	0.75	-1.86	-0.14	-0.68	-0.36	-1.65	-0.19	-0.08	-1.67	-2.55	-1.22	0.38	1.09	1.66	1.04	-0.35	0.54	0.31	1.33	0.56	0.18	1.41	-0.65	1.75	0.16	-1.89	2.27
1992	0.43	-0.88	1.91	-0.17	1.27	0.61	1.58	0.51	-0.16	1.27	1.01	1.07	-0.88	-1.42	-2.49	-1.35	0.14	-2.01	-0.91	-2.21	-1.38	0.86	0.23	1.16	-0.05	-0.12	1.81	-1.21
1993	0.22	0.68	-0.58	-0.13	-0.14	0.26	-0.34	0.34	-0.50	0.07	0.8	0.61	1.10	1.76	1.94	1.75	-1.35	1.51	0.29	1.67	0.60	1.03	-0.32	0.52	1.38	1.74	-0.05	1.08
1994	-0.84	-0.36	-1.1	-0.70	-0.82	-0.49	-2.62	-0.40	0.18	-1.05	-1.32	0.42	0.19	-1.40	-0.67	-1.45	1.64	-1.8	-1.49	-1.42	-1.30	-0.03	0.13	-1.03	-0.75	-1.45	-0.83	-0.19
1995	0.78	0.19	1.49	1.33	0.51	0.90	2.77	0.84	0.17	1.24	1.65	-0.35	0.07	0.44	0.50	0.43	-0.15	1.23	1.21	0.86	1.18	-1.78	-0.85	-0.69	-0.04	0.31	1.25	-2.47
1996	-0.71	-0.50	-0.90	-0.20	-1.67	-0.42	-0.88	-0.39	0	0.48	-1.75	-0.35	-1.26	-1.69	-0.84	-1.87	0.55	-0.04	0.39	-0.24	-0.14	2.22	0.55	0.41	-1.18	-0.35	-0.45	3.96
1997	0.62	0.44	1.57	0.12	2.60	0.36	1.64	0.23	0.19	0.27	0.13	-0.20	0.39	1.86	0.60	2.07	-0.99	0.14	-0.08	0.61	0.47	-0.99	0.67	0.97	0.59	0.15	0.87	-3.29
1998	-0.08	0.37	-1.47	-1.19	-0.77	-0.66	-2.12	-0.52	-0.34	-1.14	0.42	0.56	0.15	0.6	-0.01	0.64	-0.73	-0.13	-0.76	0.33	-0.01	0.19	-0.24	-0.09	0.45	1.03	-1.45	2.00
1999	0.81	-0.83	0.41	0.49	1.11	0.39	1.8	0.26	0.15	0.01	0.43	-0.03	0.42	-0.33	-0.02	-0.35	0.23	-0.74	-0.29	-1.29	-0.59	-0.64	-0.57	0.22	0.40	-0.64	1.10	-1.17
2000	-0.54	0.89	-0.13	0.07	-0.61	-0.21	-0.19	-0.22	0.06	-0.08	-0.42	-0.21	0.22	-0.55	-0.10	-0.59	0.7	1.03	0.48	-0.06	-0.28	0.06	0.17	-0.7	0.32	0.92	-0.28	2.3
2001	-0.51	-0.60	-0.02	-0.24	-0.32	0.11	-1.40	0.27	-0.24	0.62	0.02	0.62	-0.45	-0.8	0.01	-0.90	0.69	-0.93	-0.87	-0.57	-0.41	-0.11	-1.12	-0.17	-1.65	-0.63	-0.82	-2.28
2002	0.55	0.84	-0.57	0.40	-0.32	-1.00	0.48	-1.15	0.61	-0.62	0.67	-0.44	0.49	1.16	0.30	1.26	-1.13	1.60	1.89	1.68	1.10	0.62	1.78	0.28	2.31	0.24	0.35	1.29
2003	-0.05	-1.47	0.96	1.02	1.61	0.66	1.20	0.52	-0.06	0.62	-0.08	0.63	-0.54	-0.85	-1.54	-0.80	0.60	-1.30	-1.06	-1.58	-0.56	-0.05	-0.16	-0.02	-1.65	-0.84	0.34	-0.32
2004	-0.90	0.64	0.59	-0.56	-2.15	-0.44	-0.66	-0.38	0.19	0.01	-0.82	0.12	-1.51	-0.88	-0.62	-0.9	0.15	-0.97	-0.64	-2.08	-0.65	-0.04	-0.9	-0.83	-1.02	-0.56	-0.72	0.11
2005	0.91	-0.57	-1.55	-0.64	-0.55	0.15	-0.26	0.23	-0.05	-0.76	1.00	0.44	1.39	1.61	1.75	1.60	-0.46	0.71	0.28	2.31	0.63	0.17	0.89	0.62	2.23	1.89	0.35	-0.05
2006	-0.24	0.92	0.25	0.27	2.28	0.30	0.01	0.34	-0.42	0.42	-1.47	-0.94	-1.57	-0.73	-1.01	-0.72	-0.01	-0.39	-0.50	-0.59	-0.22	0.50	-0.43	-0.40	-0.20	-1.36	-0.93	0.94
2007	0.26	0.09	-1.00	0.99	0.37	-0.32	0.87	-0.65	0.72	0.71	1.11	-0.23	1.69	0.54	0.48	0.54	-0.24	1.53	1.19	1.39	0.97	-0.33	-0.01	-0.21	-0.59	0.33	0.98	-0.78
2008	0.61	0.47	1.70	-0.30	1.17	0.49	0.09	0.67	-0.49	-0.92	0.10	0.31	-0.01	0.68	0.13	0.69	-0.67	-1.48	-0.70	-0.93	-0.89	1.35	1.20	0.23	0.41	0.66	-0.08	-0.76
2009	-0.71	0.20	0.08	0.11	-1.23	0.17	0.17	0.17	-0.19	0.58	-0.23	-0.09	-0.54	-1.00	-0.58	-1.01	1.29	-1.09	-1.19	-1.22	0.03	-1.12	-1.39	0.02	-1.37	-0.73	-0.52	-1.46
2010	0.24	-0.10	-1.77	0.76	-0.40	0.44	0	0.54	-0.50	-0.13	-0.90	-0.09	0.54	0.01	1.59	-0.14	0.94	1.80	1.24	0.61	0.59	-0.73	-1.03	-1.67	0.29	-0.62	-0.49	0.69
2011	-0.60	-0.86	2.17	-1.21	-0.69	-0.64	0.52	-1.10	1.37	-0.59	0.84	-0.48	-0.94	-1.15	-1.54	-1.08	-0.65	0.10	0.19	-0.12	0.04	-1.33	-0.2	0.79	0.06	0.33	0.43	0.28

Appendix 4

Count of the frequency at which different recovery time brackets were observed following extreme event years. Species identified as sensitive to extreme weather events are shown in bold.

	Hot/Dry Events			Cold/Wet events		
Years to recover	**0 Yr**	**1 Yr**	**2 Yr**	**0 Yr**	**1 Yr**	**2 Yr**
Araneae	**1**	**1**		**2**	**1**	
Collembola	1		1	2		
Aphididae	1	1		2	1	
Cicadellidae	**1**	**1**		**2**	**1**	
Delphacidae	**1**		**1**	**2**	**1**	
Heteroptera	1	1		2	1	
Heteroptera adults	**1**		**1**	**1**	**2**	
Heteroptera nymphs	1	1		2		1
Heteroptera A/Y	2			3		
Thysanoptera	**1**	**1**			**1**	**1**
Braconidae	**1**	**1**		**2**		**1**
Chalcididae	2			2	1	
Carabidae	1	1		1	2	
Tachyporus		2			2	1
Tachyporus adult	1	1		2	1	
***Tachyporus* young**		**2**			**2**	**1**
Tachyporus A/Y		2		1	2	
Enicmus	**1**		**1**	**3**		
Lathridiidae	**1**		**1**	**3**		
Atomaria	2			3		
Cryptophagidae	**1**		**1**	**1**	**1**	**1**
Cecidomyiidae		1	1	1	2	
Mycetophilidae		**1**	**1**	**2**	**1**	
Empididae	1		1		3	
Lonchopteridae	1		1	1	2	
Agromyzidae	1		1	2		
Opomyzidae	2			2	1	
Drosophillidae	1	1		2	1	

Appendix 5

Analysis of habitat compositions in 100 m buffers surrounding invertebrate sampling locations in the Sussex study. Sampling locations were divided into those samples that showed an increase in invertebrate abundance and those that showed a decrease and the compositions were compared. Significant results indicate where the habitat compositions varied between the two groups. Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

Event Type	Taxa	WIlk's Lambda	d.f	P
Pre Hot	Collembola	0.956	6,204	0.153
	Aphididae	0.985	6,204	0.795
	Heteroptera	0.944	6,204	0.066
	Heteroptera Nymphs	0.955	6,204	0.145
	Heteroptera AY	0.954	6,204	0.138
	Chalcididae	0.960	6,204	0.209
	Carabidae	0.971	6,204	0.414
	Tachyporus	0.984	6,204	0.761
	***Tachyporus* Adults**	**0.918****	**6,204**	**0.007**
	Tachyporus AY	0.962	6,204	0.237
	Atomaria	0.977	6,204	0.556
	Cecidomyiidae	0.975	6,204	0.510
	Empididae	0.951	6,204	0.110
	Lonchopteridae	0.971	6,204	0.421
	Agromyzidae	0.982	6,204	0.723
	Opomyzidae	0.9433	6,204	0.061
	Drosophillidae	0.986	6,204	0.812
Pre Cold	Collembola	0.978	6,203	0.609
	Aphididae	0.948	6,203	0.090
	Heteroptera	0.982	6,203	0.718
	Heteroptera Nymphs	0.976	6,203	0.547
	Heteroptera AY	0.982	6,203	0.709
	Chalcididae	0.983	6,203	0.738
	Carabidae	0.971	6,203	0.427
	Tachyporus	0.981	6,203	0.688
	Tachyporus Adults	0.943	6,203	0.061
	Tachyporus AY	0.982	6,203	0.726
	Atomaria	0.974	6,203	0.500
	Cecidomyiidae	0.972	6,203	0.440
	Empididae	0.987	6,203	0.856
	Lonchopteridae	0.962	6,203	0.248
	Agromyzidae	0.989	6,203	0.888
	Opomyzidae	0.945	6,203	0.072
	Drosophillidae	0.981	6,203	0.672

Appendix 5 (continued).

Event Type	Taxa	WIlk's Lambda	d.f	P
Post Hot	Collembola	0.987	6,174	0.879
	Aphididae	0.962	6,174	0.332
	Heteroptera	0.959	6,174	0.283
	Heteroptera Nymphs	0.987	6,174	0.890
	Heteroptera AY	0.976	6,174	0.627
	Chalcididae	0.979	6,174	0.718
	Carabidae	0.939	6,174	0.085
	Tachyporus	0.945	6,174	0.125
	Tachyporus Adults	0.979	6,174	0.715
	Tachyporus AY	0.968	6,174	0.464
	Atomaria	0.967	6,174	0.435
	Cecidomyiidae	0.982	6,174	0.784
	Empididae	0.955	6,174	0.230
	Lonchopteridae	0.921	6,174	**0.024***
	Agromyzidae	0.971	6,174	0.527
	Opomyzidae	0.958	6,174	0.272
	Drosophillidae	0.964	6,174	0.377
Post Cold	Collembola	0.977	6,230	0.482
	Aphididae	0.983	6,230	0.693
	Heteroptera	0.983	6,230	0.674
	Heteroptera Nymphs	0.997	6,230	0.992
	Heteroptera AY	0.990	6,230	0.886
	Chalcididae	0.992	6,230	0.926
	Carabidae	0.965	6,230	0.220
	Tachyporus	0.979	6,230	0.555
	Tachyporus Adults	0.968	6,230	0.280
	Tachyporus AY	0.968	6,230	0.273
	Atomaria	0.995	6,230	0.973
	Cecidomyiidae	0.991	6,230	0.914
	Empididae	0.971	6,230	0.344
	Lonchopteridae	0.953	6,230	0.084
	Agromyzidae	0.981	6,230	0.602
	Opomyzidae	0.992	6,230	0.932
	Drosophillidae	0.9525	6,230	0.080

Appendix 6

Table 1. Sensitivity to hot, dry events from generalised linear modelling of changes in invertebrate abundance in the event year relative to the pre-event year for those taxa shown to not be sensitive to extreme weather events on a field-by-field basis. Wald statistics (for models including all effects) excluding (a) and including the number of pesticide applications in the event year (b). Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

	Degrees of freedom	Collembola	Aphididae	Heteroptera	Heteroptera (nymphs)	Heteroptera AY	Chalcididae	Carabidae	Tcyporus	Tacyporus adults	*Tachyporus* AY	*Atomaria*	Cecidomyiidae	Empididae	Lonchopteridca e	AAgromyzidae	Opomyzidae	Drosphiliidae
a. Overall: Sample size = 181																		
Year	3	1.37	4.24	7.60	7.76	2.53	0.35	2.99	**7.99***	**26.16*****	2.82	**23.14*****	4.22	5.22	**8.73***	**12.86****	4.77	2.87
Crop	2	0.80	0.40	2.76	2.73	1.04	1.66	**6.36***	2.05	0.48	0.87	1.07	**6.29***	2.92	4.33	**7.50***	4.75	0.31
Aspect	3	0.19	1.47	7.53	**8.18***	4.05	1.48	0.38	3.67	1.75	0.99	0.88	4.34	6.23	3.17	6.17	4.49	**10.46***
Field boundary density	1	0.76	2.13	0.34	0.94	**4.19***	2.01	0.61	0.75	2.98	0.15	2.08	0.13	0.75	0.10	0.93	0.32	0.56
Slope	1	3.30	0.79	1.09	0.34	0.73	0.21	0.55	0.13	0.10	0.01	0.23	0.49	0.56	1.15	0.19	2.20	3.63
Elevation	1	1.78	0.17	0.79	1.44	1.25	0.70	0.08	0.06	**4.43***	2.09	0.80	0.03	0.01	0.74	0.75	**4.76***	0.34
Patch density (log)	1	0.12	2.30	0.15	0.02	1.04	0.09	0.46	0.32	0.01	0.21	0.63	0.35	1.19	0.01	0.30	2.44	1.00
Field area (log)	1	0.02	0.31	0.55	0.95	1.28	0.04	0.50	0.10	0.21	0.93	2.82	2.26	0.98	0.18	0.17	0.32	1.08
b. Overall: Sample size = 92																		
Year	3	1.02	-	2.49	1.67	1.08	4.99	0.92	1.73	0.59	0.48	2.87	2.57	1.18	4.45	1.98	0.91	3.10
Crop	2	2.09	-	0.15	0.99	2.94	2.62	3.17	**10.79****	1.37	2.65	3.53	5.38	4.09	2.77	4.70	2.94	5.08
Aspect	3	2.22	-	7.12	4.19	3.97	4.09	2.03	**8.28***	0.54	1.95	1.94	4.17	**10.84***	0.75	7.13	2.75	2.58
Field boundary density	1	0.83	-	0.35	0.75	1.84	1.04	0.01	1.44	1.48	0.03	1.15	0.83	3.42	0.43	0.34	0.36	1.43
Slope	1	0.01	-	0.02	0.58	1.66	0.16	3.95	0.02	1.82	0.33	0.69	0.01	0.47	0.01	0.11	0.79	0.98
Elevation	1	0.85	-	0.08	0.01	0.39	0.20	0.84	0.04	0.05	0.12	0.36	0.74	**4.39***	1.37	0.31	2.44	**7.89****
Patch density (log)	1	0.13	-	0.01	0.24	1.03	0.36	0.71	0.39	1.43	0.23	0.30	2.45	0.46	1.78	1.89	1.73	**5.75***
Field area (log)	1	0.57	-	2.98	2.86	0.07	0.09	0.08	0.06	0.33	0.43	2.96	0.19	0.04	0.30	0.69	1.34	1.47
Herbicide	1	0.01	-	1.52	0.06	2.10	0.02	0.01	0.57	0.70	0.25	2.29	0.02	0.34	0.57	1.56	0.14	0.06
Fungicide	1	0.16	-	0.19	0.62	0.36	0.20	0.27	0.85	1.12	0.05	0.22	1.63	2.64	2.62	0.23	1.60	0.47
Insecticide	1	0.02	-	0.04	1.04	2.79	2.40	0.07	2.88	0.56	3.17	0.10	0.29	0.50	**5.93***	**7.09***	1.63	0.26

Table 2. Sensitivity to cold, wet events from generalised linear modelling of changes in invertebrate abundance in the event year relative to the pre-event year for those taxa shown to not be sensitive to extreme weather events on a field-by-field basis. Wald statistics (for models including all effects) excluding (a) and including the number of pesticide applications in the event year (b). Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

	Degrees of freedom	Collembola	Aphididae	Heteroptera	HEteroptera (nymphs)	Heteroptera AY	Chalcididae	Carabidae	*Tachyporus*	*Tachyporus* adults	*Tachyporus* AY	*Atomaria*	Cecidomyiidae	Empididae	Lonchopteridcae	Agromyzidae	Opomyzidae	Drosphiliidae
a. Overall: Sample size = 210																		
Year	3	5.04	0.17	**11.62***	**7.99***	1.75	**8.27***	**8.62***	0.26	0.94	1.46	1.73	3.17	4.68	1.80	0.52	1.70	1.20
Crop	2	1.47	1.87	0.48	0.58	0.68	1.18	**6.57***	0.33	1.66	0.83	0.59	**6.13***	1.91	5.54	2.09	**7.00***	0.10
Aspect	3	0.77	**8.08***	5.97	3.89	0.55	2.11	4.11	**10.74***	4.22	**10.94***	2.16	7.04	**17.52*****	**10.18***	**8.02***	1.50	7.24
Field boundary density	1	0.27	0.11	**3.94***	2.93	0.35	0.08	0.49	0.43	0.20	0.06	0.34	0.16	0.04	0.88	0.07	0.01	0.17
Slope	1	0.13	0.75	0.79	0.91	0.25	0.02	0.01	0.27	0.21	0.01	0.28	3.32	0.17	0.01	2.01	0.07	0.01
Elevation	1	2.44	0.54	2.49	3.39	3.28	2.33	0.95	0.73	2.24	0.01	2.79	0.89	**3.99***	0.49	0.14	0.09	2.45
Patch density (log)	1	0.94	0.16	1.22	0.83	0.11	0.32	1.06	0.85	0.43	0.66	0.07	0.50	0.20	0.28	0.13	0.07	0.01
Field area (log)	1	0.51	2.62	0.38	0.19	0.02	0.14	1.32	1.00	0.35	0.07	0.04	1.98	0.13	0.41	0.01	0.10	3.27
b. Overall: Sample size =126																		
Year	3	1.56	0.95	3.00	3.54	3.19	5.79	**11.96***	2.09	3.79	2.40	0.42	0.56	2.97	1.19	2.93	2.45	2.48
Crop	2	1.14	1.78	0.90	0.79	0.62	1.68	3.33	0.47	0.42	3.22	0.05	**6.34***	0.96	3.06	0.40	3.15	1.43
Aspect	3	0.77	3.02	4.01	3.26	1.33	1.85	2.80	2.76	2.03	5.14	3.37	1.80	5.01	6.70	1.74	0.98	5.80
Field boundary density	1	0.88	1.71	1.70	1.63	0.26	1.80	0.01	0.01	1.55	0.61	0.39	3.29	0.10	0.02	0.09	0.21	2.99
Slope	1	0.56	**3.99***	0.28	0.26	0.05	1.16	0.42	0.01	0.68	0.25	0.01	1.87	0.14	0.01	3.01	0.89	0.18
Elevation	1	0.73	0.55	**5.27***	**4.97***	0.98	0.15	0.26	0.96	0.38	0.59	1.24	2.14	2.92	0.33	0.01	0.49	1.40
Patch density (log)	1	2.09	0.82	2.42	2.52	1.74	2.62	0.32	0.19	0.64	**4.49***	0.06	0.17	0.40	0.01	0.26	0.82	0.11
Field area (log)	1	0.18	**6.88***	0.01	0.03	0.14	0.56	1.65	0.15	0.01	0.06	0.04	2.37	0.36	0.33	0.36	0.21	0.11
Herbicide	1	1.55	0.19	0.01	0.01	0.01	0.08	0.03	1.66	2.19	0.01	0.02	1.54	0.01	0.15	3.18	0.06	0.01
Fungicide	1	**4.22***	0.04	0.35	0.09	0.60	0.01	0.02	0.25	0.04	0.23	2.57	0.93	1.12	0.13	1.25	0.38	0.99
Insecticide	1	0.51	0.16	1.24	1.13	0.27	1.41	2.07	0.01	0.03	0.11	1.86	0.52	0.34	0.04	1.28	0.01	0.75

Table 3. Resilience to hot, dry events from generalised linear modelling of changes in invertebrate abundance in the post-event year relative to the event year for taxa shown to not be sensitive to extreme weather events on a field-by-field basis. Wald statistics (for models including all effects) excluding (a) and including the number of pesticide applications in the year following the event year. Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

	Degrees of freedom	Collembola	Aphididae	Heteroptera	Heteroptera (nymphs)	Heteroptera AY	Chalcididae	Carabidae	Tcyporus	Tacyporus adults	*Tachyporus* AY	*Atomaria*	Cecidomyiidae	Empididae	Lonchopteridca e	AAgromyzidae	Opomyzidae	Drosphiliidae
a. Overall: Sample size = 181																		
Year	3	3.34	1.55	**11.23***	**10.18***	0.77	1.38	2.63	3.39	1.00	6.97	4.46	6.99	2.23	0.63	3.19	0.20	1.11
Crop	2	1.22	0.76	**8.06***	**8.99***	4.19	0.37	0.42	5.17	0.83	**6.57***	1.14	0.87	0.81	4.75	**6.96***	3.06	0.86
Aspect	3	2.56	0.67	2.50	2.98	4.26	2.89	2.28	1.14	1.97	0.05	3.50	0.78	0.64	0.43	3.61	1.90	1.80
Field boundary density	1	0.08	2.36	0.23	0.27	0.24	0.87	0.66	0.74	3.00	0.01	0.48	0.07	0.66	0.83	0.60	0.43	0.27
Slope	1	0.49	0.01	0.01	0.06	0.37	0.01	0.02	0.17	0.17	0.09	0.14	0.14	0.06	0.28	2.75	0.02	0.39
Elevation	1	**3.94***	0.52	2.51	**5.92***	**7.89****	3.63	0.02	0.57	**5.53***	**7.93****	3.79	2.36	1.06	1.02	1.06	0.24	0.78
Patch density (log)	1	0.07	0.88	0.41	0.07	0.10	0.73	1.00	0.31	1.49	0.43	0.70	1.23	0.03	0.01	0.89	0.32	0.34
Field area (log)	1	0.04	2.01	**4.72***	3.26	0.11	0.05	0.03	0.81	0.01	1.64	1.64	0.01	0.02	0.20	0.78	0.01	2.59
b. Overall: Sample size = 92																		
Year	3	2.30	2.55	1.47	1.31	0.22	1.42	1.38	1.51	0.29	1.45	0.44	2.65	1.09	4.43	3.44	0.99	1.86
Crop	2	1.99	0.93	0.67	1.65	3.35	1.24	2.61	**10.64****	3.28	3.01	3.49	5.29	2.82	2.93	**6.33***	2.67	5.39
Aspect	3	3.62	2.78	6.61	4.27	3.89	3.04	2.46	6.15	0.42	1.23	2.84	3.97	**11.78***	1.16	8.33	4.33	2.15
Field boundary density	1	0.35	0.02	0.18	1.33	3.72	0.14	0.22	1.53	1.06	0.49	0.38	1.62	3.41	0.42	1.33	0.42	2.41
Slope	1	0.06	0.07	0.35	1.16	1.49	0.04	2.21	0.07	0.53	0.60	0.12	0.02	0.01	0.11	0.01	0.61	0.14
Elevation	1	1.36	2.38	0.01	0.01	0.02	2.51	0.74	0.81	0.63	0.87	3.93	0.95	**6.80***	1.50	0.08	1.41	**6.07***
Patch density (log)	1	0.22	0.42	0.01	0.29	1.32	0.48	0.80	1.10	1.24	0.01	0.01	1.91	0.78	1.42	1.88	1.03	3.54
Field area (log)	1	0.06	0.92	**4.37***	2.10	0.33	0.21	0.03	0.19	0.01	0.14	0.80	0.22	0.01	0.06	0.89	1.58	0.96
Herbicide	1	0.68	0.89	0.99	0.11	1.18	1.07	0.13	0.11	0.01	0.01	0.29	0.29	0.14	1.53	3.14	0.94	1.63
Fungicide	1	0.31	0.39	1.27	0.71	0.01	0.04	0.32	0.44	0.25	0.08	0.01	0.50	1.53	2.88	0.49	1.20	0.17
Insecticide	1	0.79	2.04	0.09	0.02	0.65	1.43	0.20	0.34	1.20	0.01	0.14	0.13	1.22	**4.71***	**4.33***	0.89	0.35

Table 4. Resilience to cold, wet events from generalised linear modelling of changes in invertebrate abundance in the post-event year relative to the event year for taxa shown to not be sensitive to extreme weather events on a field-by-field basis. Wald statistics (for models including all effects) excluding (a) and including the number of pesticide applications in the year following the event year. Significant results highlighted in bold (*P < 0.05, ** P < 0.01, and*** P < 0.001).

	Degrees of freedom	Collembola	Aphididae	Heteroptera	Heteroptera (nymphs)	Heteroptera AY	Chalcididae	Carabidae	*Tachyporus*	*Tachyporus* adults	*Tachyporus* AY	*Atomaria*	Cecidomyiidae	Empididae	Lonchopteridcae	Agromyzidae	Opomyzidae	Drosphiliidae
a. Overall: Sample size = 237																		
Year	3	**14.86****	**10.82***	**8.38***	**9.93***	4.88	0.22	2.24	3.95	2.00	4.41	0.42	3.37	3.51	1.05	1.09	1.93	0.51
Crop	2	0.48	4.91	**6.87***	**10.92****	**7.40***	0.11	3.48	4.54	3.11	0.12	1.29	1.44	2.32	4.24	1.03	5.38	0.78
Aspect	3	2.72	1.86	2.45	2.61	3.88	0.27	2.27	4.57	7.30	1.75	1.11	1.41	6.56	1.83	1.89	0.69	0.79
Field boundary density	1	1.78	0.01	**5.42***	**5.85***	2.32	0.17	0.17	0.23	**4.85***	1.60	2.71	1.03	0.05	0.25	0.27	0.83	0.01
Slope	1	0.01	0.22	0.15	0.42	1.27	0.11	0.32	0.55	0.12	0.77	1.73	0.18	0.90	2.30	1.19	0.09	0.35
Elevation	1	0.07	0.26	0.26	0.61	0.36	0.01	0.23	0.01	0.64	0.66	0.46	0.01	0.50	1.21	0.37	2.40	0.62
Patch density (log)	1	1.82	0.03	3.51	2.83	0.09	0.27	0.51	**4.24***	**8.39****	0.22	**5.99***	0.21	0.01	0.62	0.03	0.30	0.06
Field area (log)	1	1.88	0.60	**6.07***	3.63	0.10	0.68	0.58	0.07	0.67	0.01	**4.71***	1.21	0.41	0.13	0.01	2.25	0.16
b. Overall: Sample size =139																		
Year	3	**10.96***	2.95	1.55	2.50	4.55	0.58	4.00	1.74	1.57	3.78	4.03	3.95	3.59	1.37	0.63	1.31	1.53
Crop	2	2.34	3.58	1.77	2.63	4.08	1.65	1.45	0.07	2.62	4.28	1.28	2.36	3.09	5.21	1.80	1.72	0.15
Aspect	3	2.00	3.91	2.95	2.24	1.88	2.52	4.07	2.01	4.30	0.95	0.76	0.88	1.55	0.27	0.80	2.44	3.38
Field boundary density	1	2.57	0.86	0.81	1.38	2.10	0.20	0.09	1.41	3.73	0.02	3.70	1.52	0.01	0.71	0.08	0.48	2.14
Slope	1	0.01	3.37	1.37	2.29	**4.44***	0.27	0.70	0.32	0.02	0.31	0.25	0.02	0.56	0.40	0.92	0.01	0.01
Elevation	1	0.02	**6.80***	1.05	0.21	1.01	0.20	0.40	0.58	0.64	0.01	0.71	2.16	2.76	0.26	0.23	0.07	0.21
Patch density (log)	1	**4.17***	0.09	2.70	2.43	0.31	0.01	0.56	**5.31***	**5.23***	0.33	3.31	0.83	0.01	0.25	0.01	0.10	1.35
Field area (log)	1	1.72	0.70	**6.34***	2.70	1.29	0.80	0.01	1.27	0.28	0.01	0.08	1.16	1.35	0.56	0.76	1.10	1.48
Herbicide	1	0.42	0.15	0.14	0.36	0.91	0.19	0.35	0.82	2.49	3.48	3.57	1.30	1.62	1.25	0.75	0.01	0.43
Fungicide	1	0.02	0.55	0.85	0.04	1.59	0.90	0.01	1.05	0.53	0.69	0.18	0.14	0.25	3.50	0.01	0.34	0.37
Insecticide	1	0.01	0.54	0.49	0.61	0.10	0.03	0.18	0.17	0.76	0.59	0.01	1.98	0.38	0.06	0.01	0.03	0.39

Appendix 7

Table 1. Mean change (± 1 SE) in abundance of invertebrates in relation to aspect of sampling location following a significant result for aspect within a mixed model (Appendix 6– Table 2a). Means are adjusted for other factors in the model, and ones that are not different ($P < 0.05$) are labelled with the same letter.

Aspect	Aphididae	*Tachyporus*	*Tachyporus* AY	Empididae	Lonchopteridcae	Agromyzidae
North	1.544 ± 0.568 $_{b}$	0.981 ± 0.552 $_{bc}$	-0.226 ± 0.175 $_{a}$	1.969 ± 0.497 $_{b}$	0.920 ± 0.495 $_{c}$	-0.328 ± 0.450 $_{ab}$
East	-0.237 ± 0.336 $_{a}$	-0.439 ± 0.323 $_{a}$	0.245 ± 0.102 $_{b}$	-0.180 ± 0.295 $_{a}$	-0.215 ± 0.292 $_{ab}$	-0.244 ± 0.266 $_{ab}$
South	-0.042 ± 0.188 $_{a}$	-0.146 ± 0.181 $_{ab}$	-0.036 ± 0.057 $_{a}$	-0.126 ± 0.166 $_{a}$	-0.396 ± 0.164 $_{a}$	-0.387 ± 0.149 $_{a}$
West	-0.059 ± 0.250 $_{a}$	0.513 ± 0.237 $_{c}$	-0.131 ± 0.075 $_{a}$	0.183 ± 0.221 $_{a}$	0.190 ± 0.216 $_{bc}$	0.285 ± 0.199 $_{b}$

Table 2. Mean change (± 1 SE) in abundance of invertebrates in relation to aspect of sampling location following a non-significant result for aspect within a mixed model (Appendix 6 – Table 2a). Means are adjusted for other factors in the model.

Aspect	Collembola	Heteroptera	Heteroptera (nymphs)	Heteroptera AY	Chalcididae	Carabidae	*Tachyporus* adults	*Atomaria*	Cecidomyiidae	Opomyzidae	Drosphiliidae
North	-0.815 ± 1.157	-0.191 ± 0.548	-0.227 ± 0.552	0.106 ± 0.159	-0.319 ± 0.52	0.08 ± 0.263	0.207 ± 0.285	0.204 ± 0.454	1.401 ± 0.583	0.348 ± 0.507	1.002 ± 0.559
East	-0.024 ± 0.678	-0.4 ± 0.319	-0.317 ± 0.324	0.024 ± 0.094	-0.244 ± 0.309	-0.065 ± 0.156	0.075 ± 0.164	-0.048 ± 0.264	-0.262 ± 0.344	-0.082 ± 0.3	0.244 ± 0.332
South	-0.116 ± 0.38	0.249 ± 0.179	0.178 ± 0.181	0.004 ± 0.053	-0.156 ± 0.174	-0.201 ± 0.088	-0.163 ± 0.091	-0.249 ± 0.147	0.182 ± 0.193	-0.258 ± 0.168	-0.217 ± 0.186
West	0.223 ± 0.499	0.5 ± 0.233	0.413 ± 0.238	-0.019 ± 0.07	0.195 ± 0.233	0.061 ± 0.117	0.054 ± 0.119	0.025 ± 0.192	0.442 ± 0.256	-0.229 ± 0.223	0.335 ± 0.248

Appendix 8

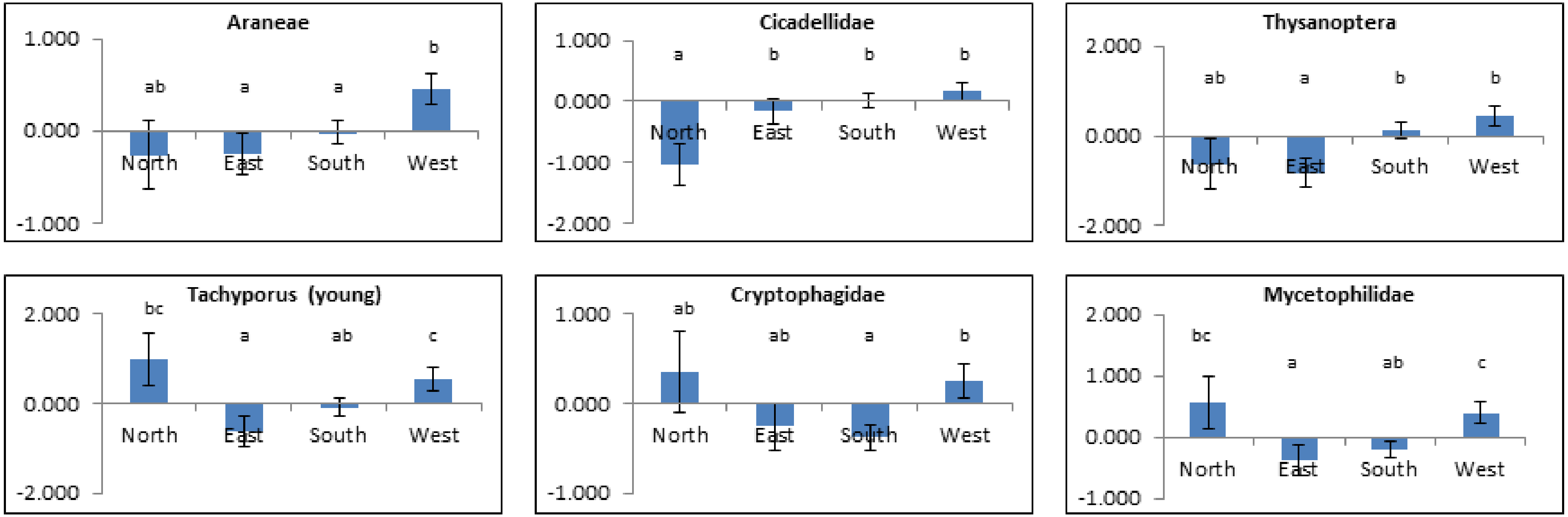


Figure 1. Mean change in abundance of sensitive invertebrate taxa in relation to aspect of sampling location following a significant result for aspect within a mixed model (Table 9a). Error bars show ± 1 SE.

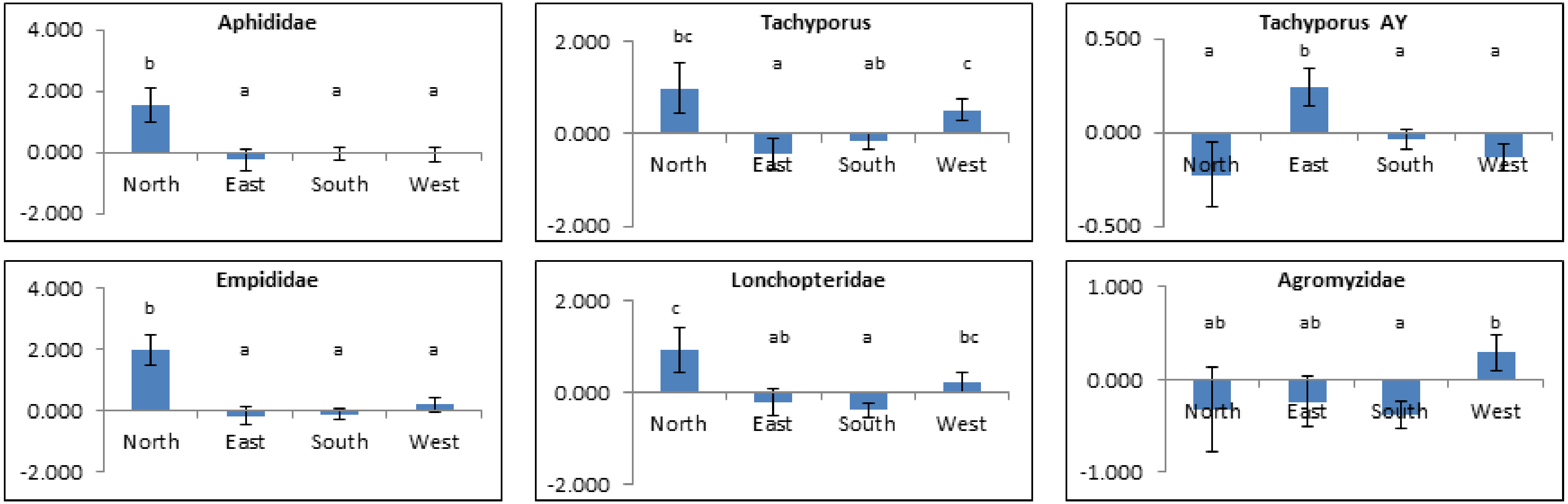


Figure 2. Mean change in abundance of non-sensitive invertebrate taxa in relation to aspect of sampling location following a significant result for aspect within a mixed model (Appendix 6–Table 2a). Error bars show ± 1 SE.

Appendix 9

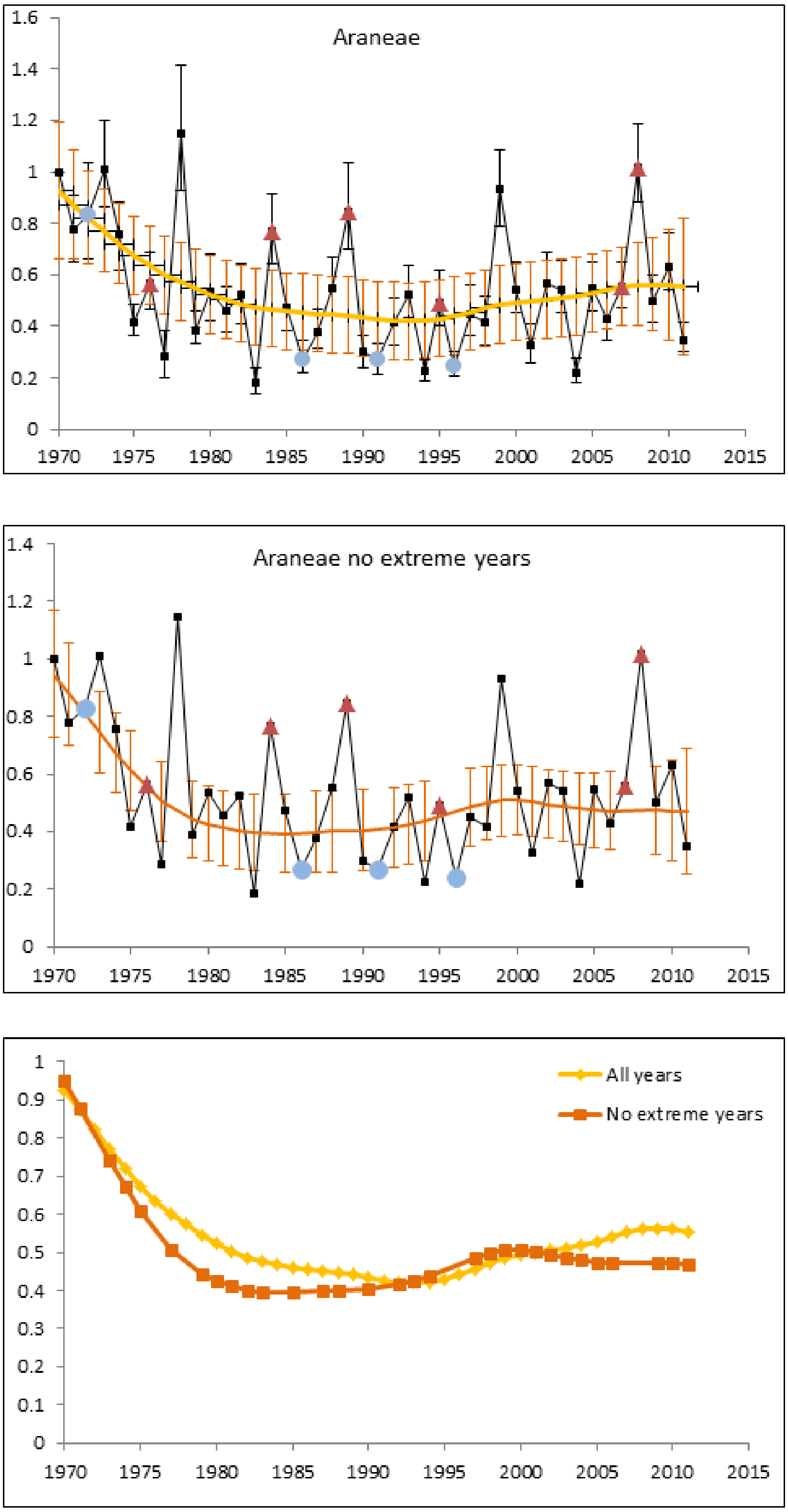


Figure 1. Long term trends in Araneae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

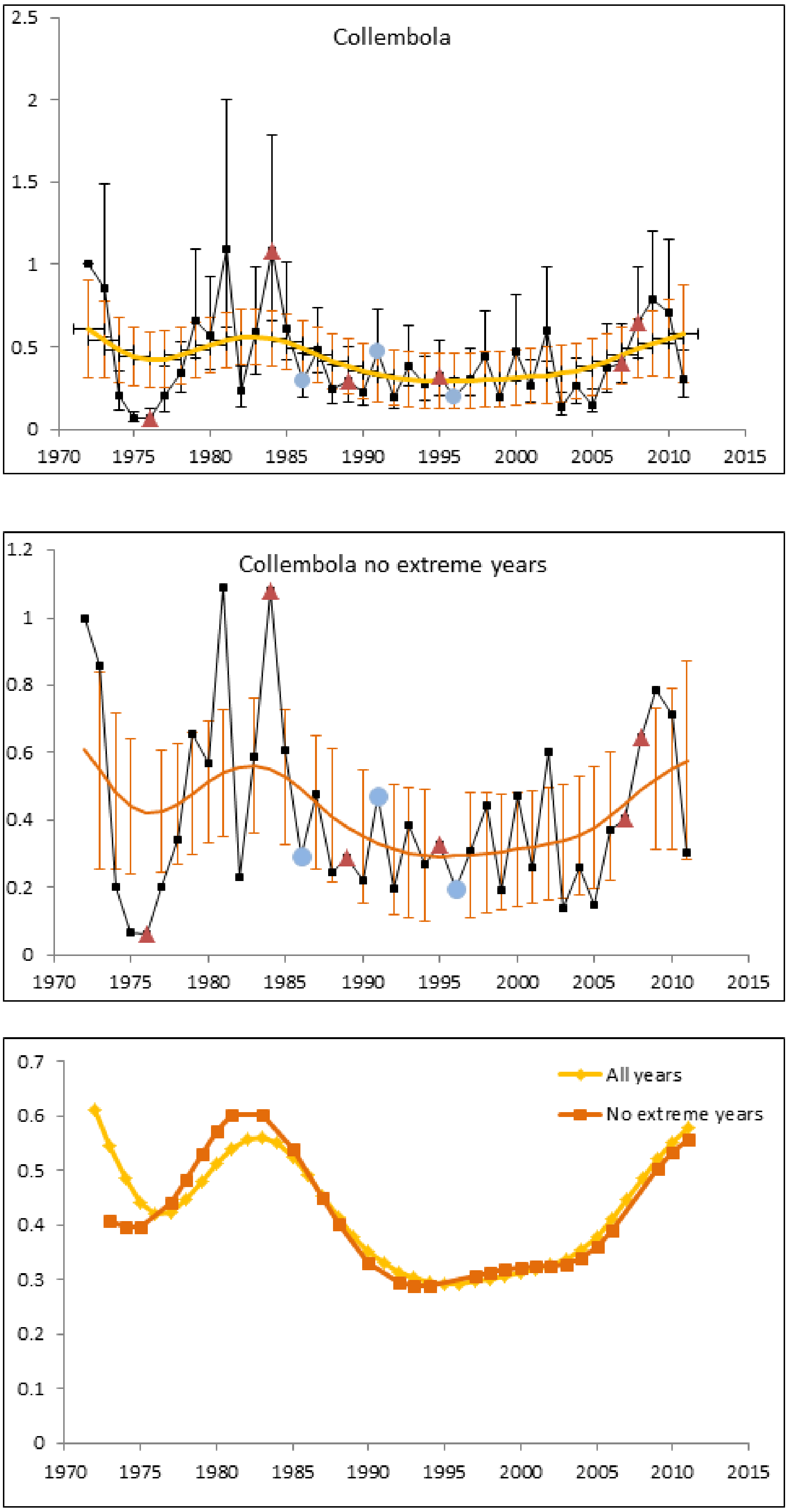


Figure 2. Long term trends in Collembola: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

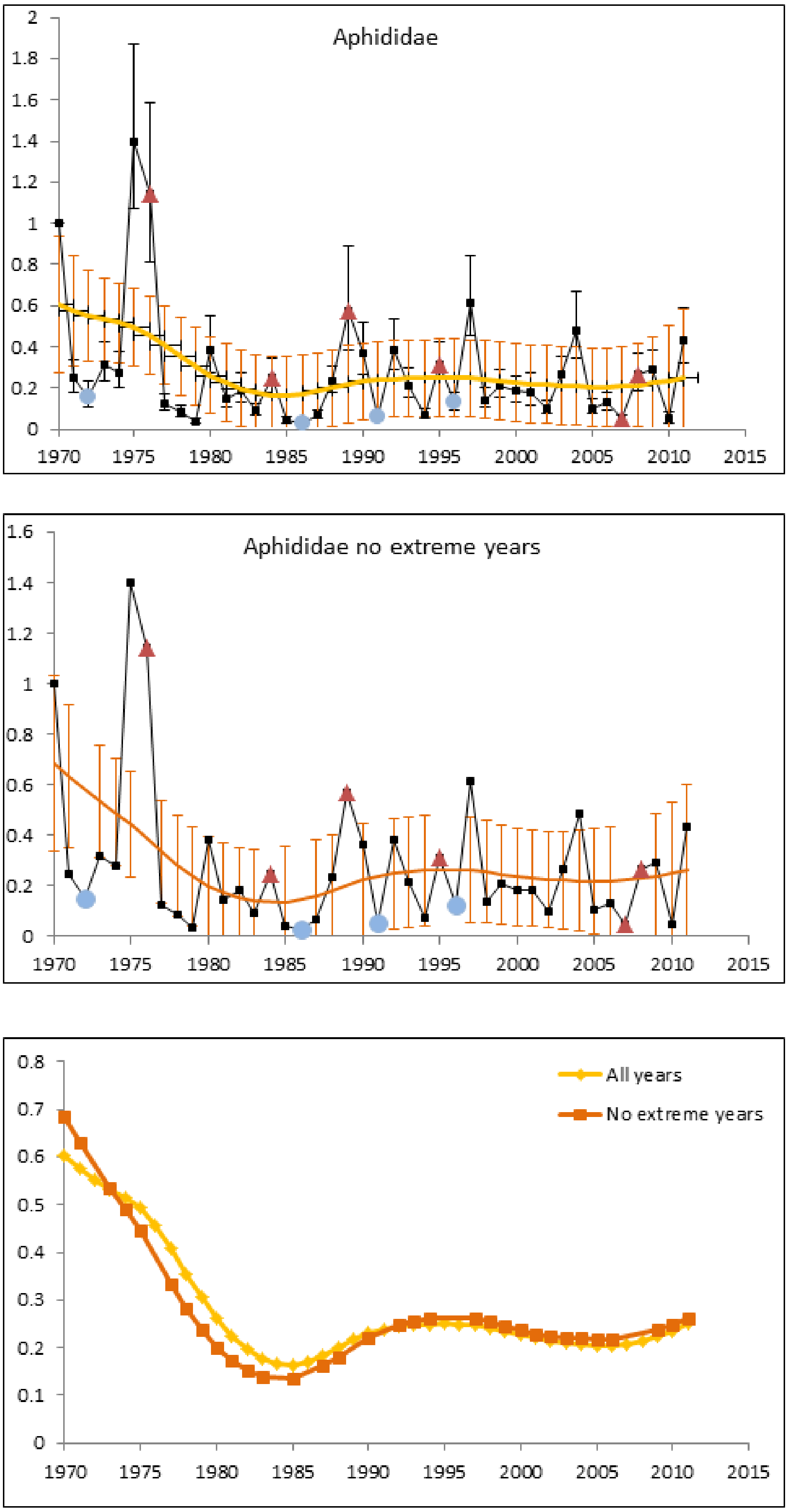


Figure 3. Long term trends in Aphididae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

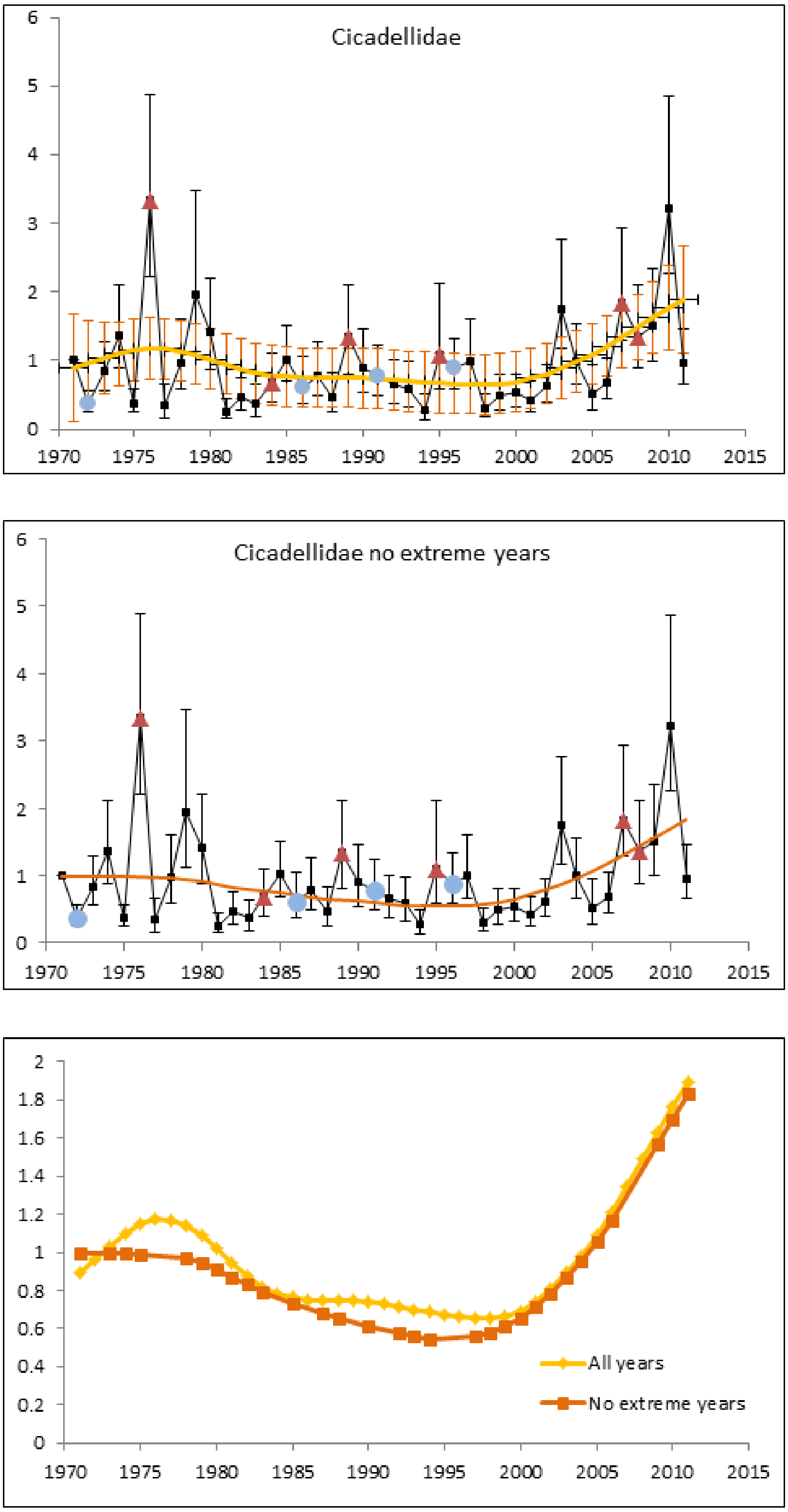


Figure 4. Long term trends in Cicadellidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

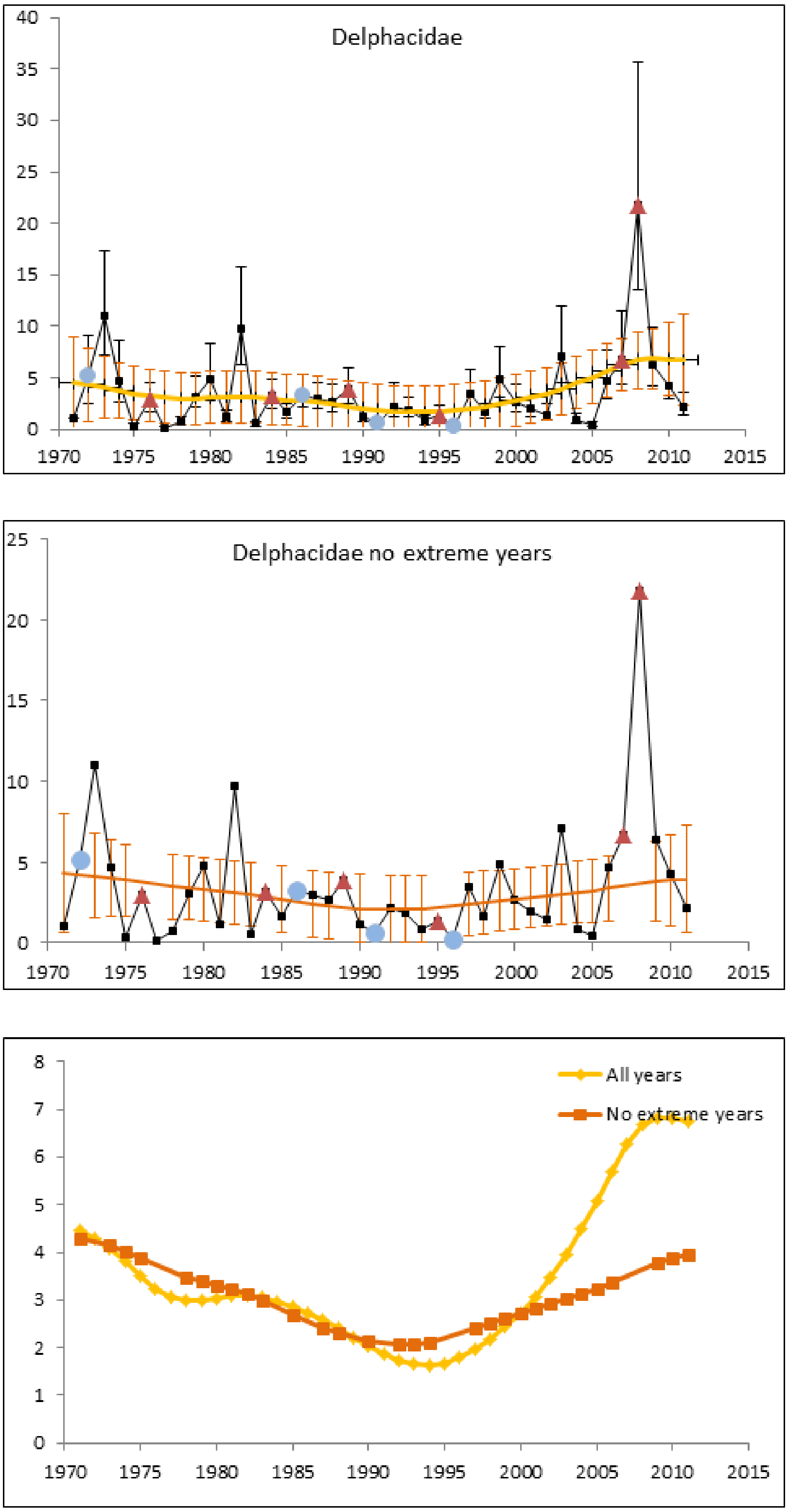


Figure 5. Long term trends in Delphacidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

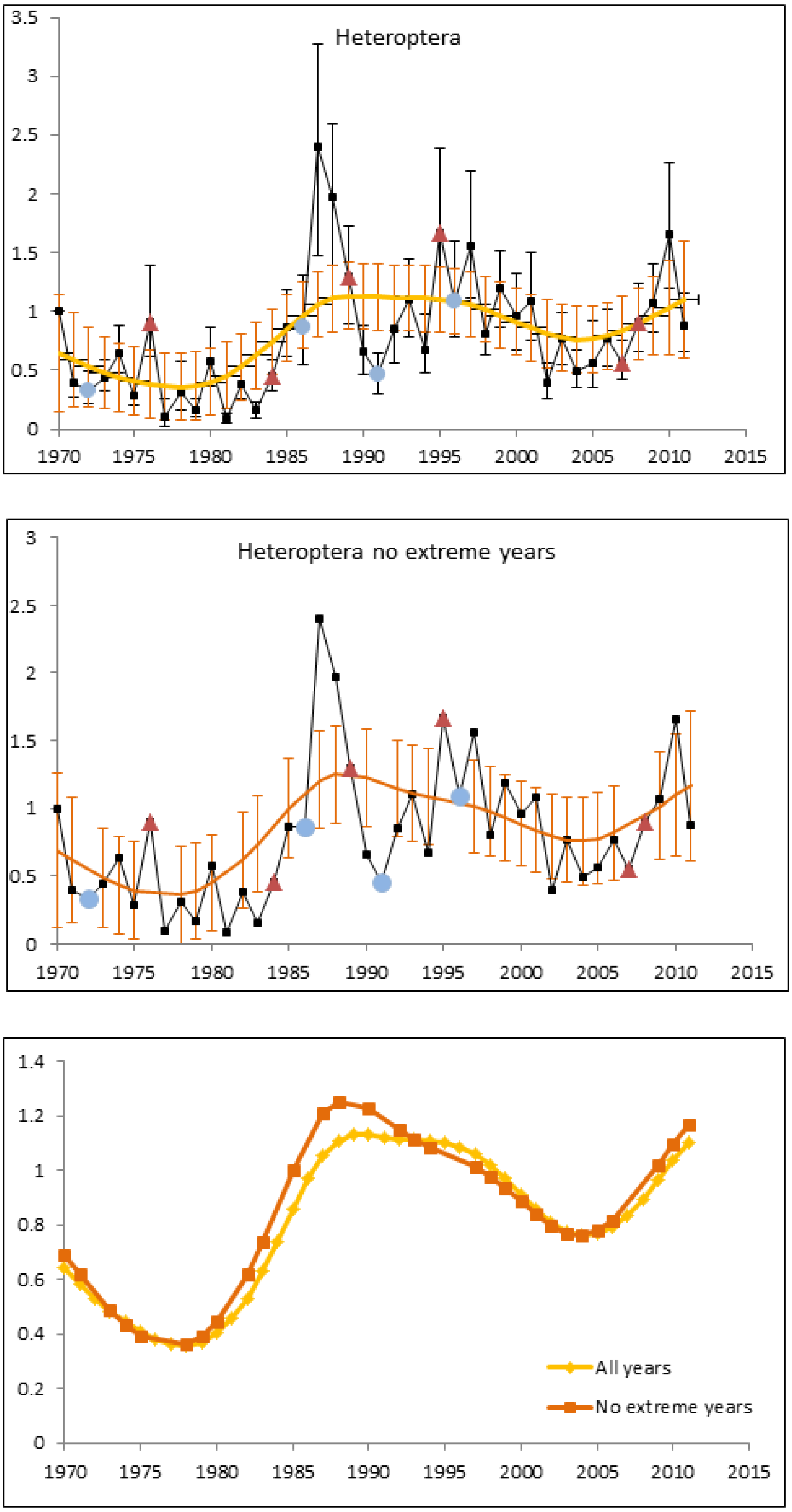


Figure 6. Long term trends in Heteroptera: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

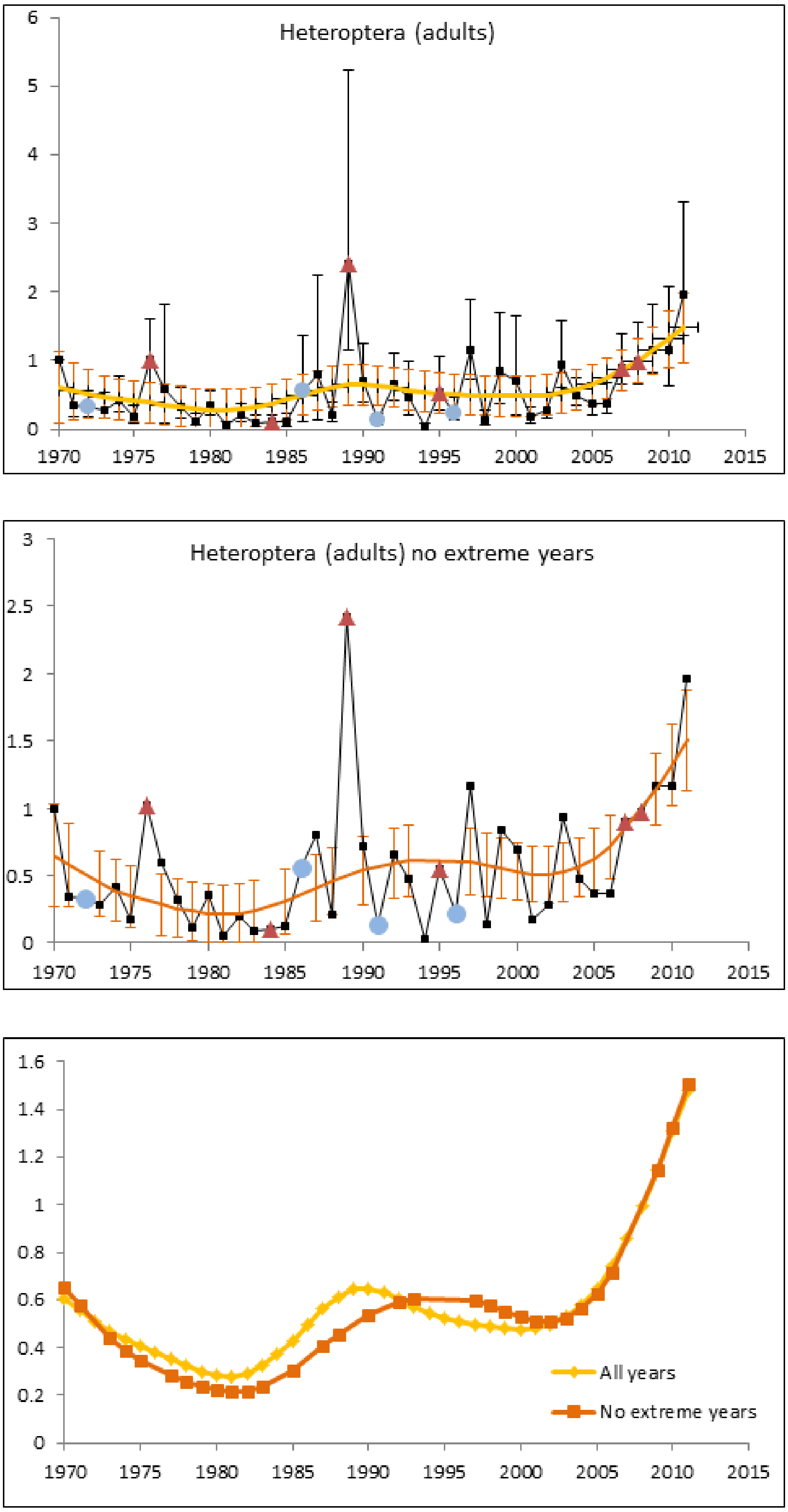


Figure 7. Long term trends in Heteroptera adults: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

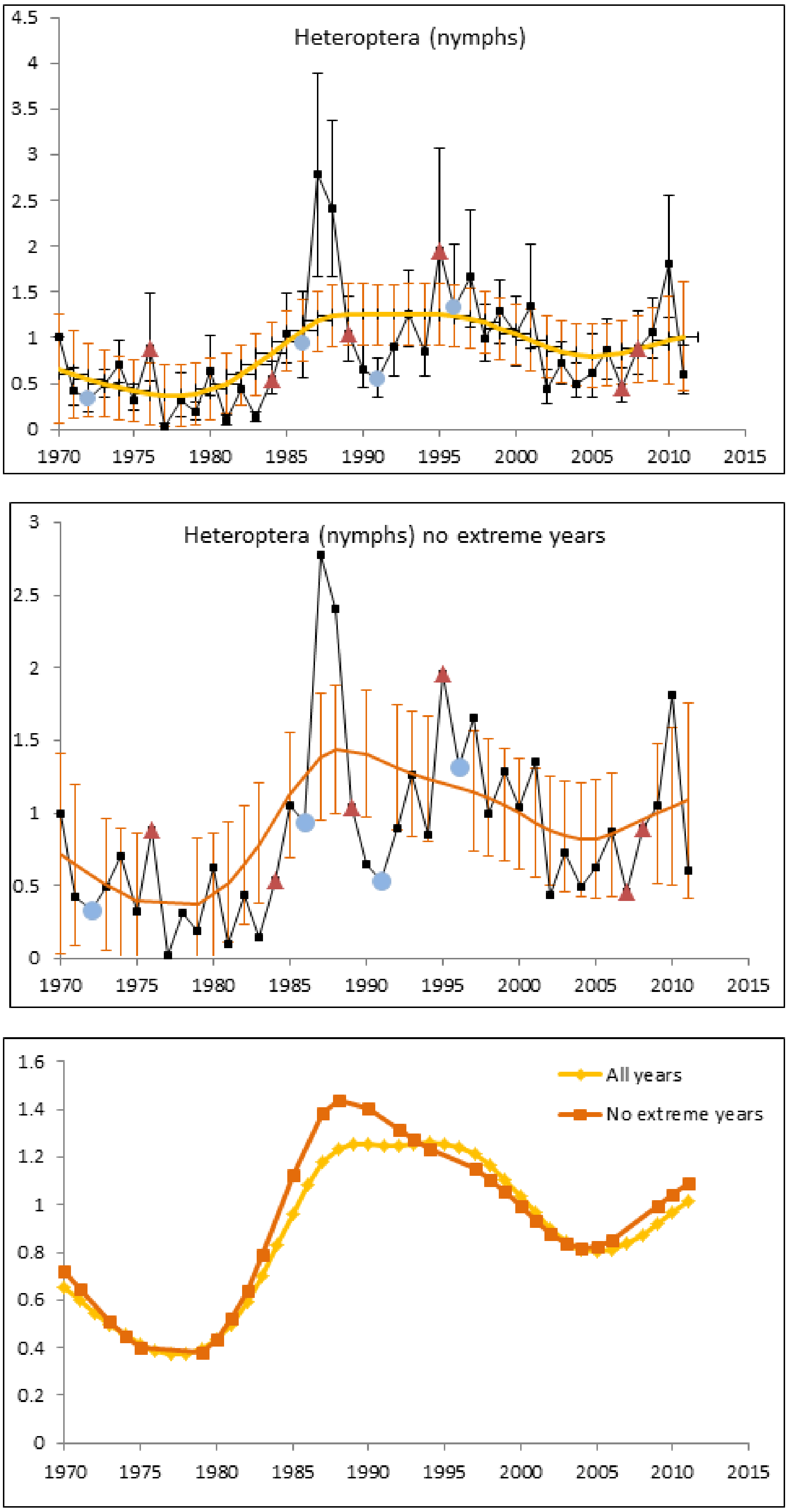


Figure 8. Long term trends in Heteroptera nymphs: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

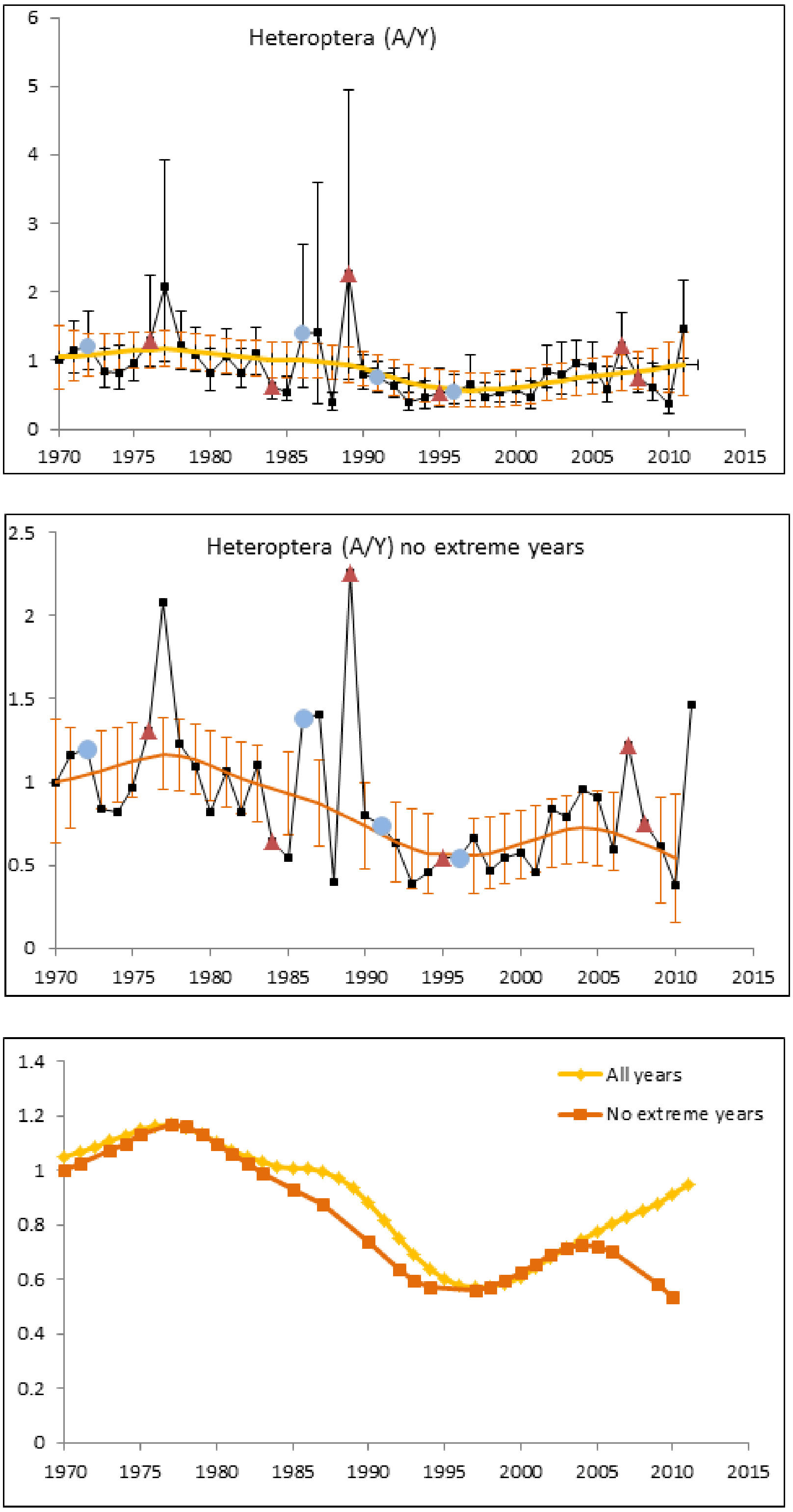


Figure 9. Long term trends in the ratio of Heteroptera adults to nymphs: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

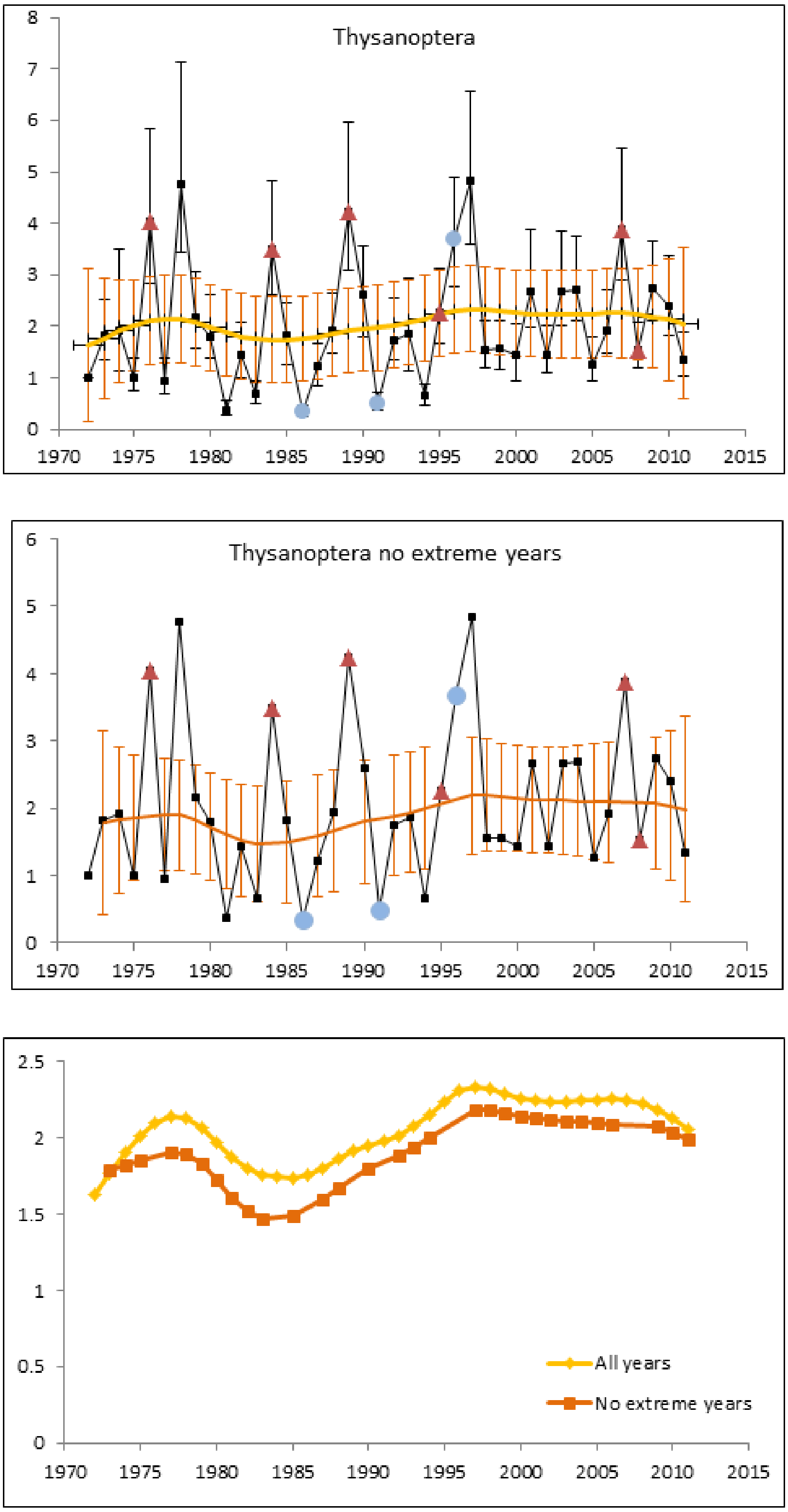


Figure 10. Long term trends in Thysanoptera: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

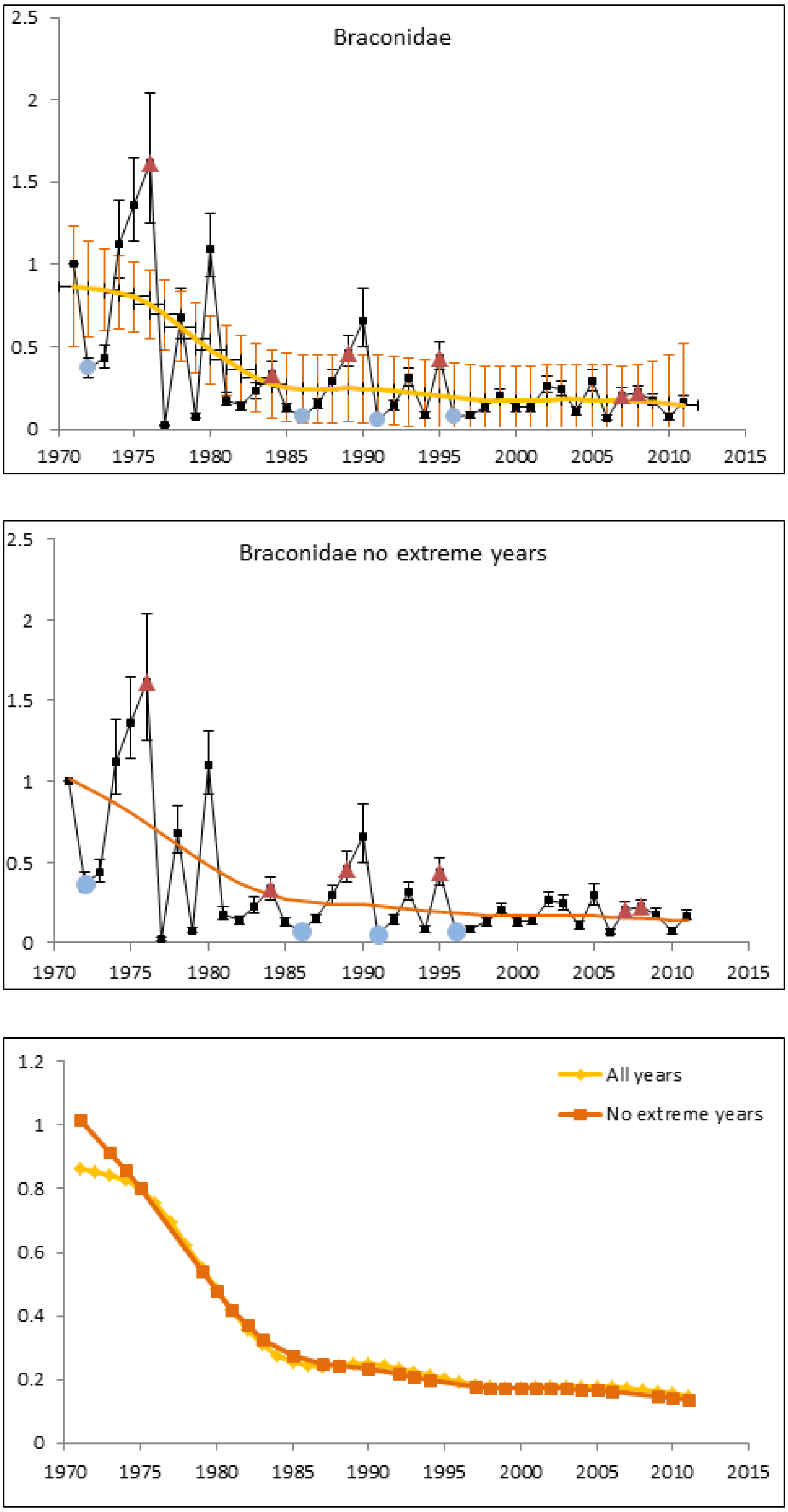


Figure 11. Long term trends in Braconidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

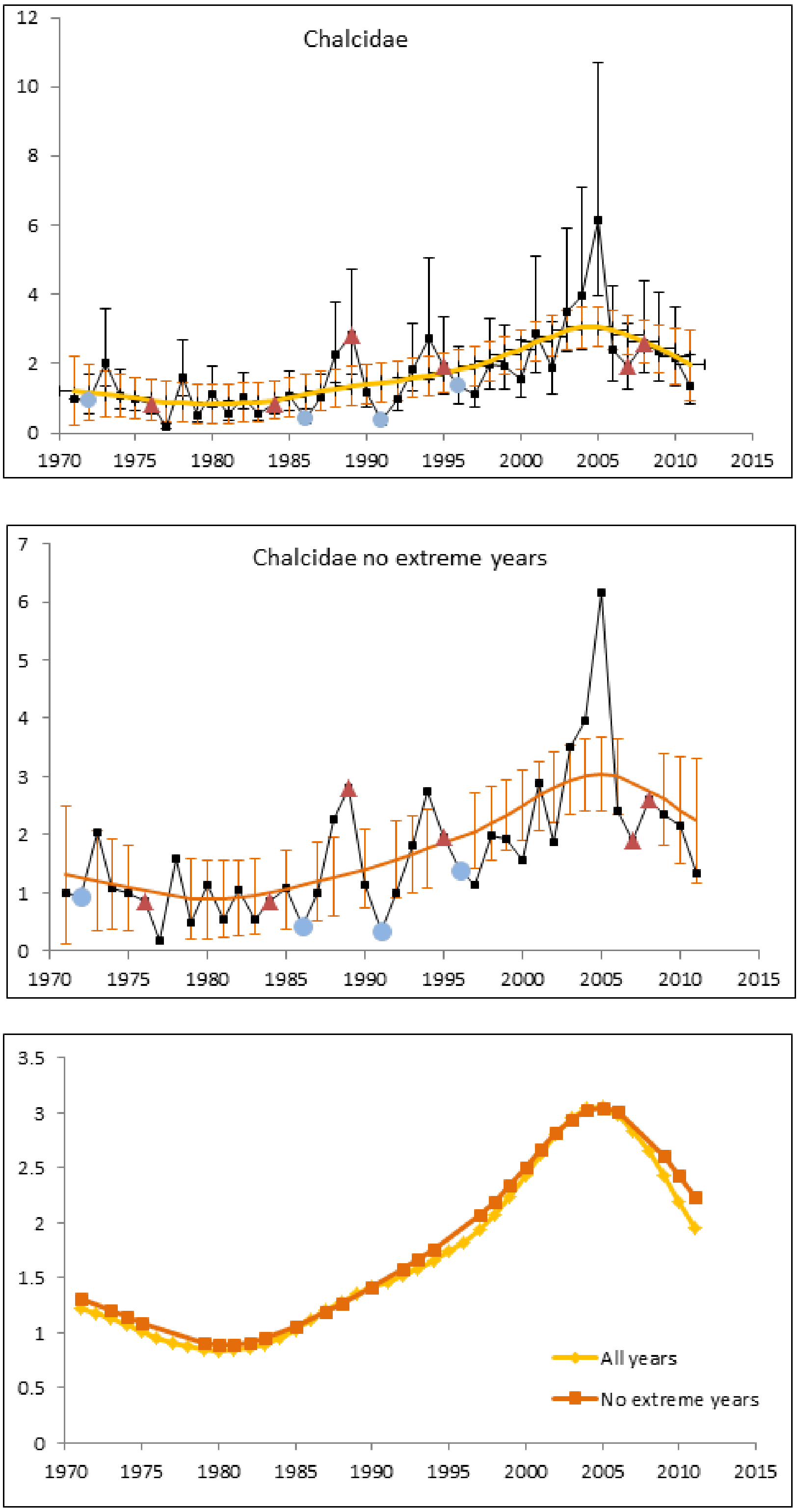


Figure 12. Long term trends in Chalcididae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

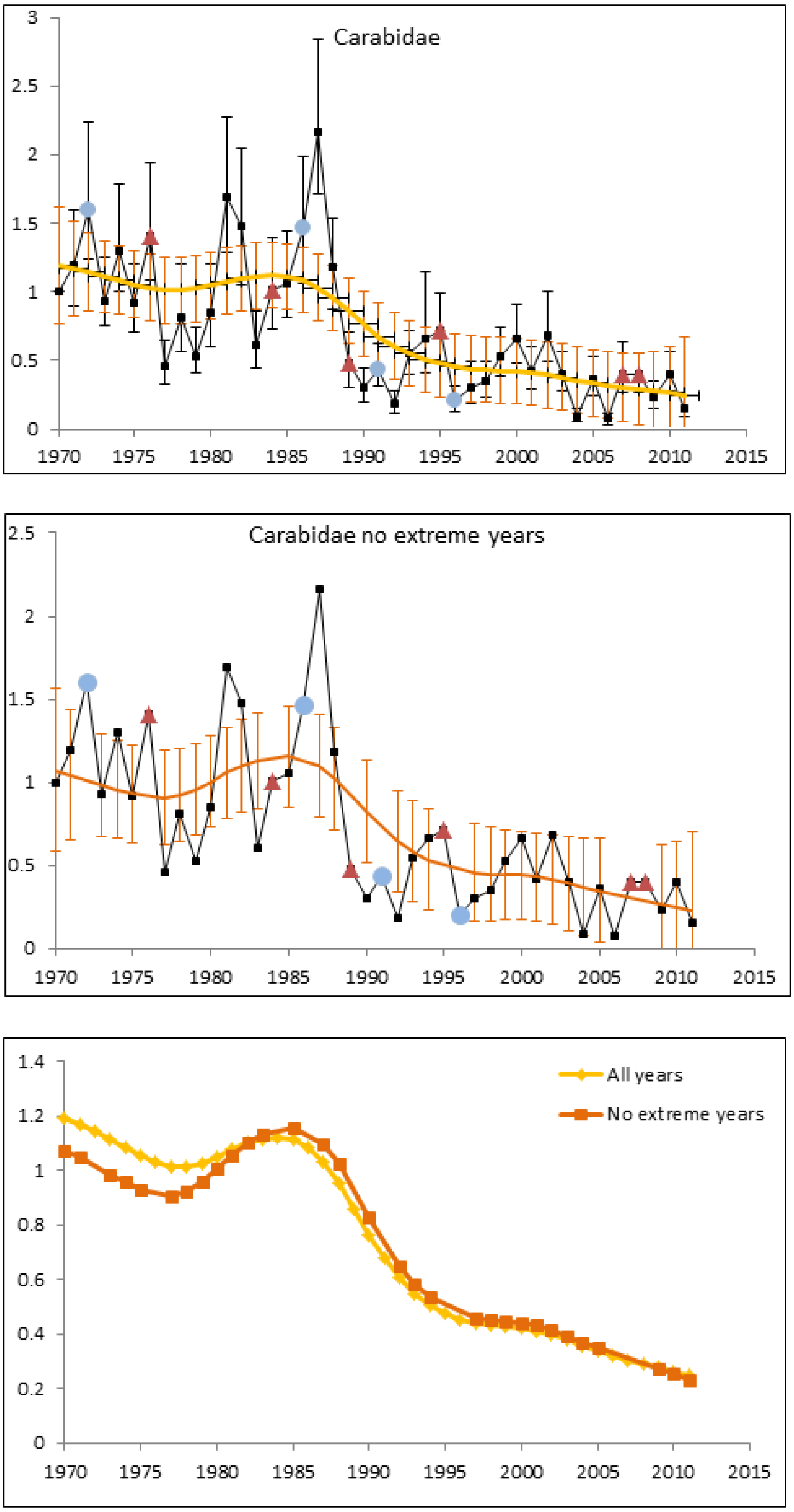


Figure 13. Long term trends in Carabidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

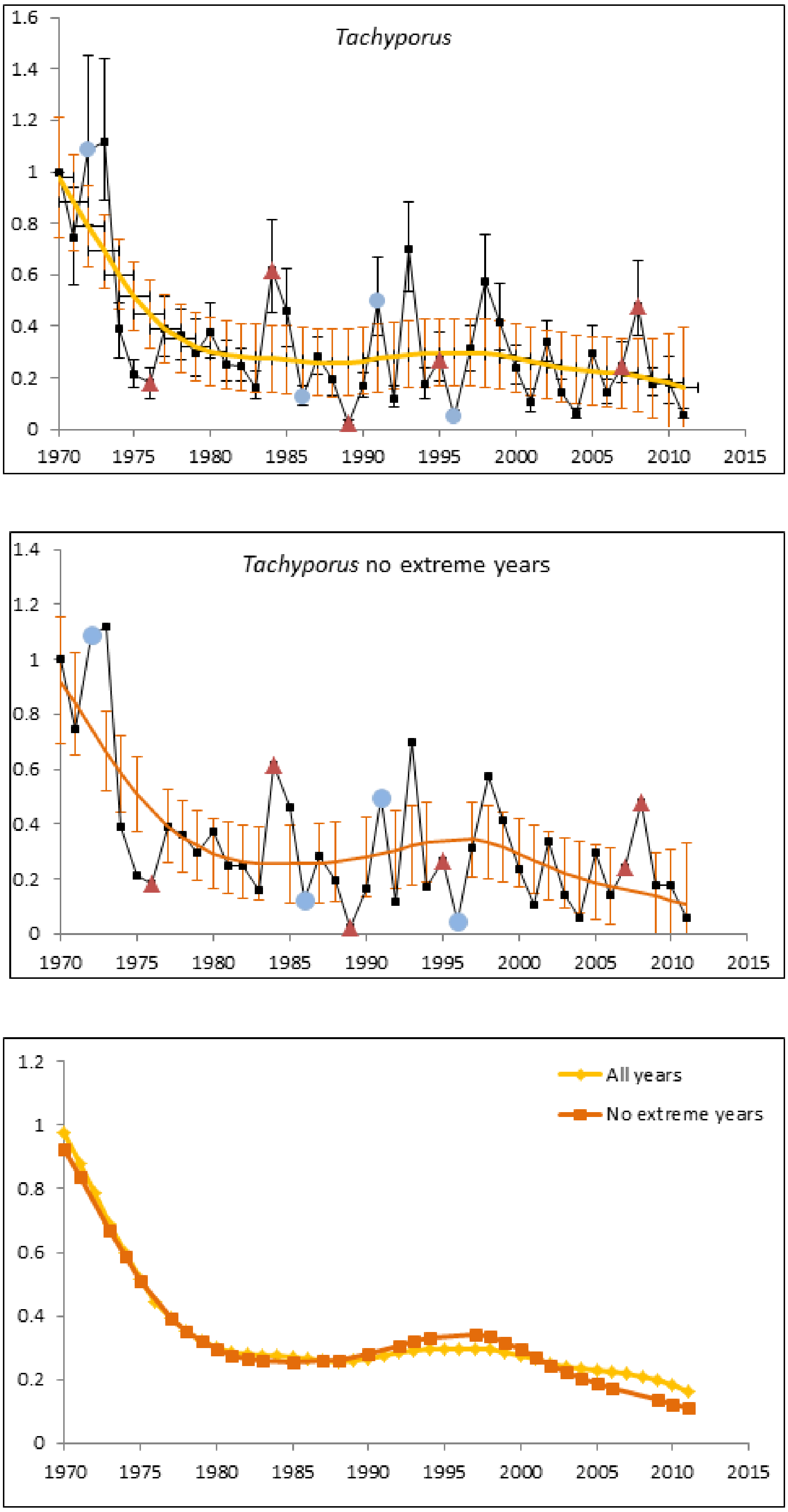


Figure 14. Long term trends in *Tachyporus*: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

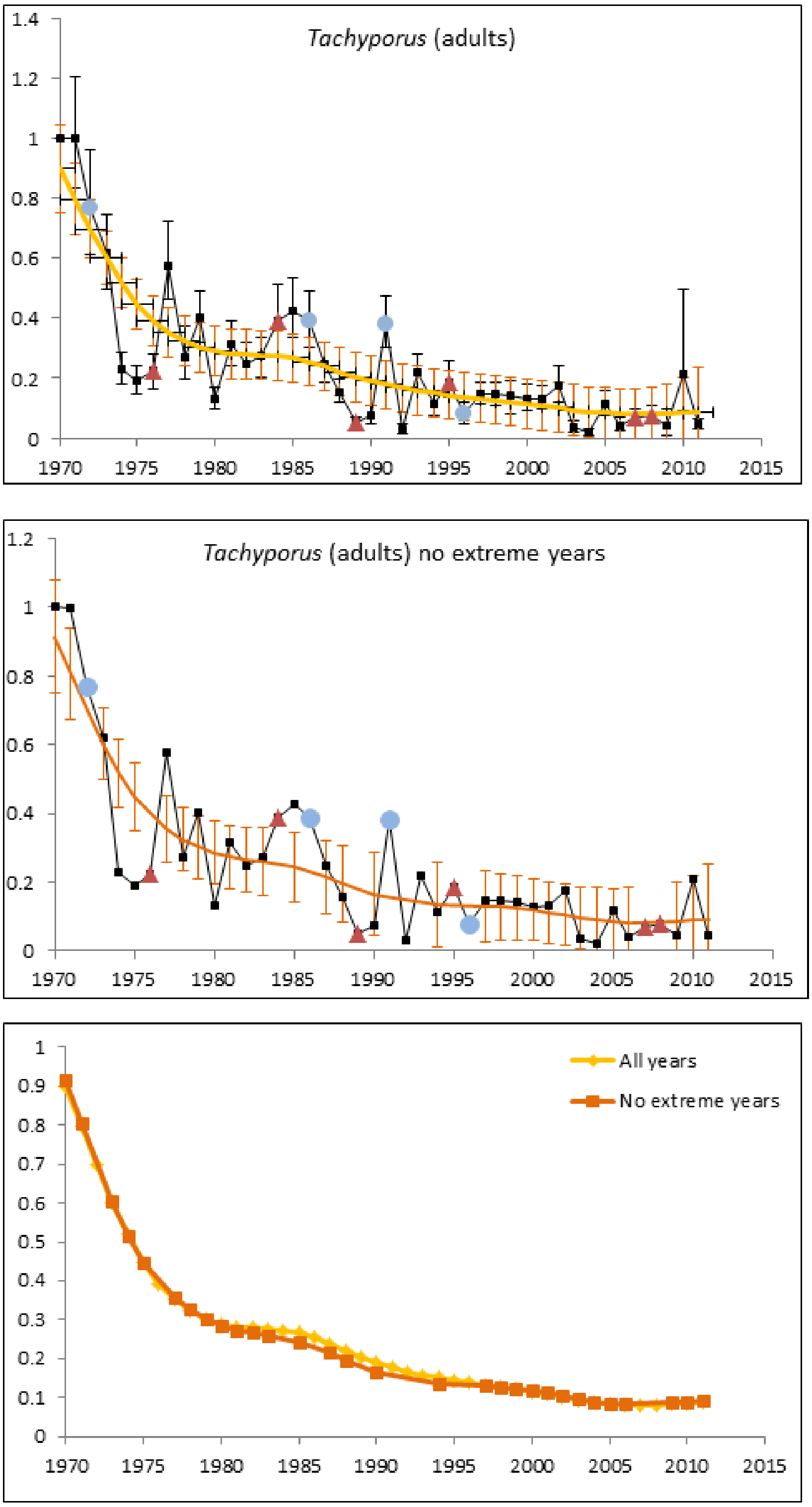


Figure 15. Long term trends in *Tachyporus* adults: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

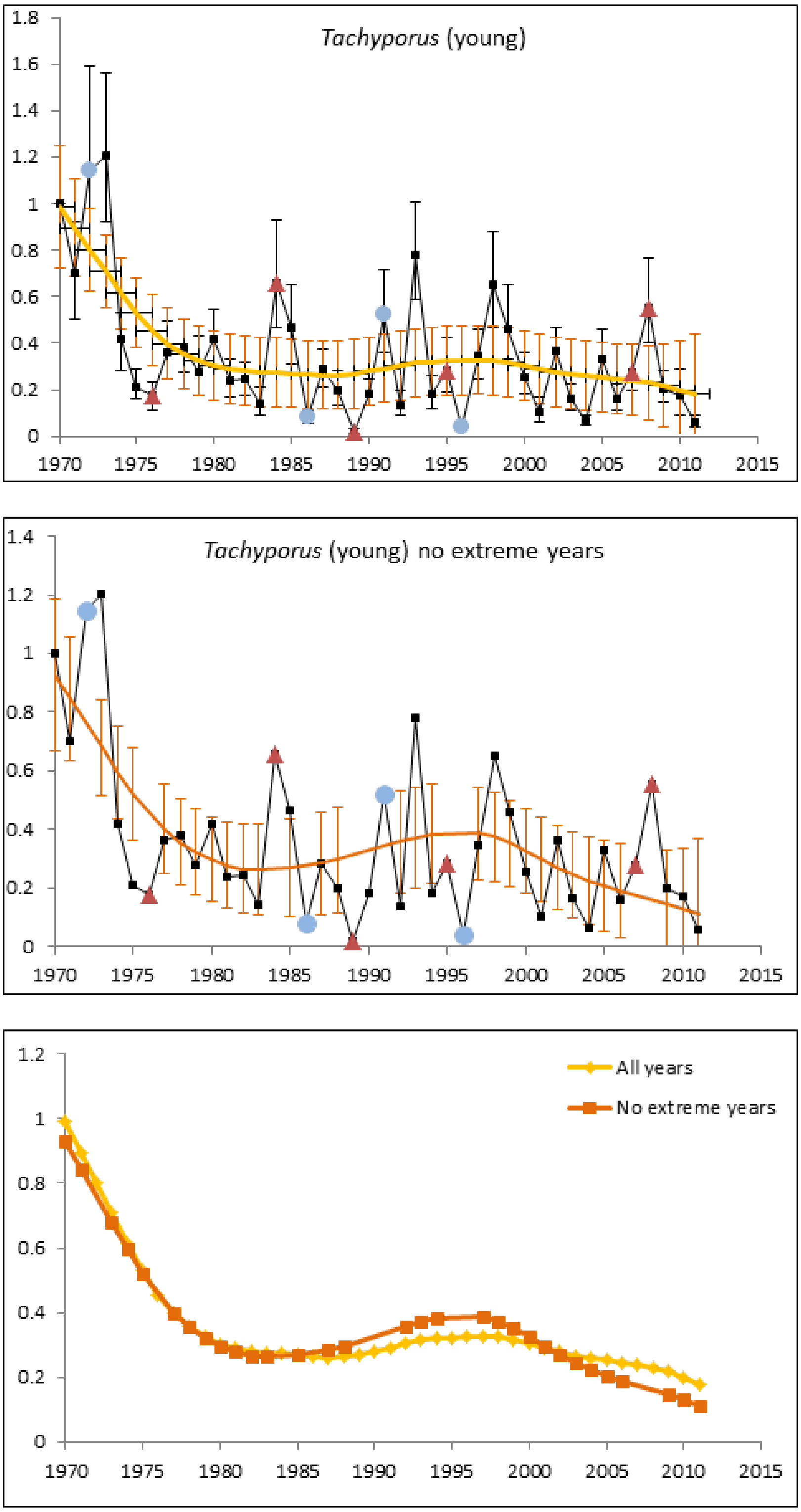


Figure 16. Long term trends in *Tachyporus* nymphs: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

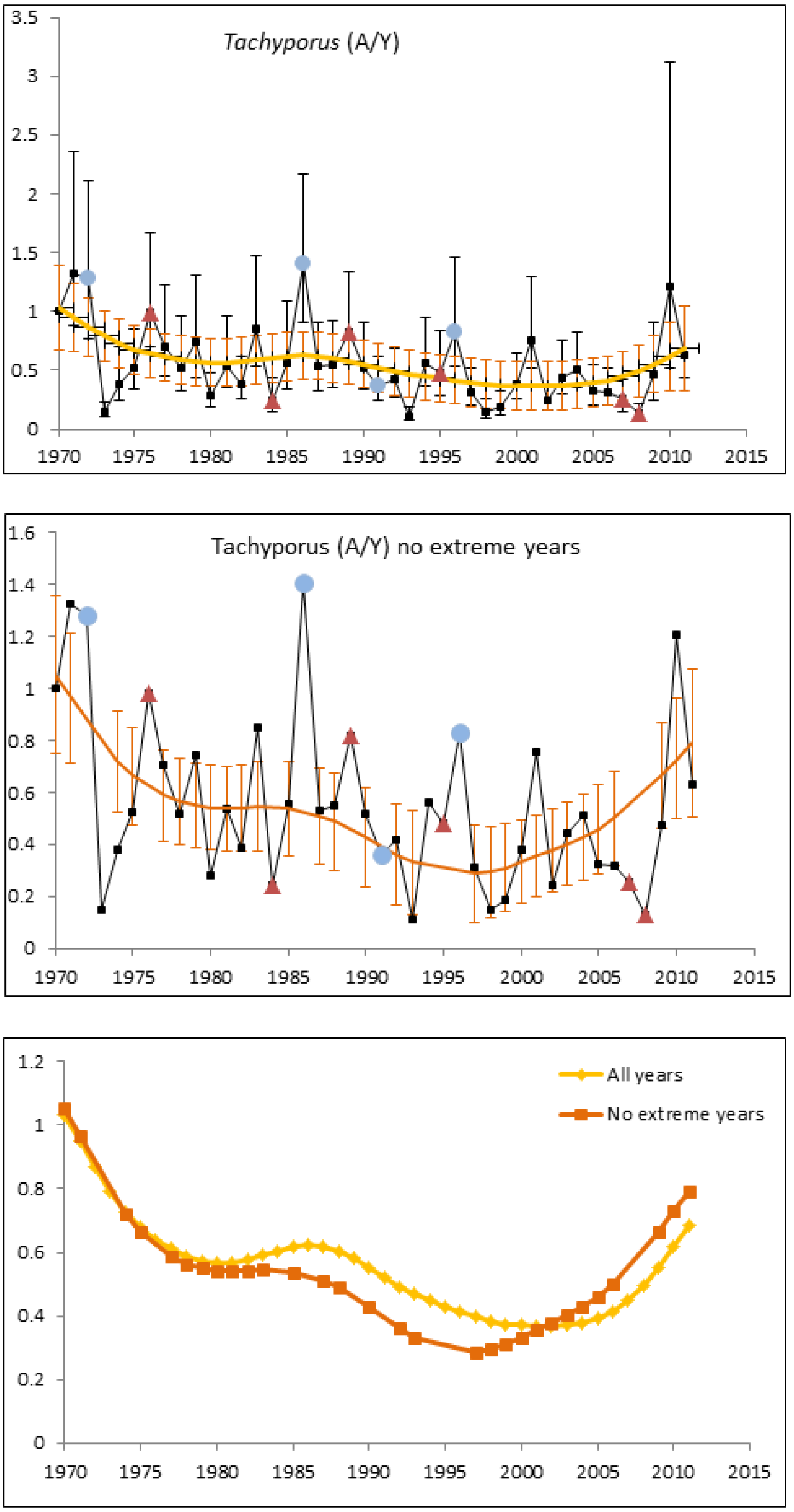


Figure 17. Long term trends in the ratio of *Tachyporus* adults to nymphs: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

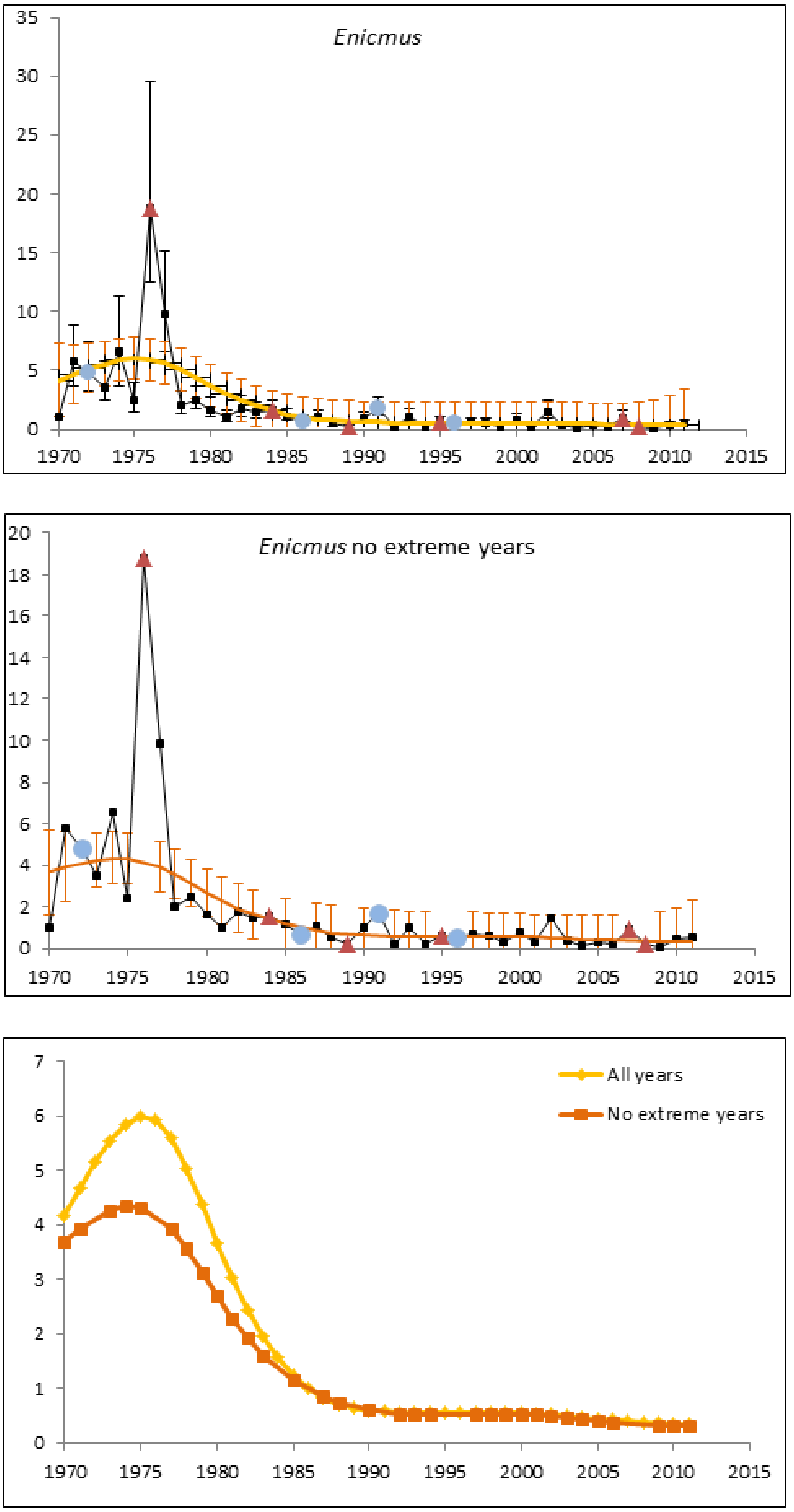


Figure 18. Long term trends in *Enicmus*: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

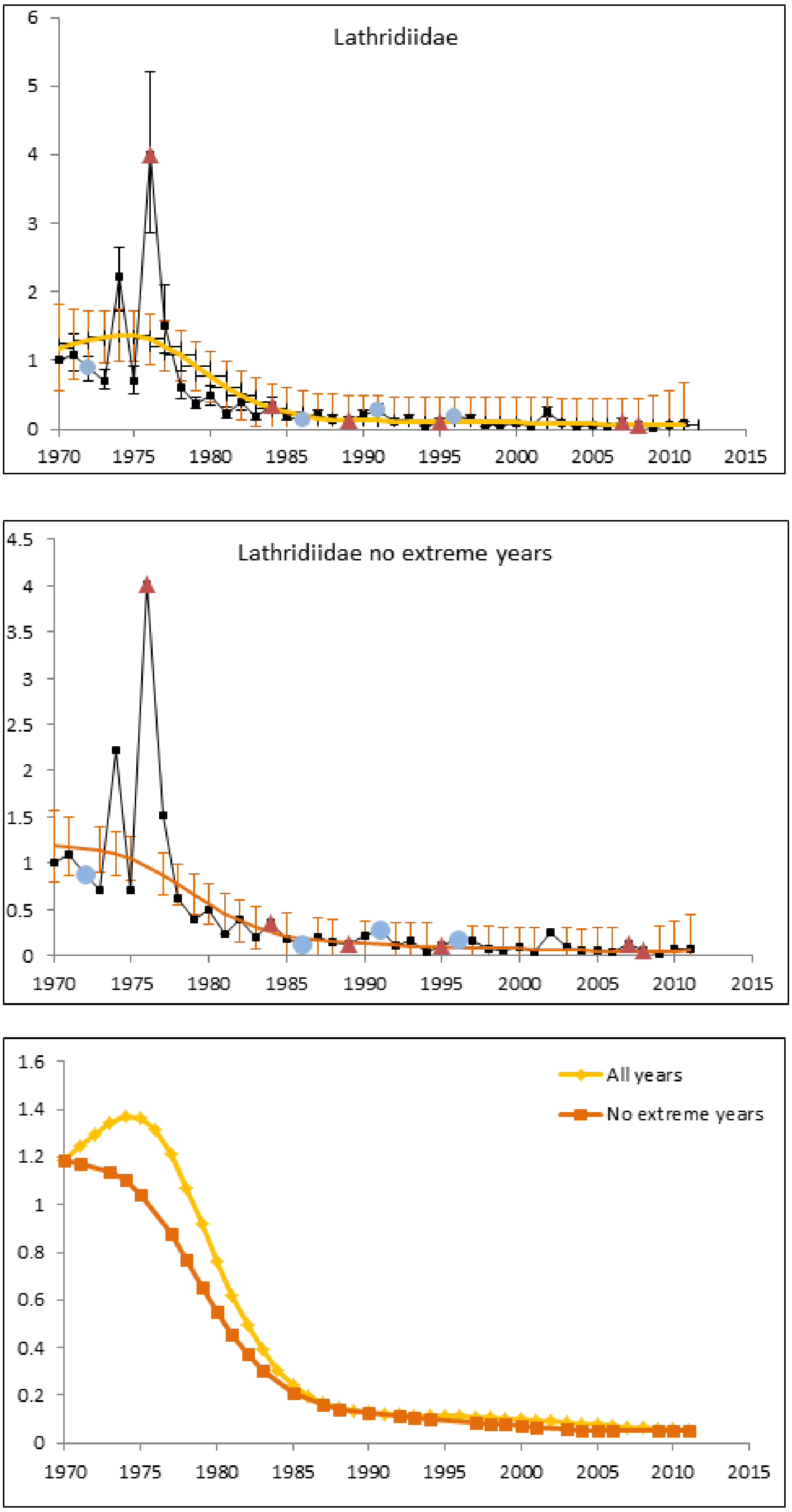


Figure 19. Long term trends in Lathridiidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

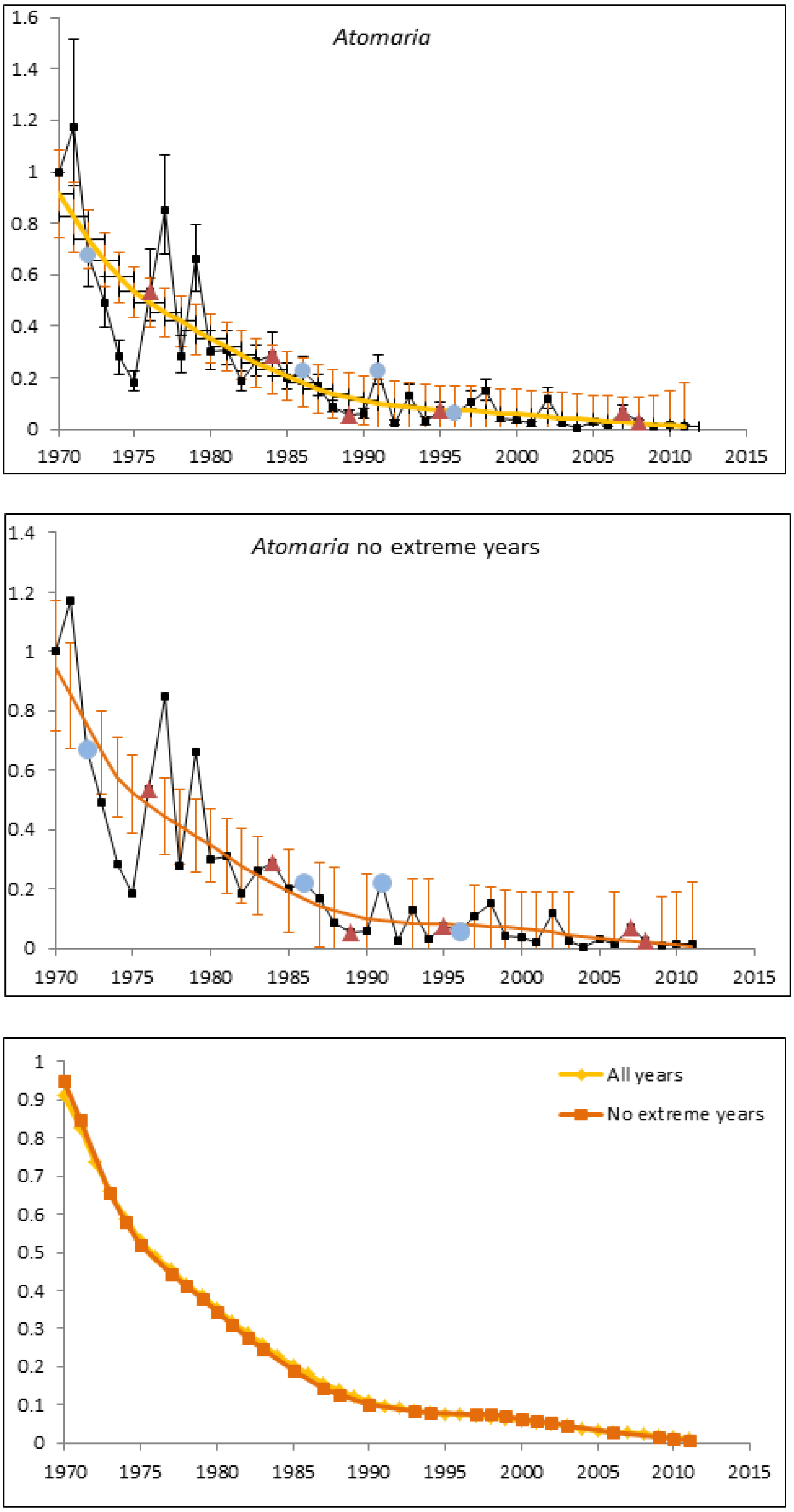


Figure 20. Long term trends in *Atomaria*: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

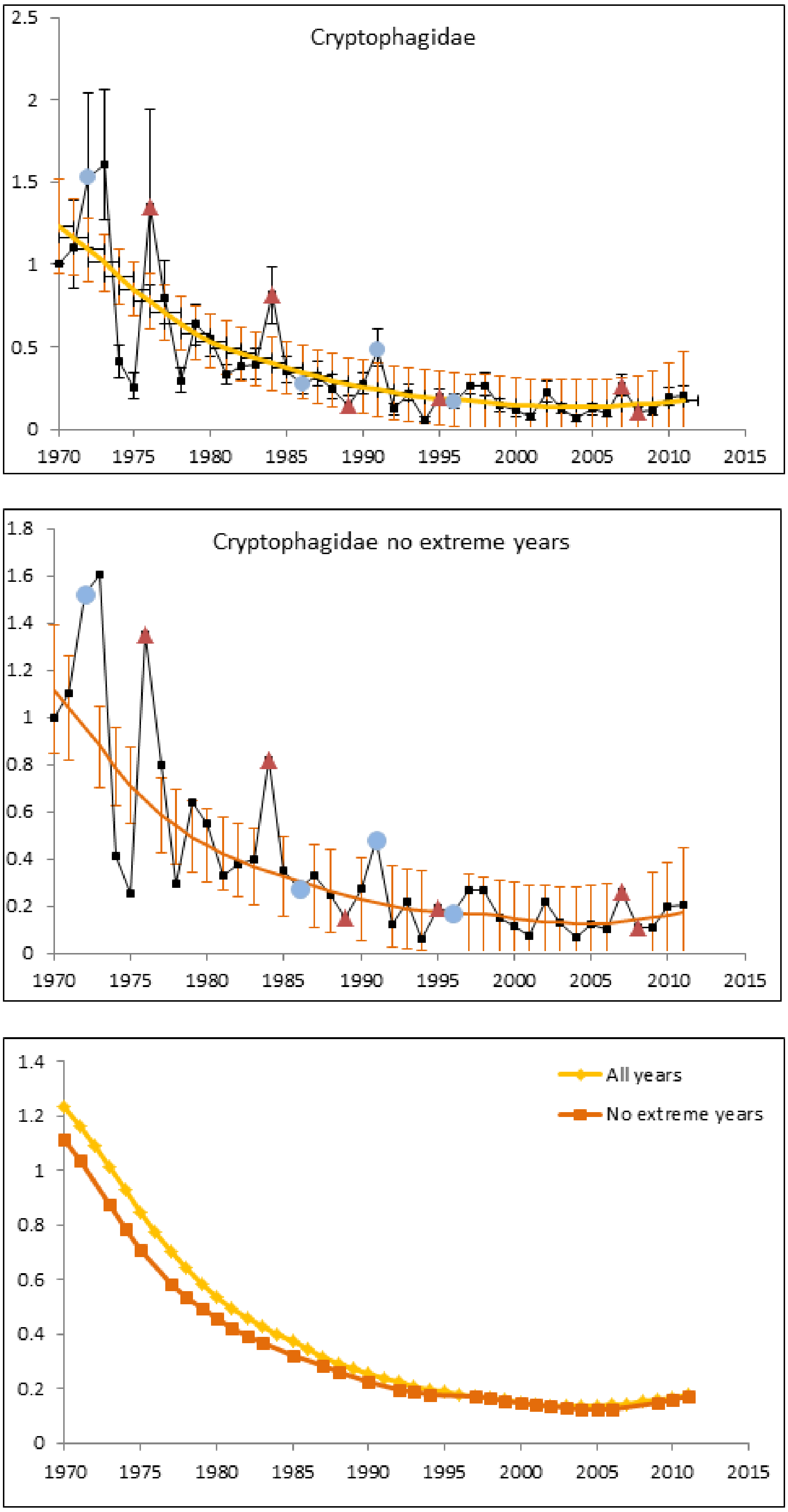


Figure 21. Long term trends in Cryptophagidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

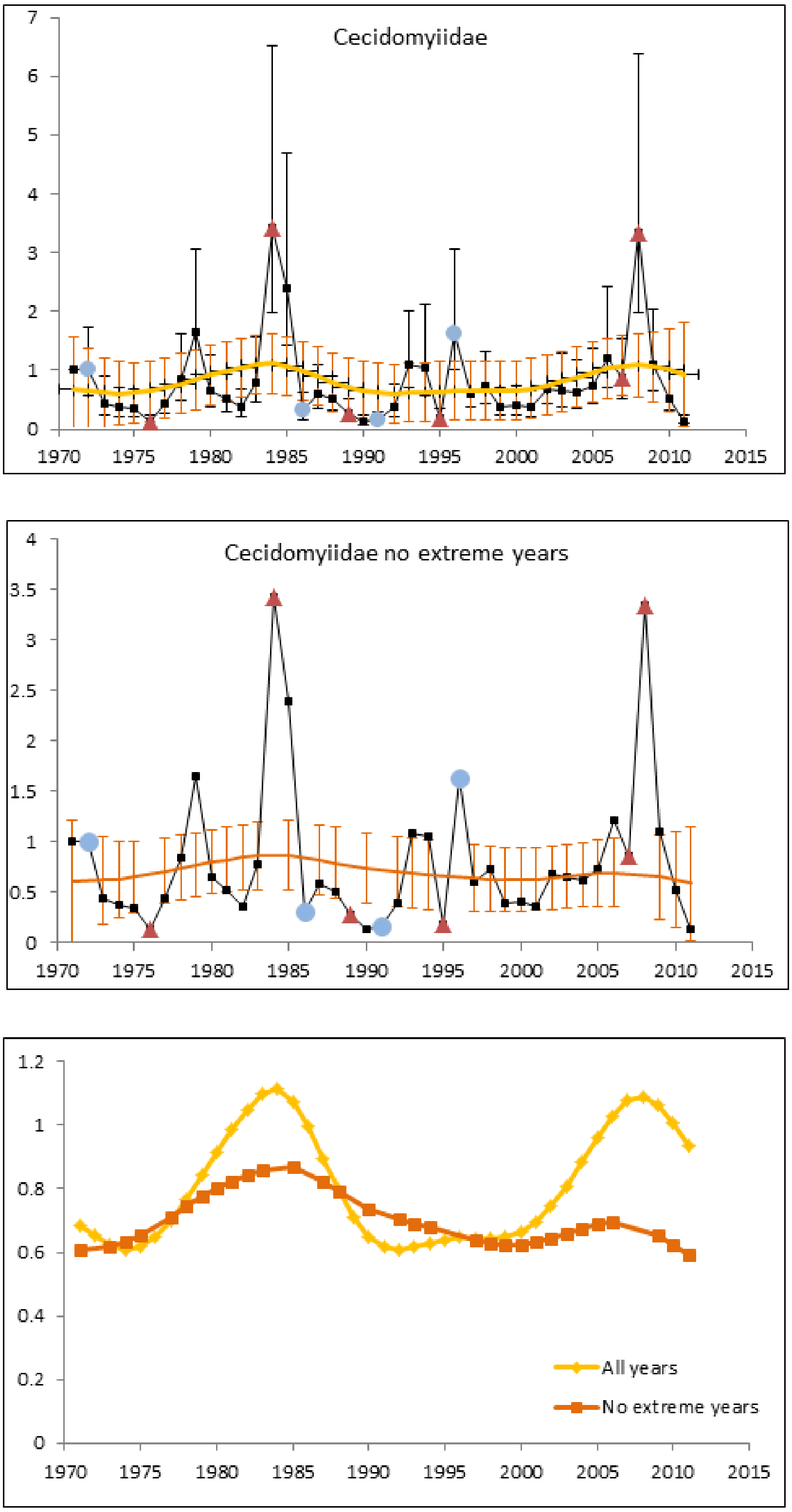


Figure 22. Long term trends in Cecidomyiidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

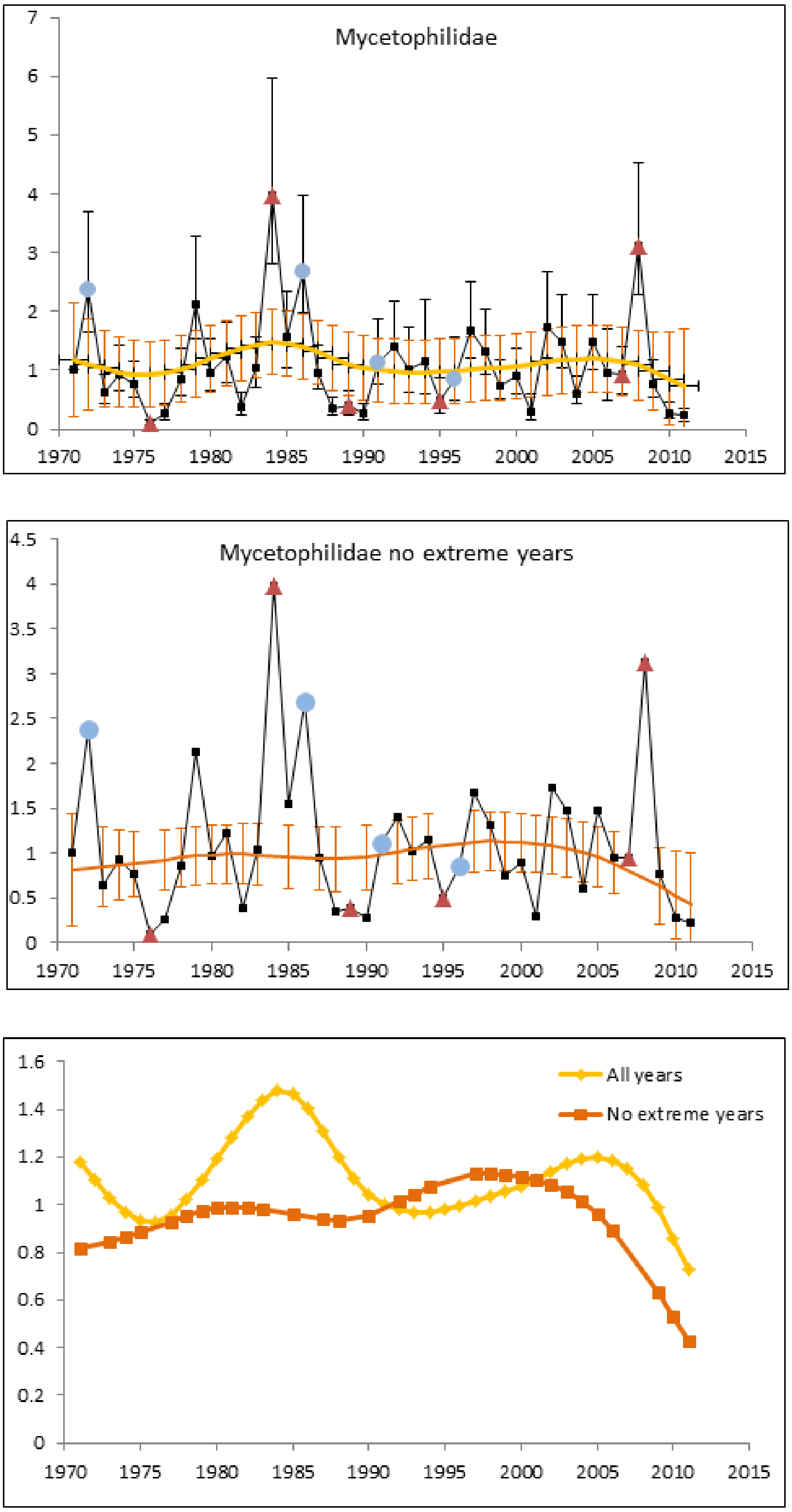


Figure 23. Long term trends in Mycetophilidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

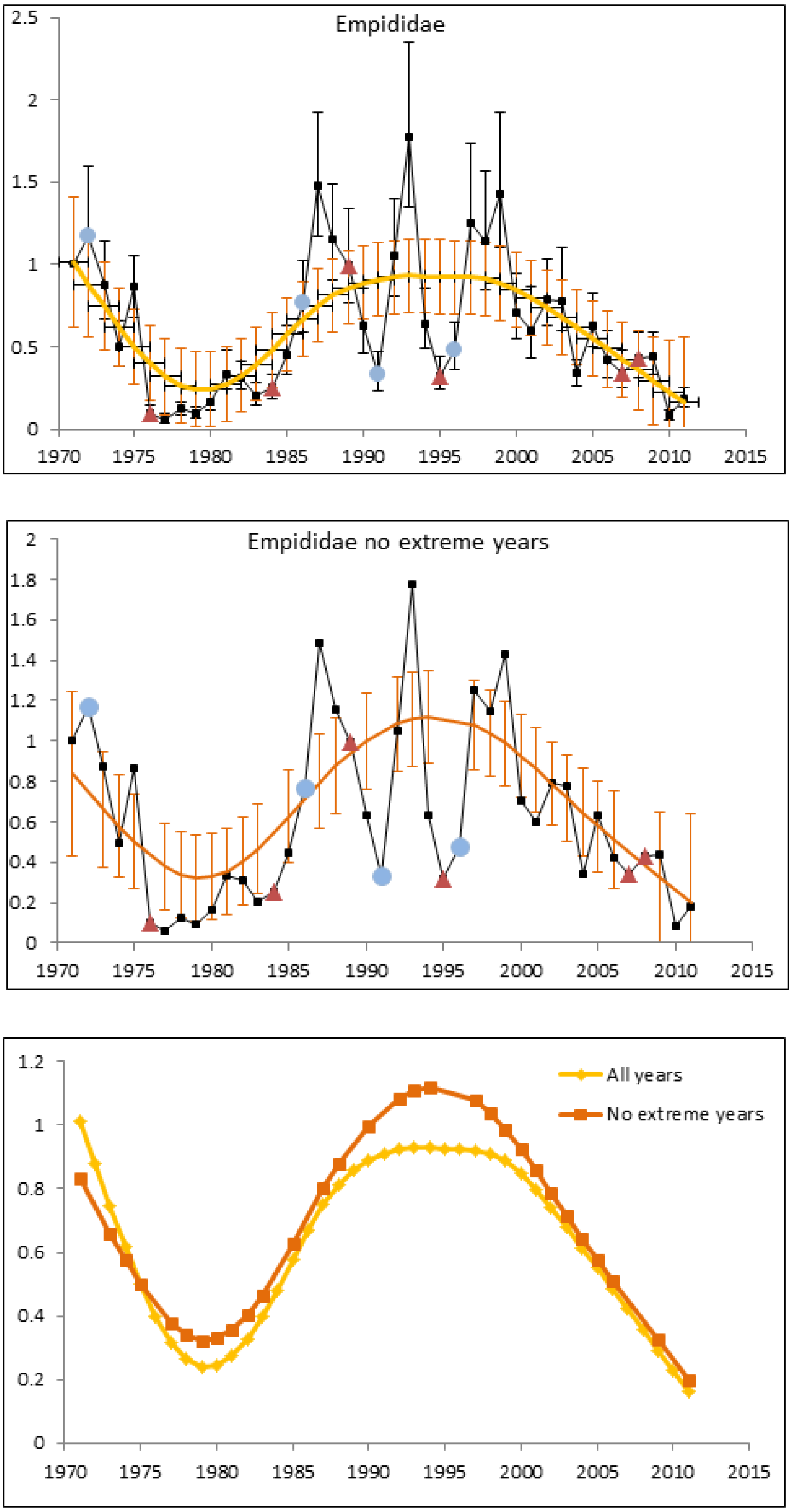


Figure 24. Long term trends in Empididae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

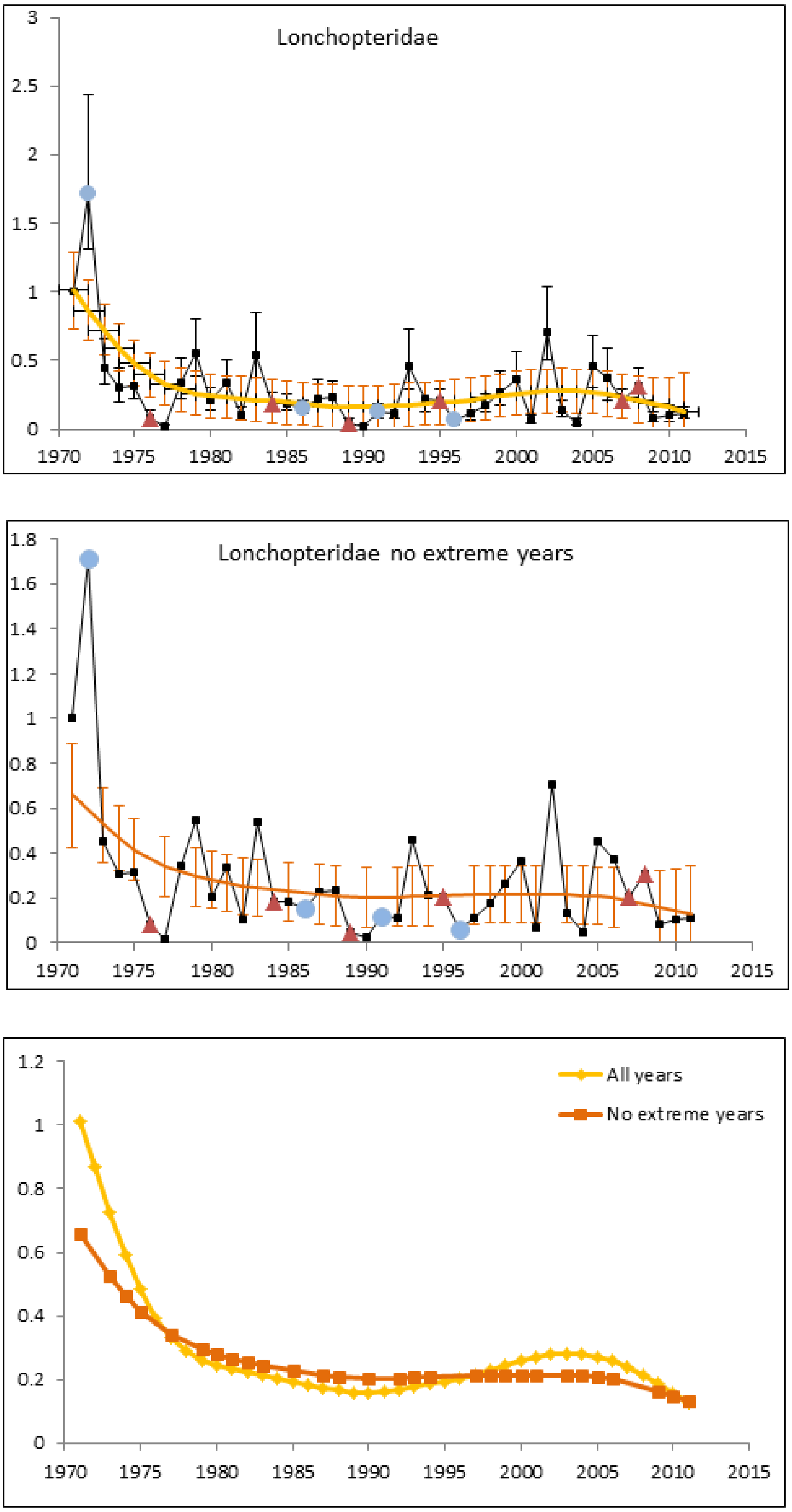


Figure 25. Long term trends in Lonchopteridae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

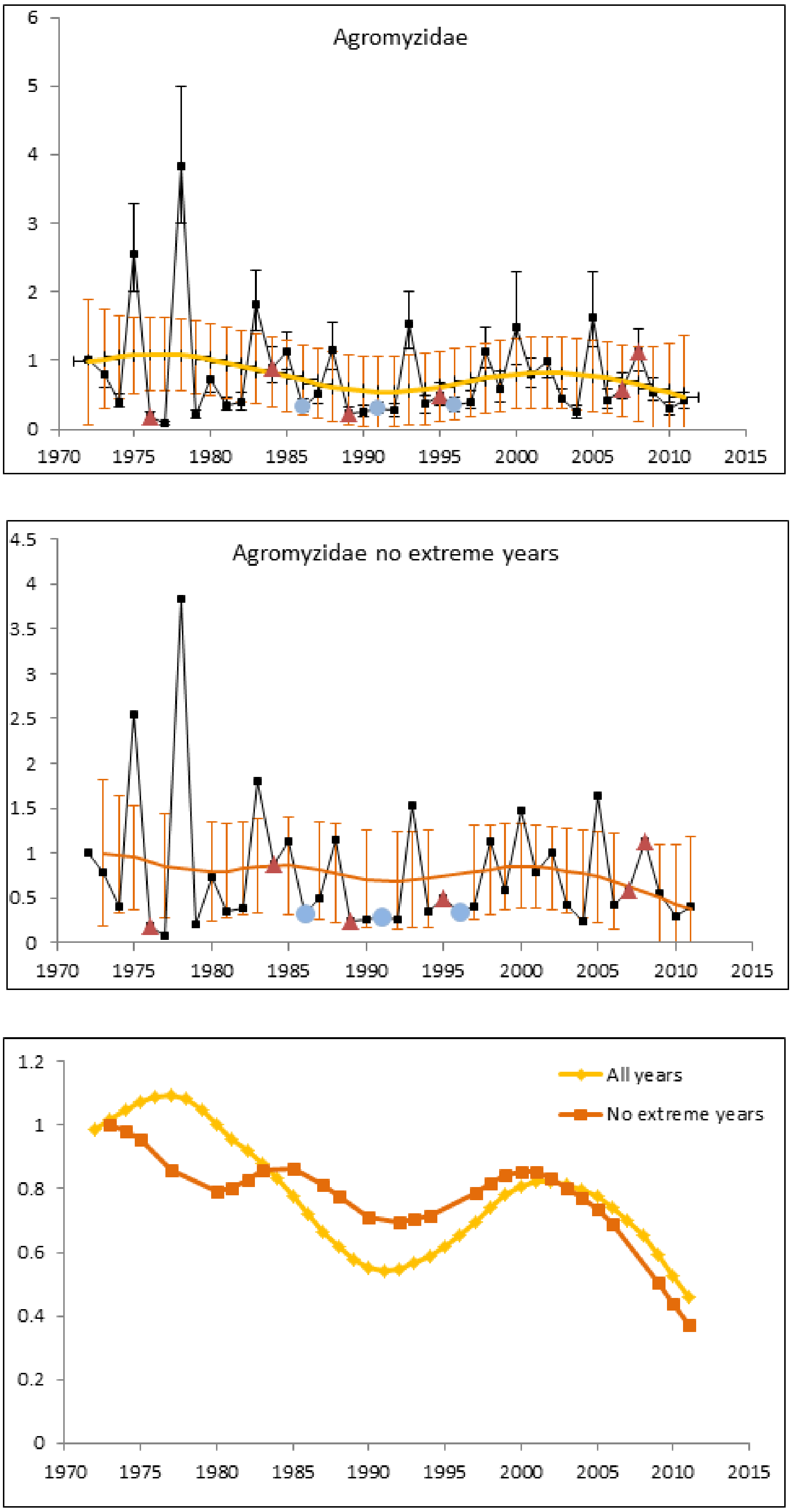


Figure 26. Long term trends in Agromyzidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

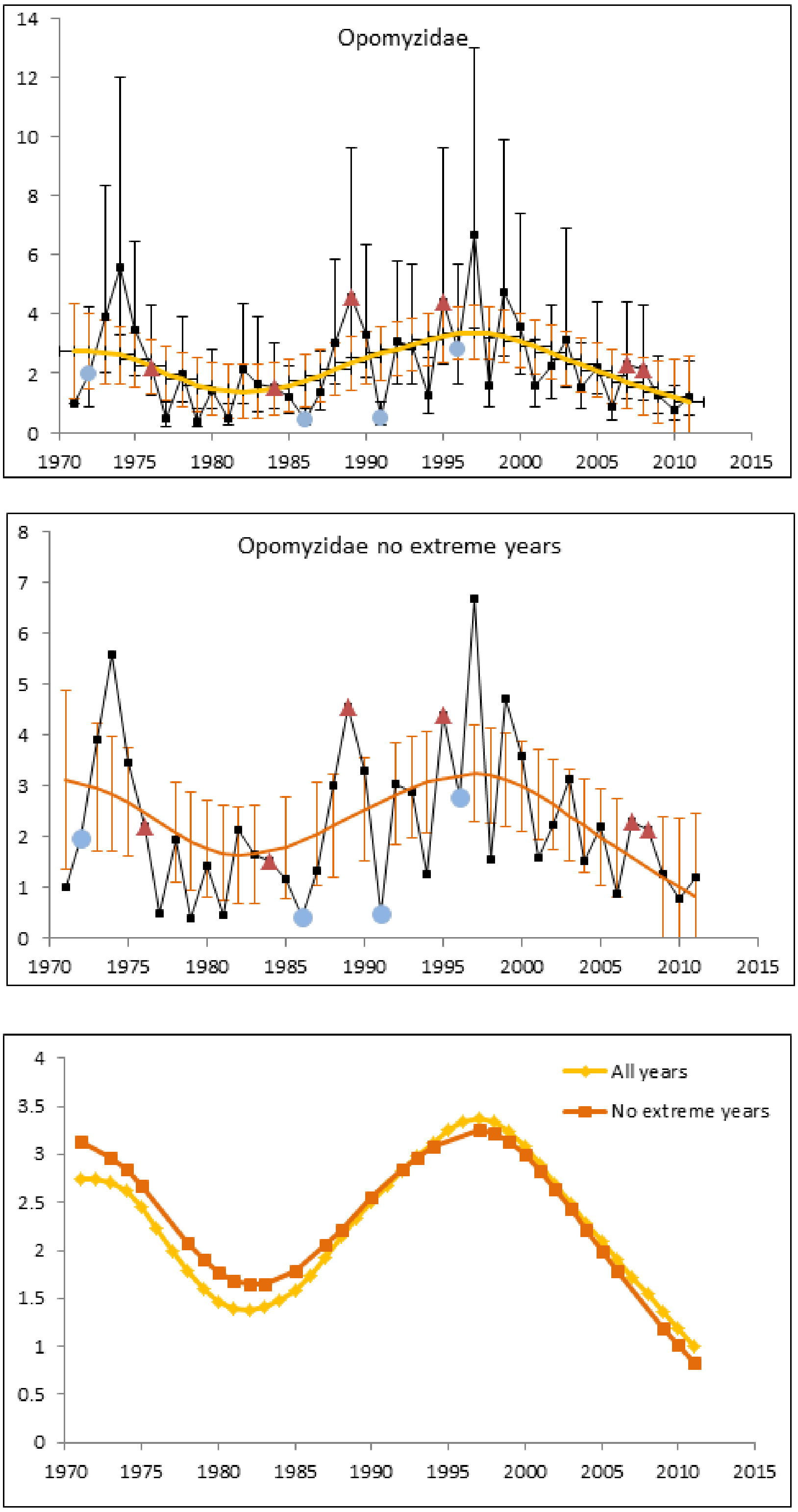


Figure 27. Long term trends in Opomyzidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

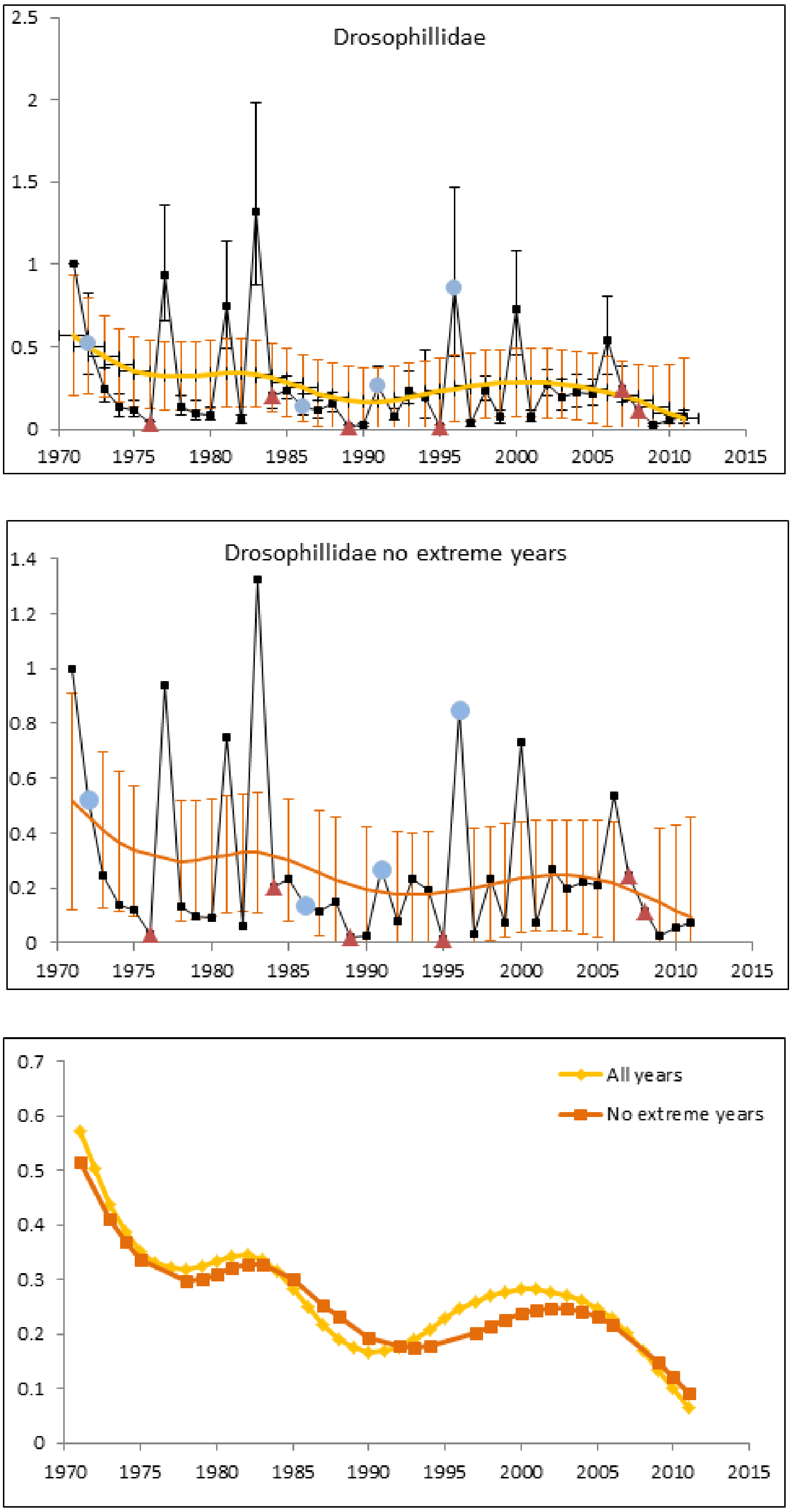
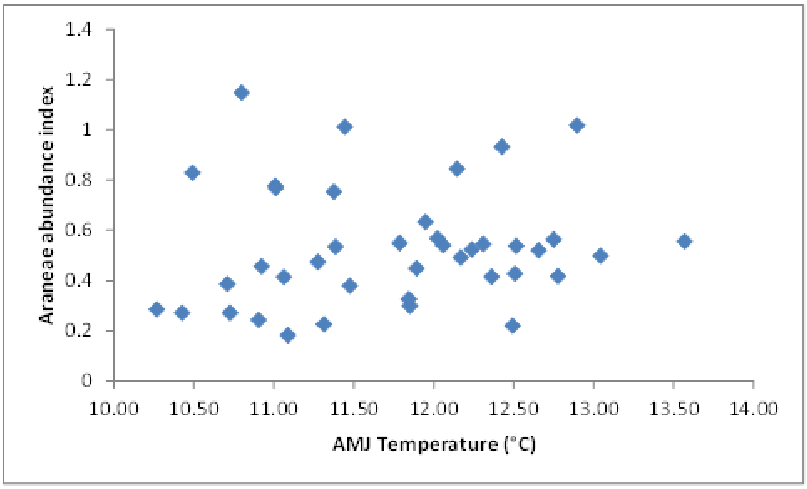
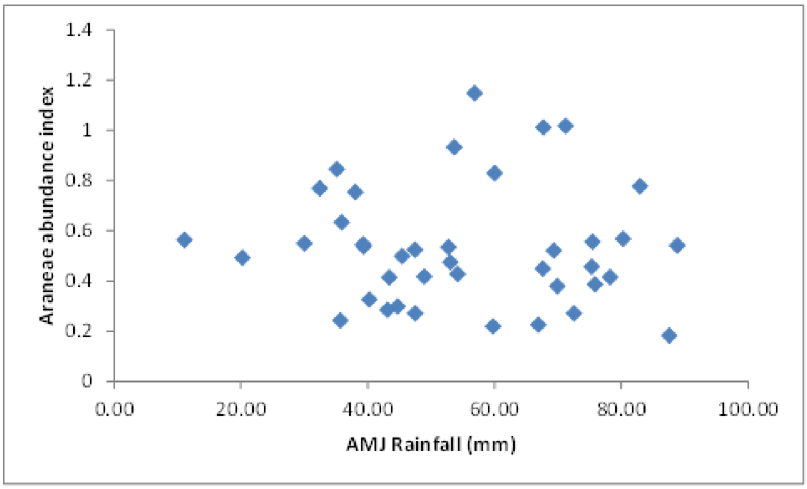


Figure 28. Long term trends in Drosophillidae: (A.) All years with trend and 95% confidence interval, (B.) trend without extreme years, and (C). comparison of the two long-term trends from the top two graphs. Hot/dry extremes are indicated by red triangles, cold/wet years by blue circles.

Appendix 10





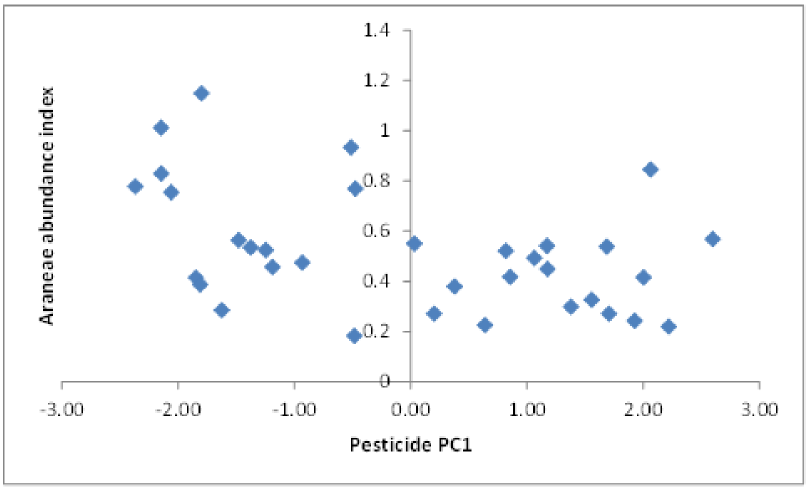


Figure 1. Correlation between Araneae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

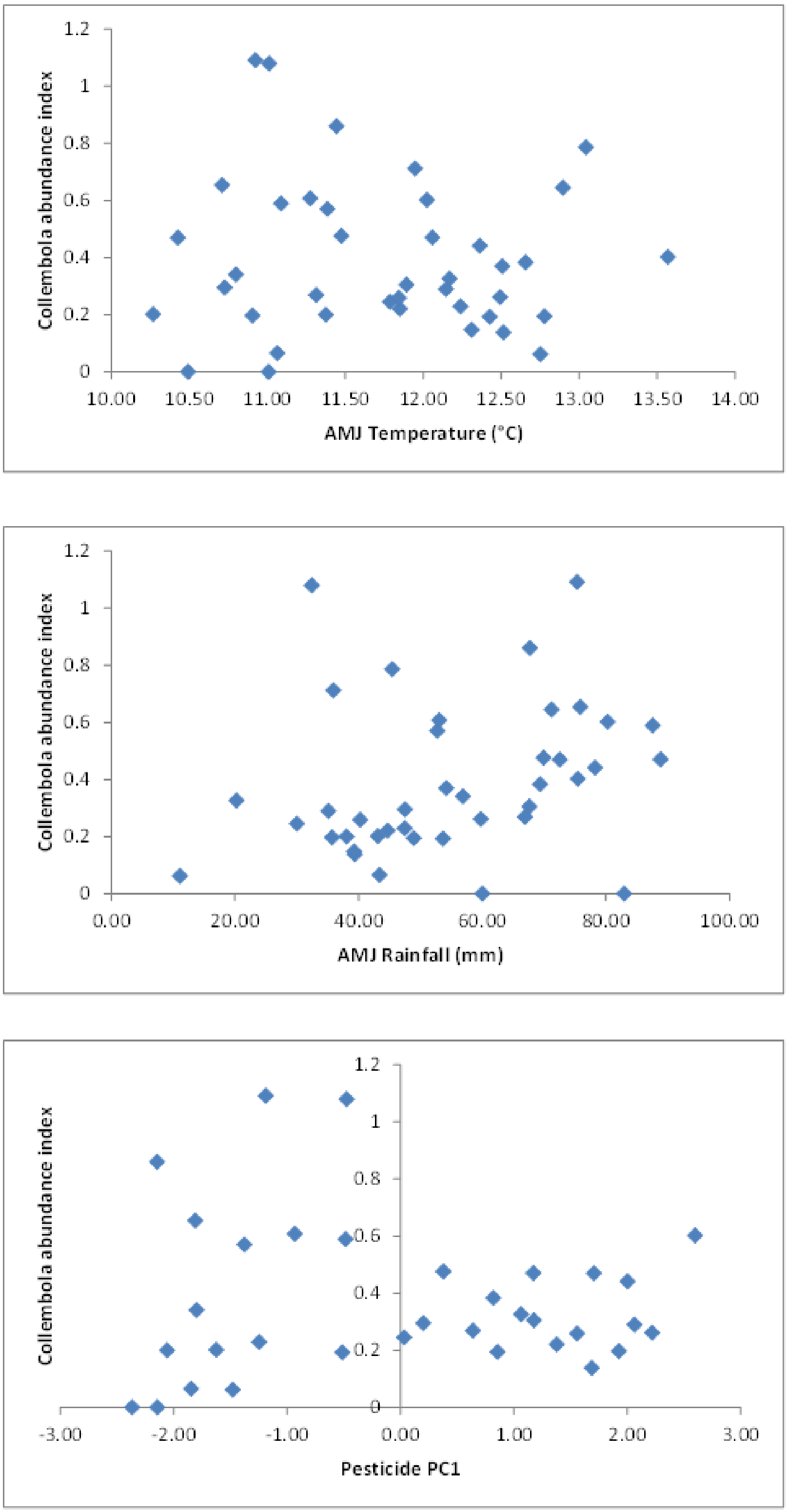


Figure 2. Correlation between Collembola abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

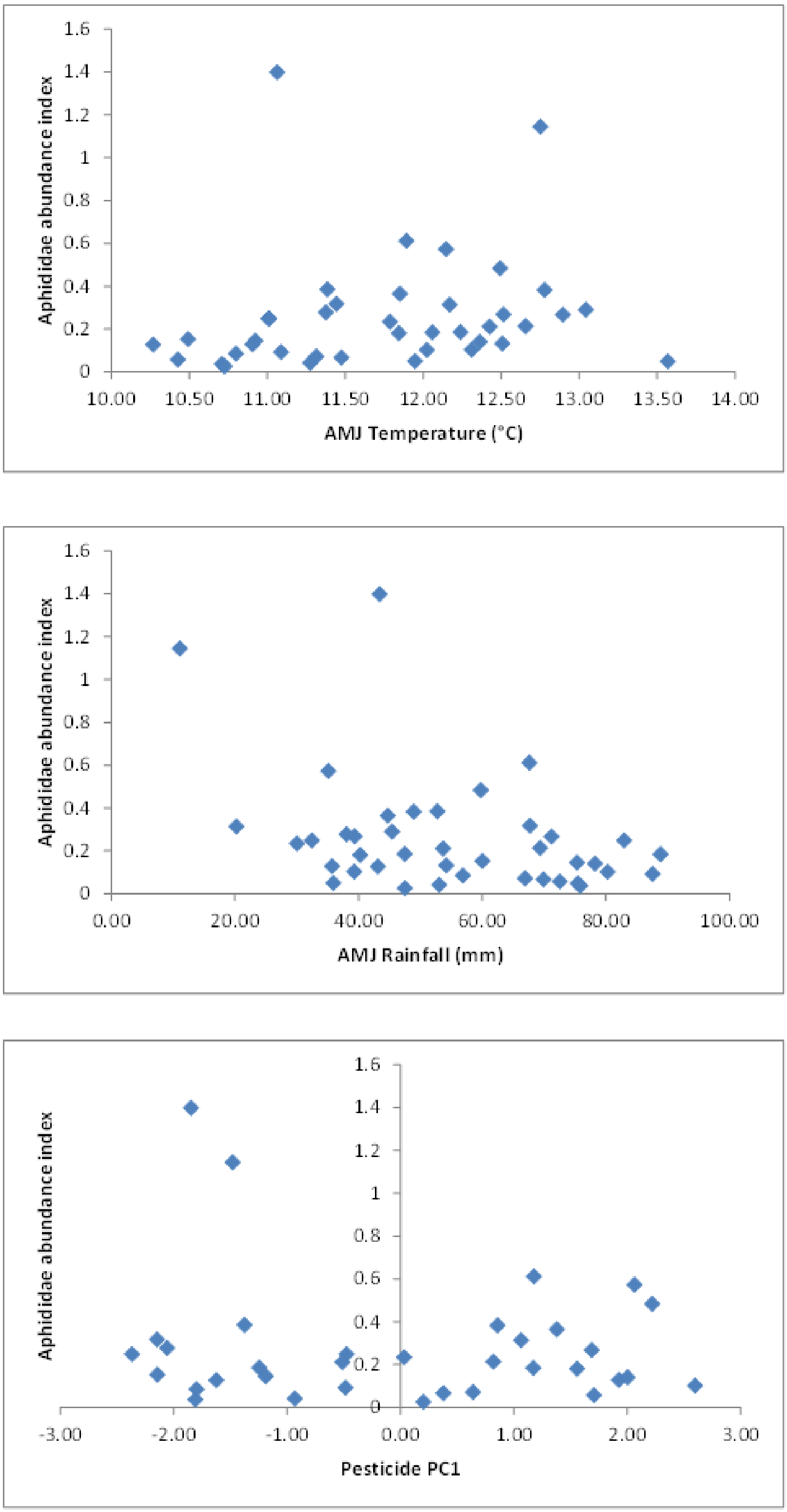
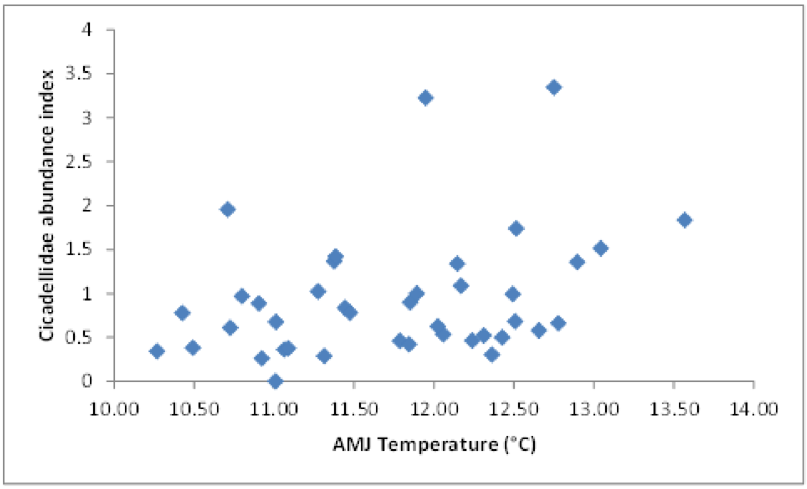
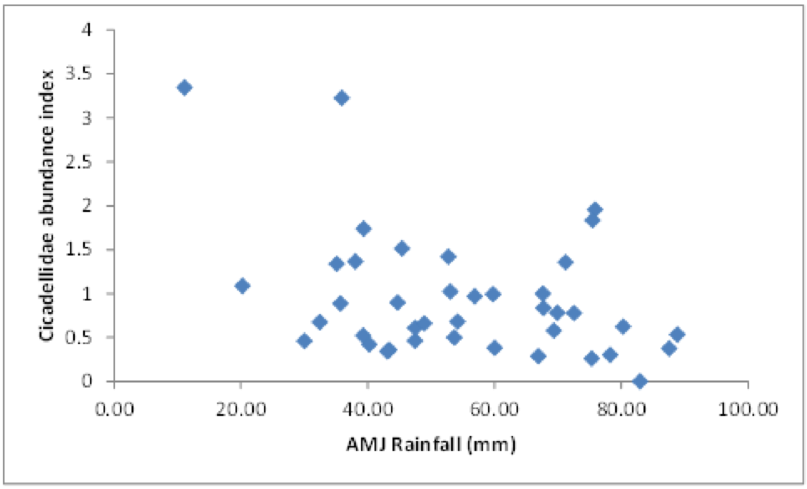


Figure 3. Correlation between Aphididae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.





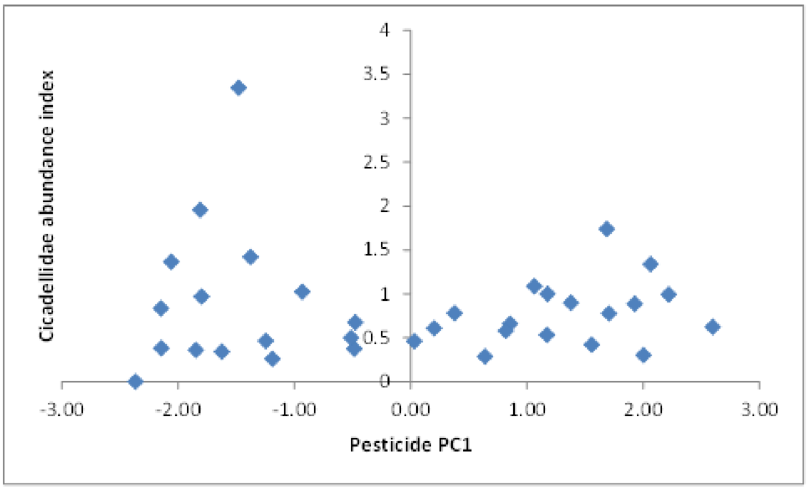


Figure 4. Correlation between Cicadellidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

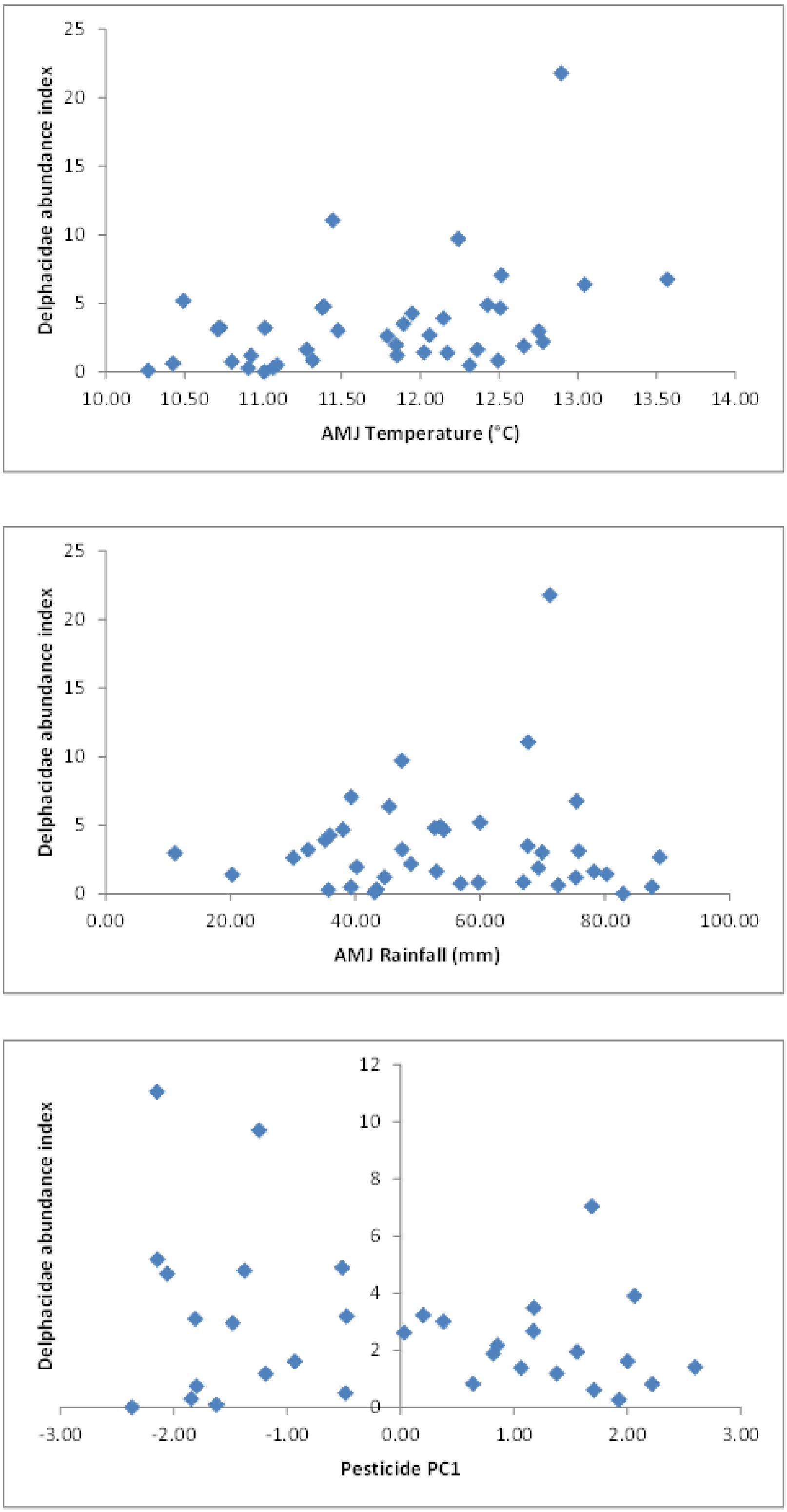
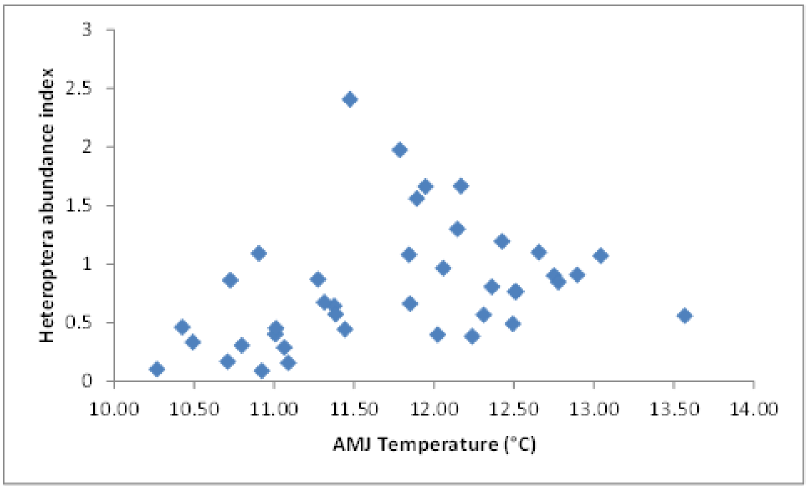
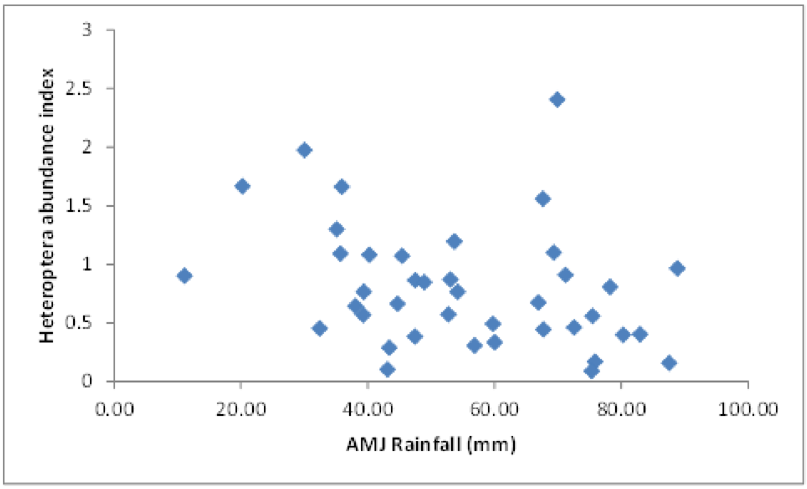


Figure 5. Correlation between Delphacidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.





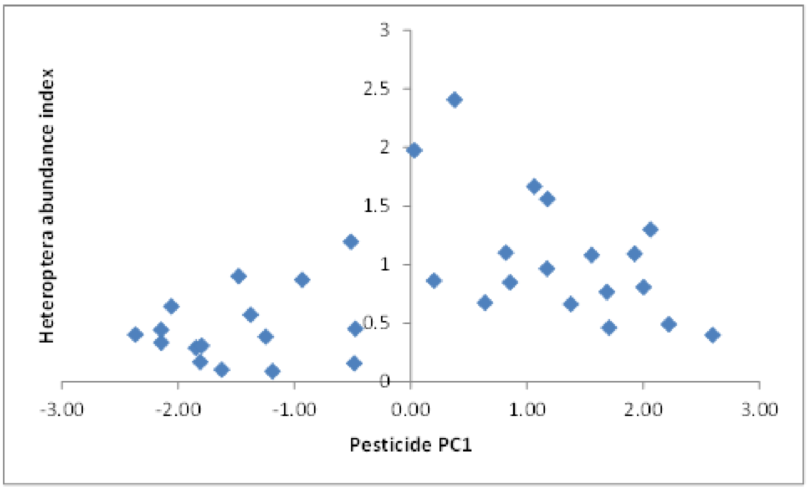


Figure 6. Correlation between Heteroptera abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

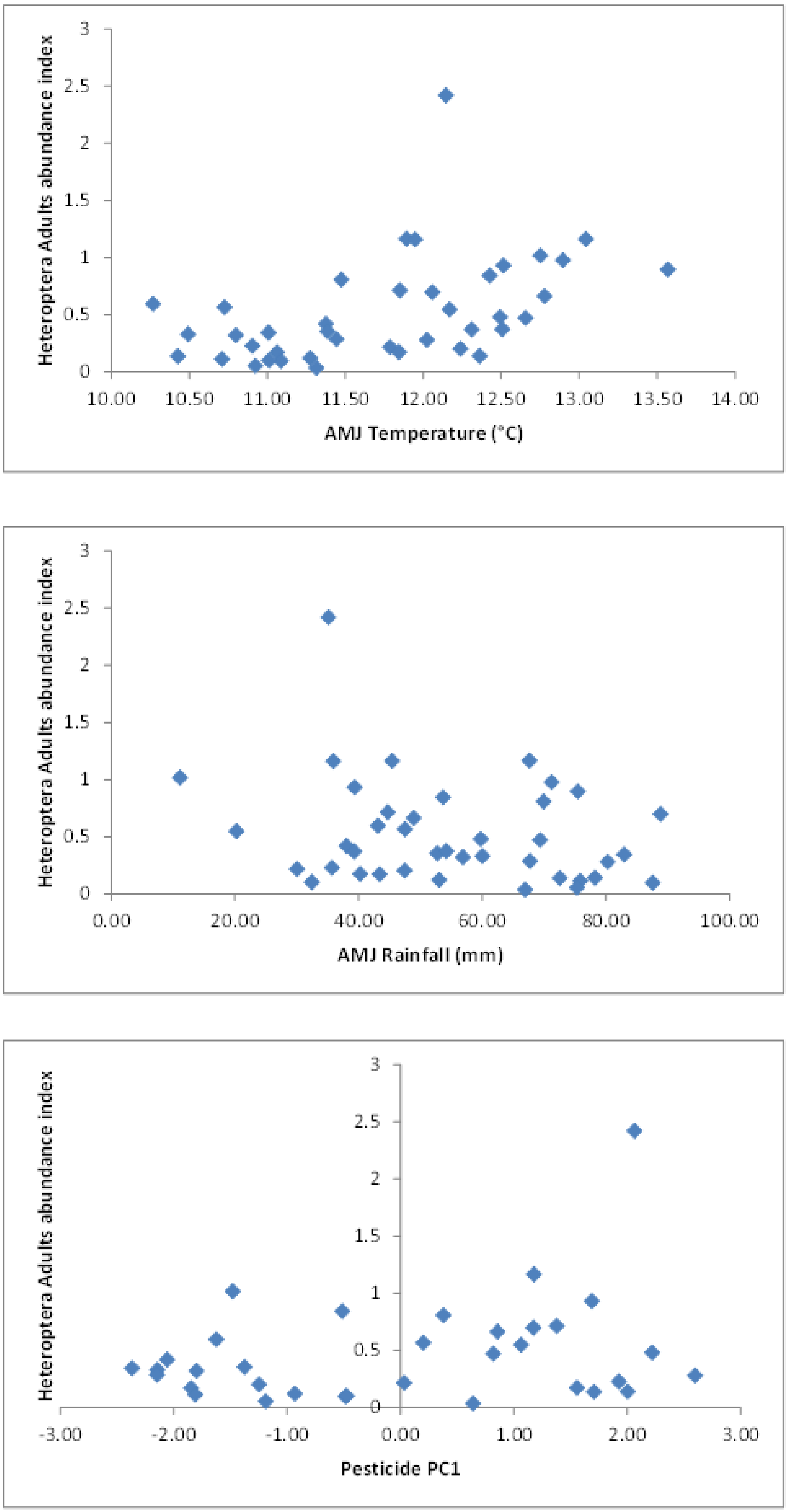


Figure 7. Correlation between Heteroptera adult abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

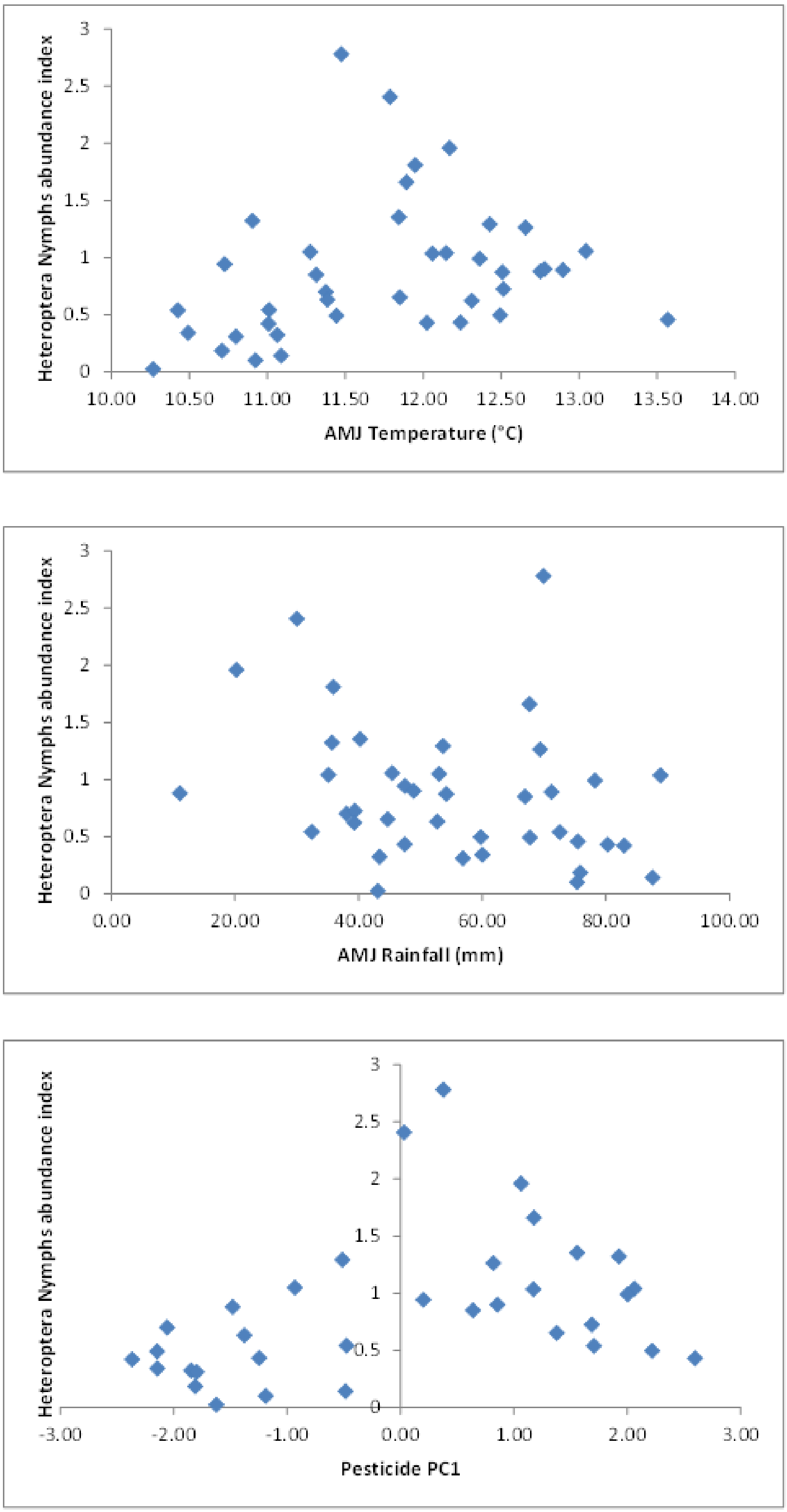


Figure 8. Correlation between Heteroptera young abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

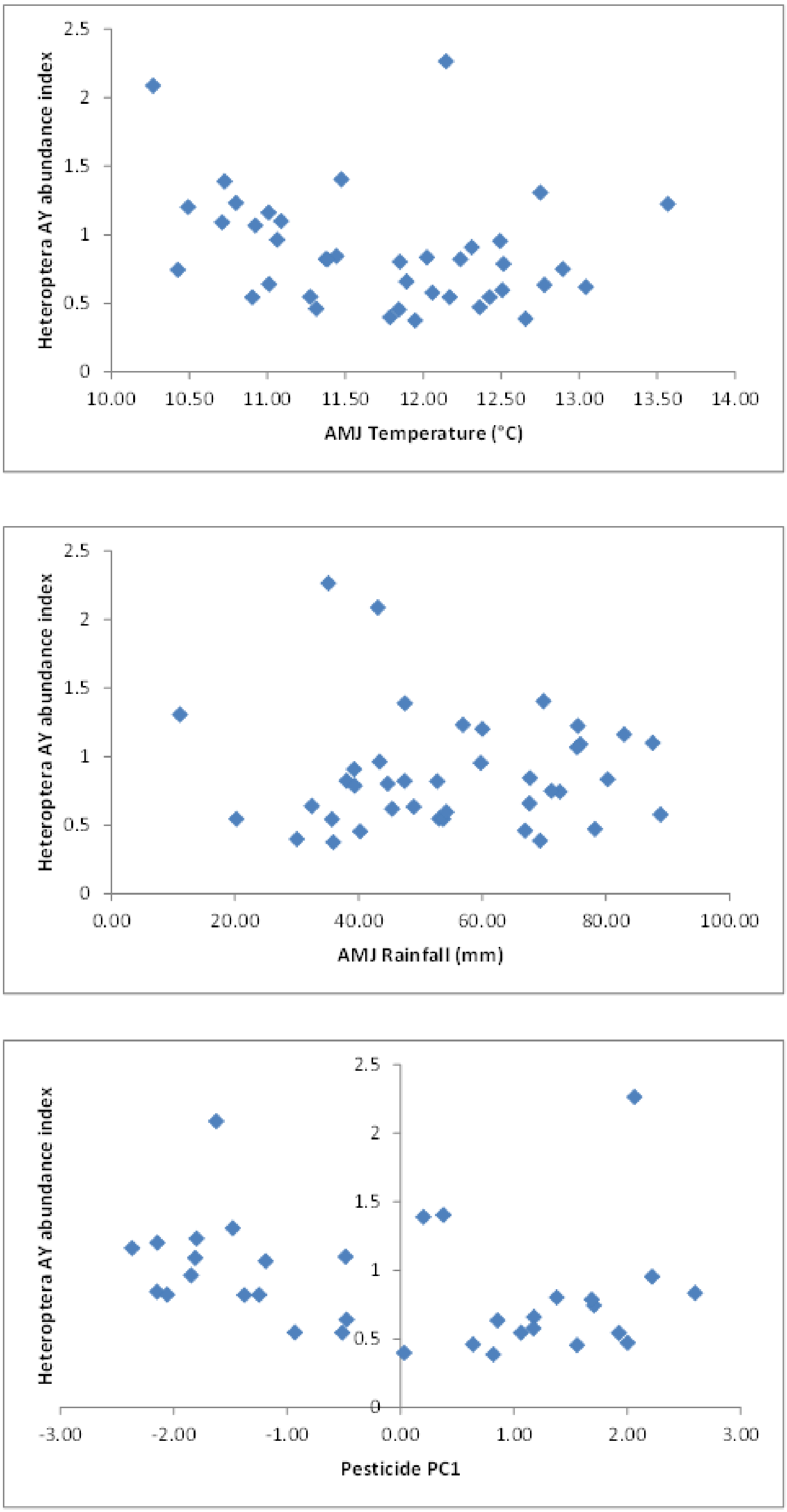


Figure 9. Correlation between Heteroptera AY abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

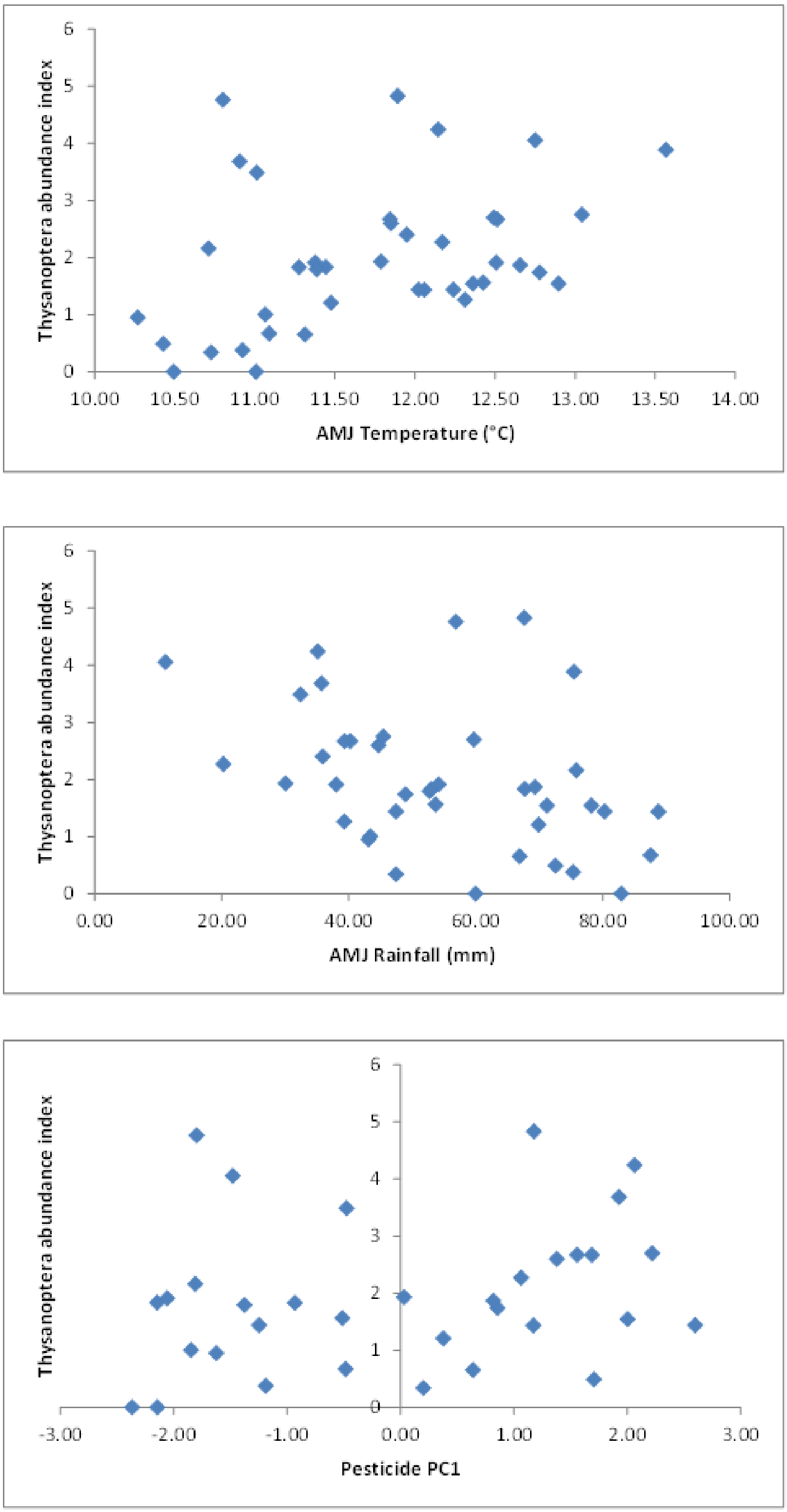


Figure 10. Correlation between Thysanoptera abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

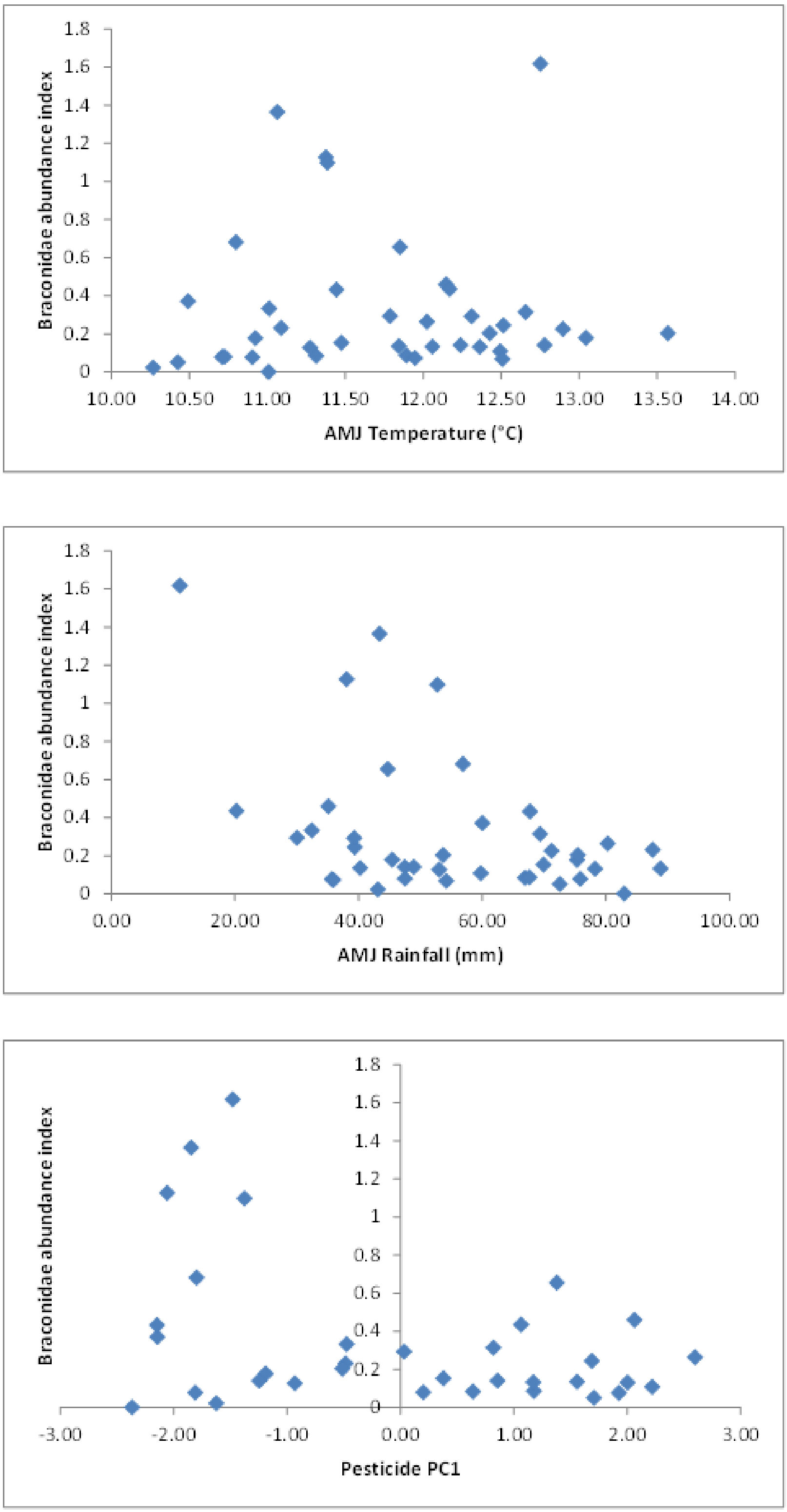


Figure 11. Correlation between Braconidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

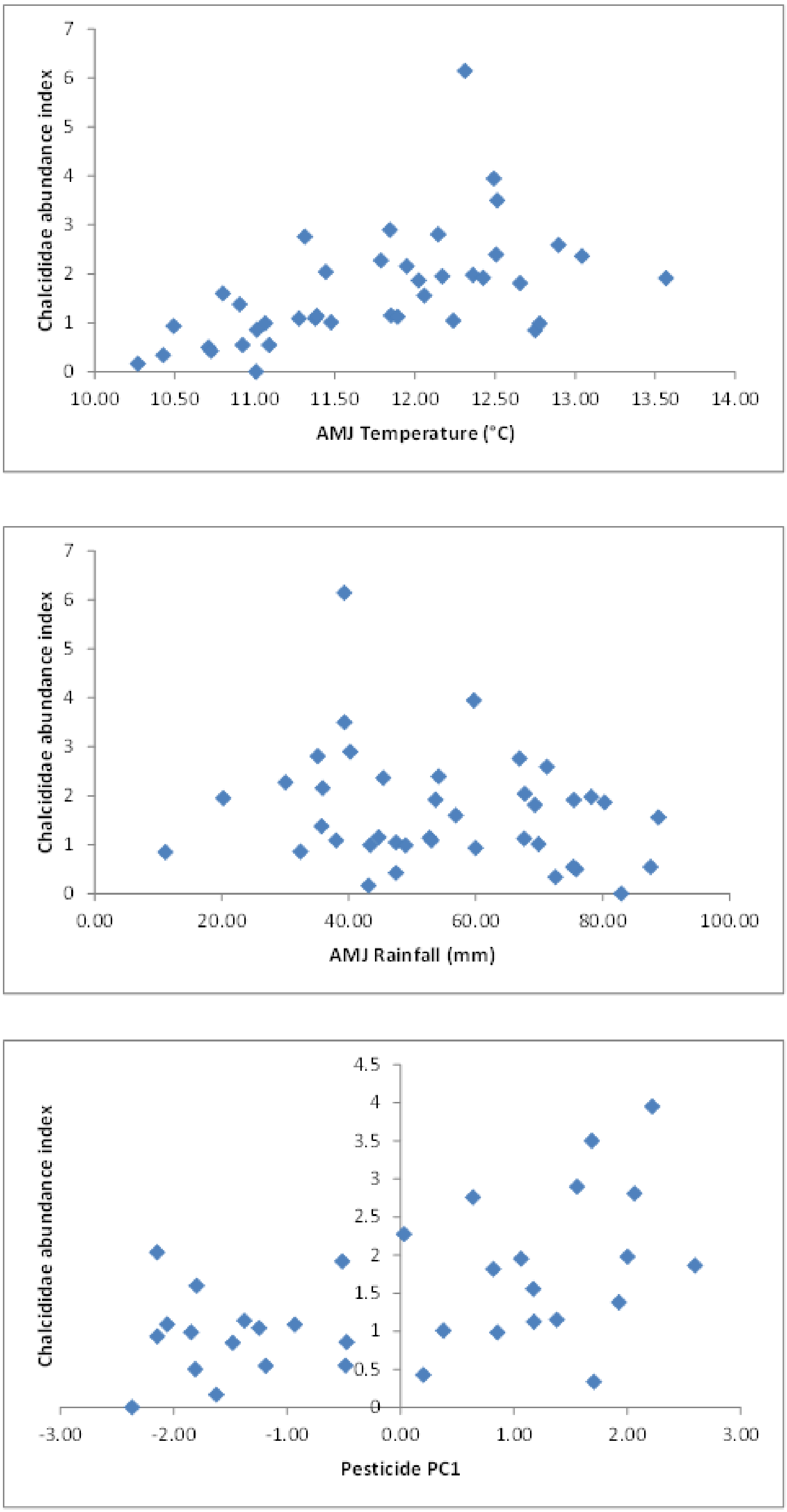


Figure 12. Correlation between Chalcididae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

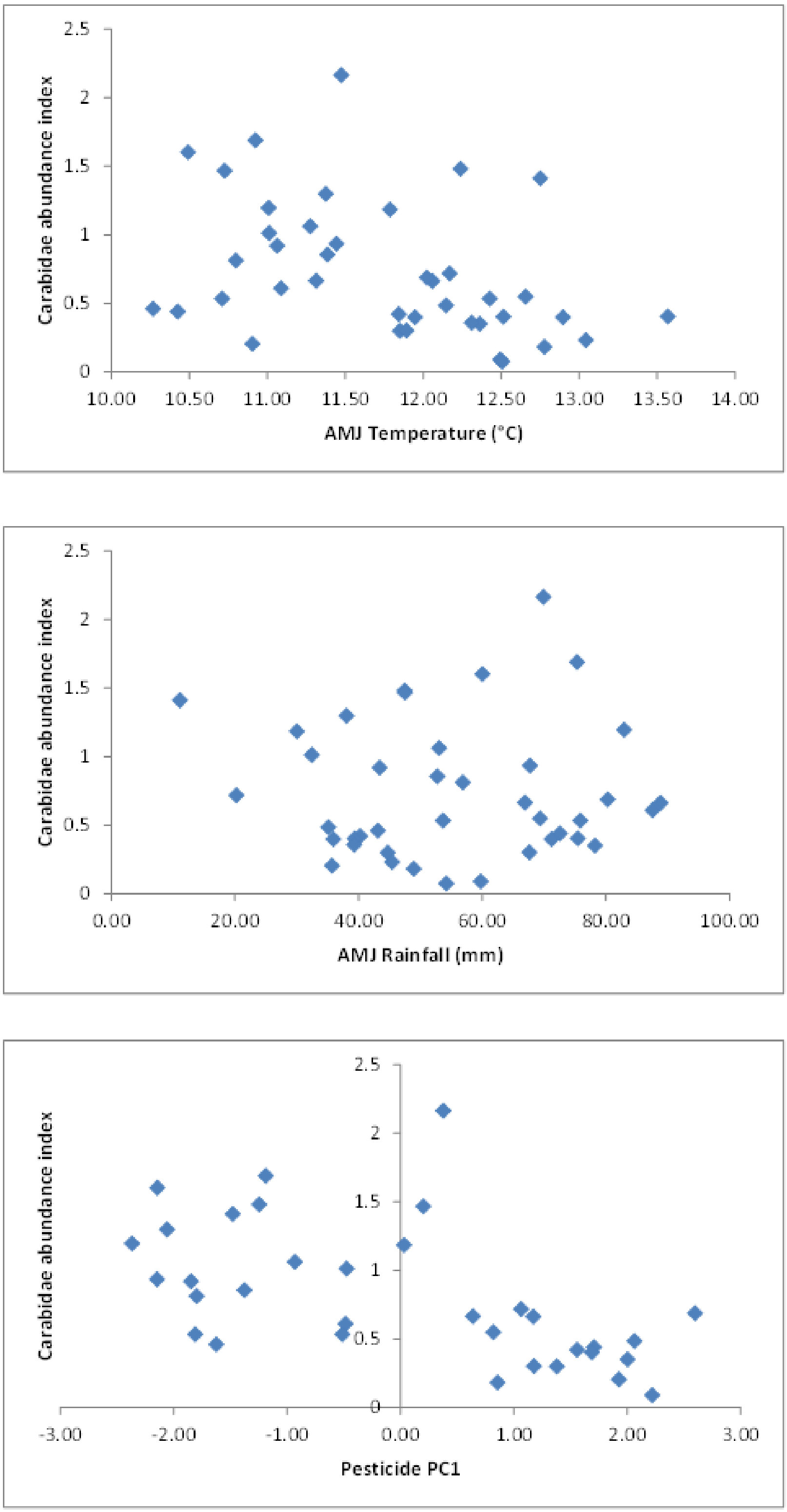


Figure 13. Correlation between Carabidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

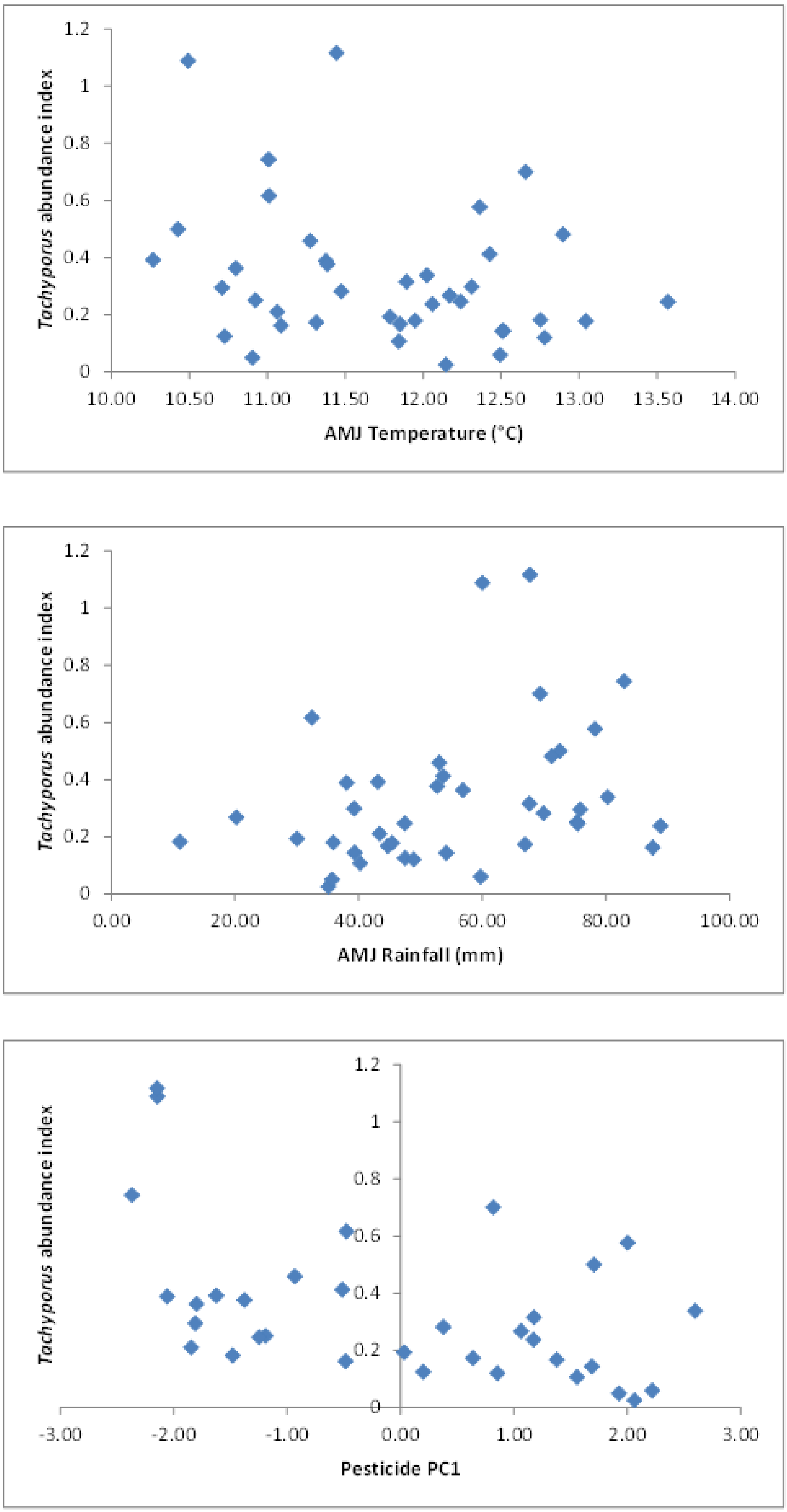


Figure 14. Correlation between *Tachyporus* abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

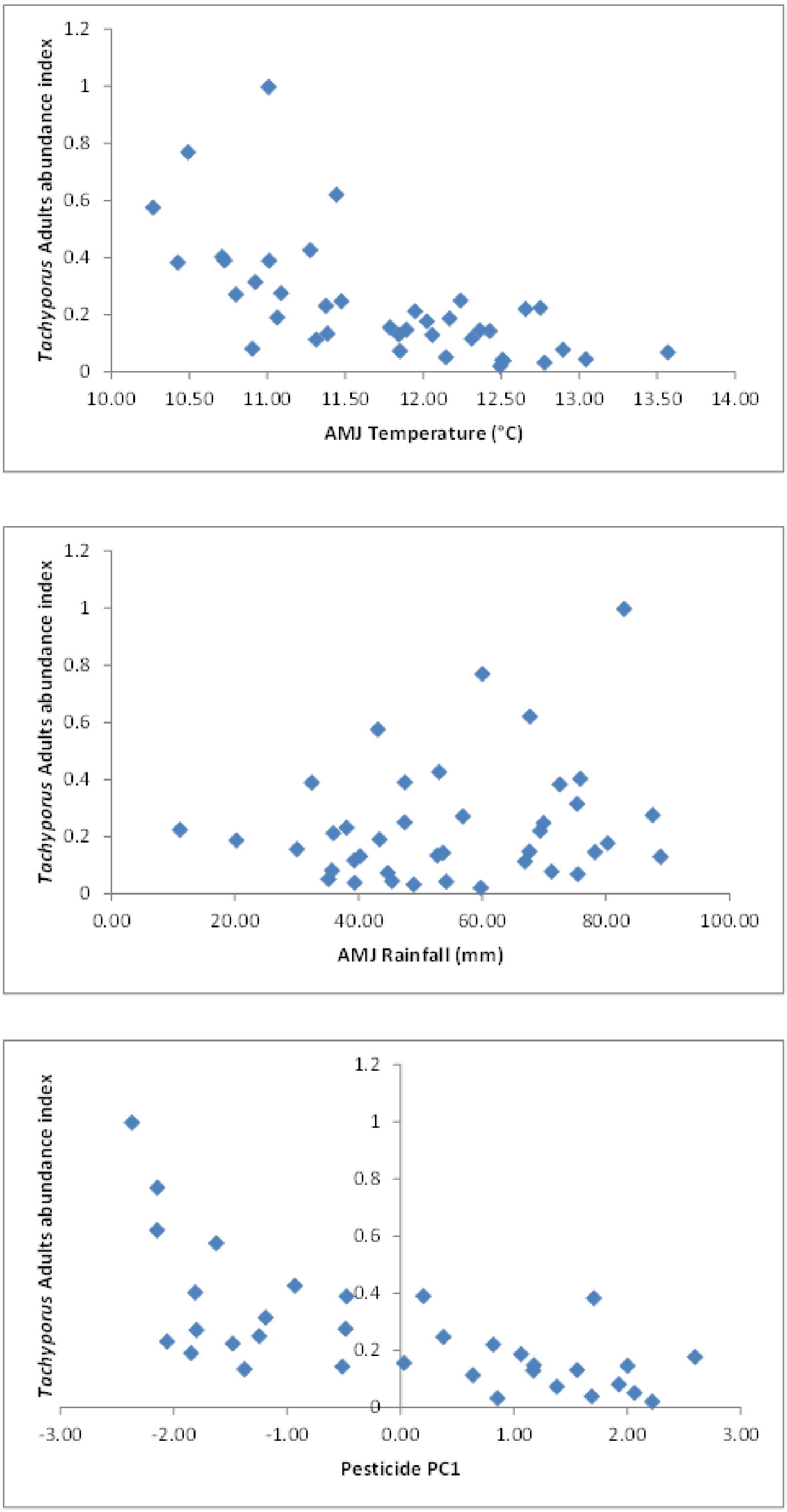


Figure 15. Correlation between *Tachyporus* Adult abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

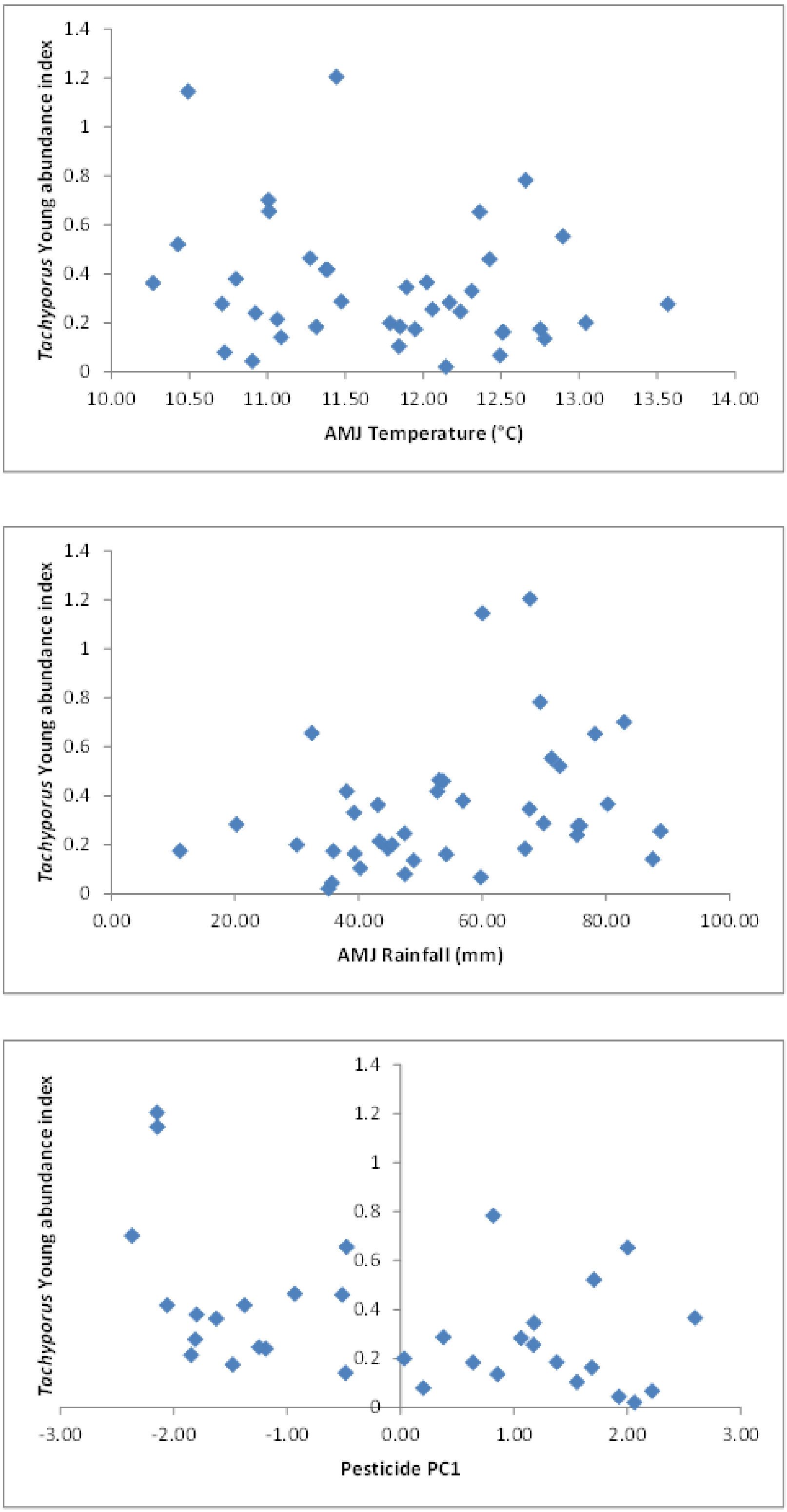


Figure 16. Correlation between *Tachyporus* Young abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

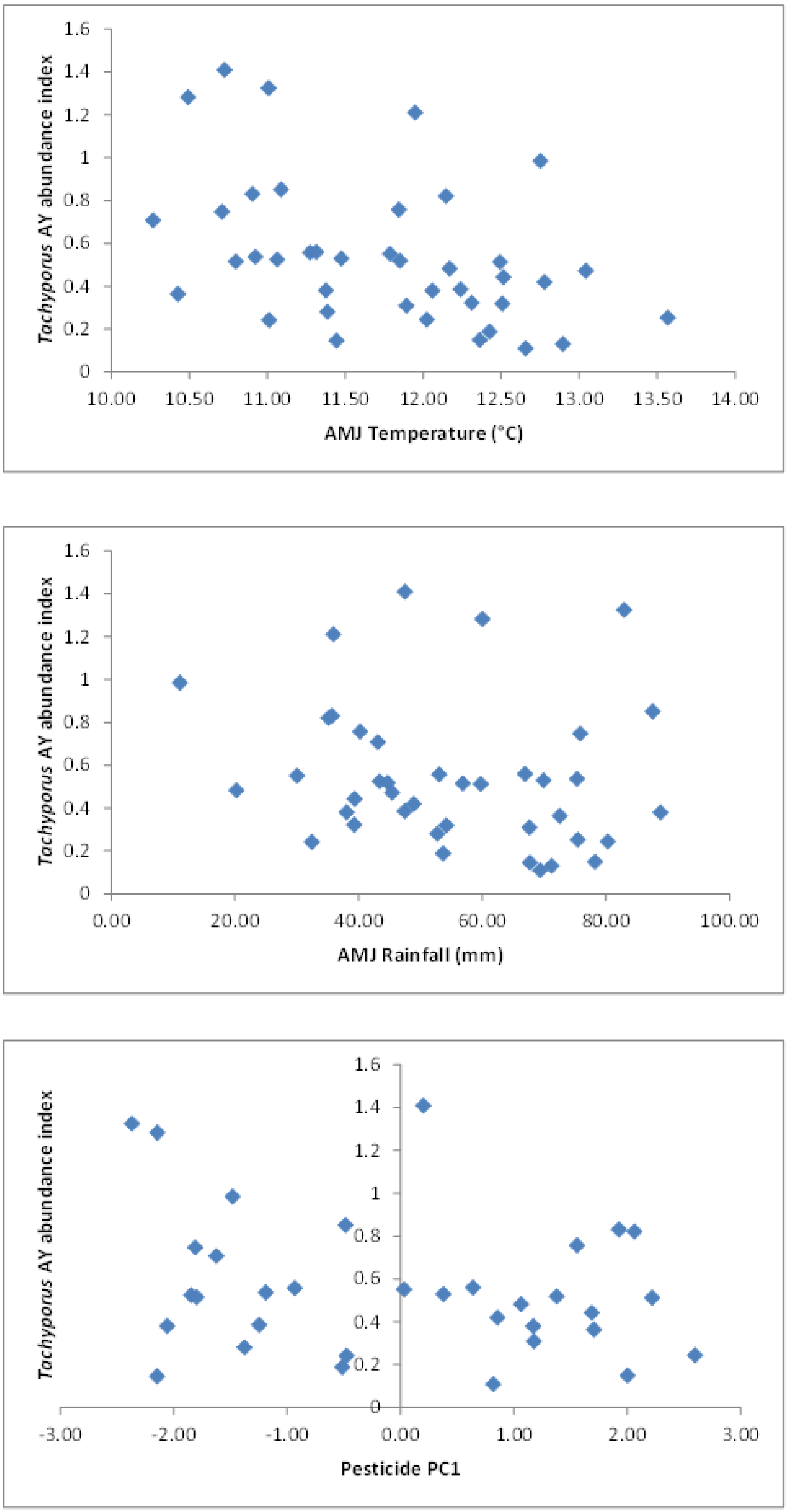


Figure 17. Correlation between *Tachyporus* AY abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

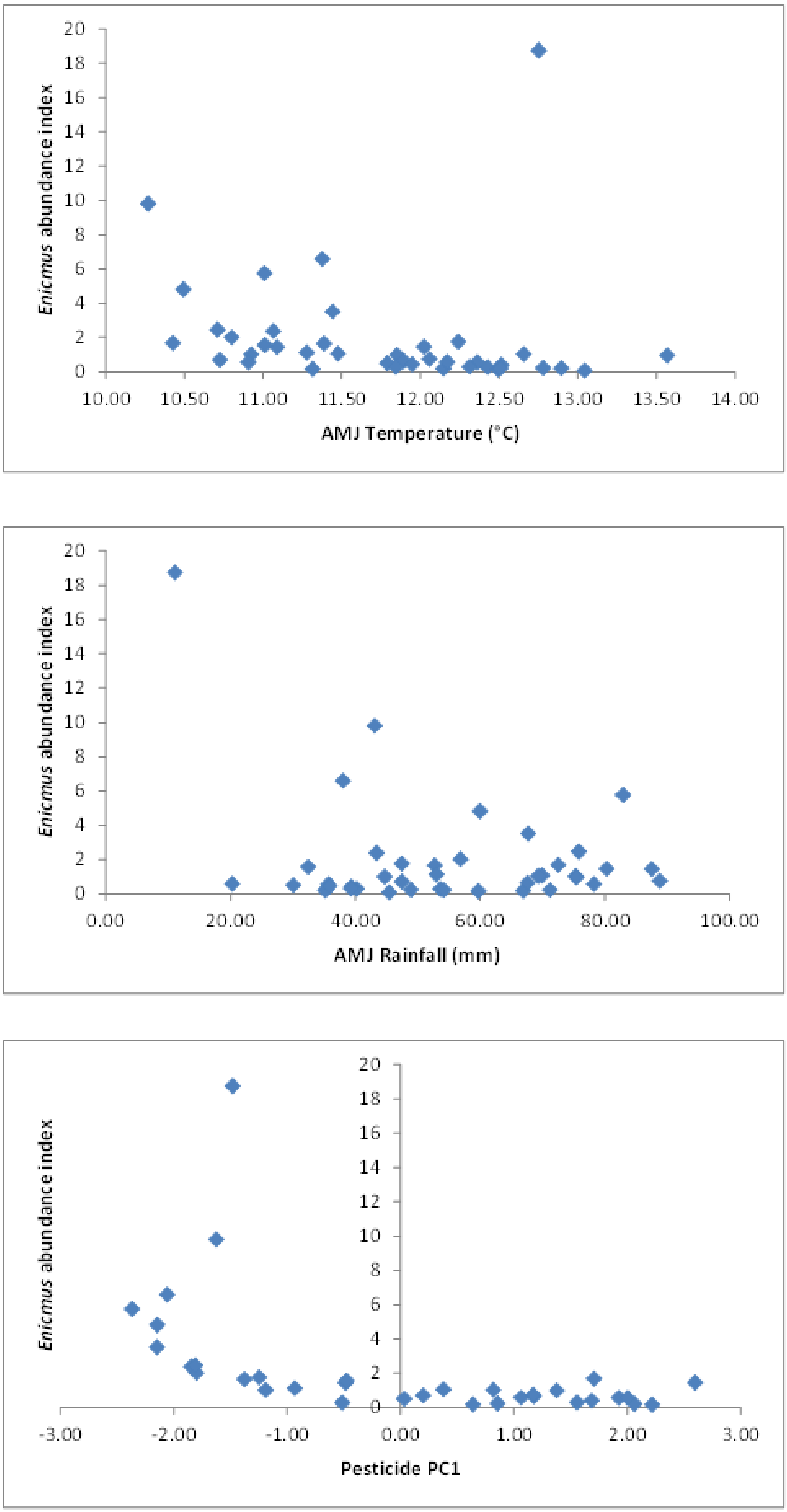


Figure 18. Correlation between *Enicmus* abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

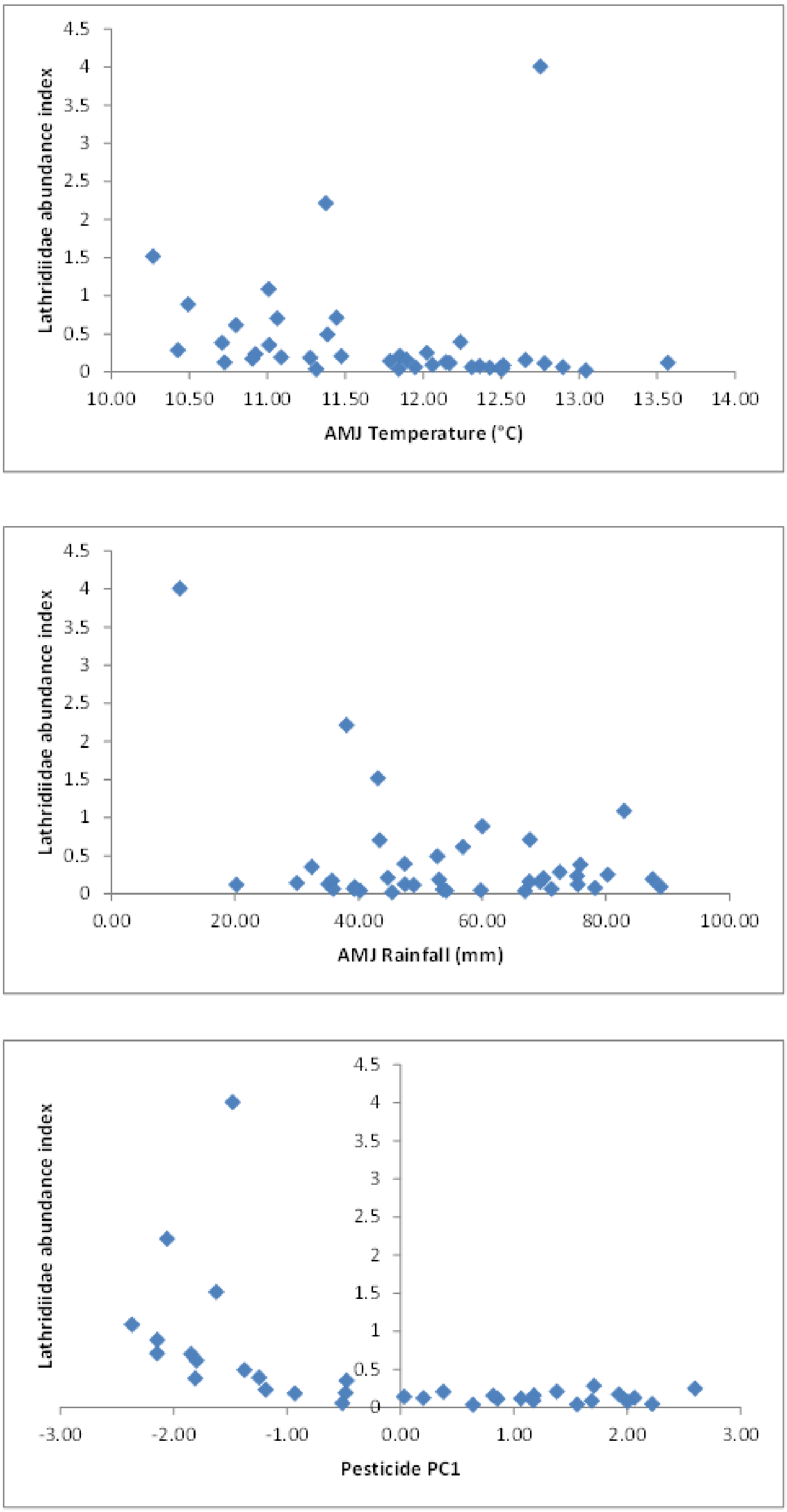


Figure 19. Correlation between Lathridiidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

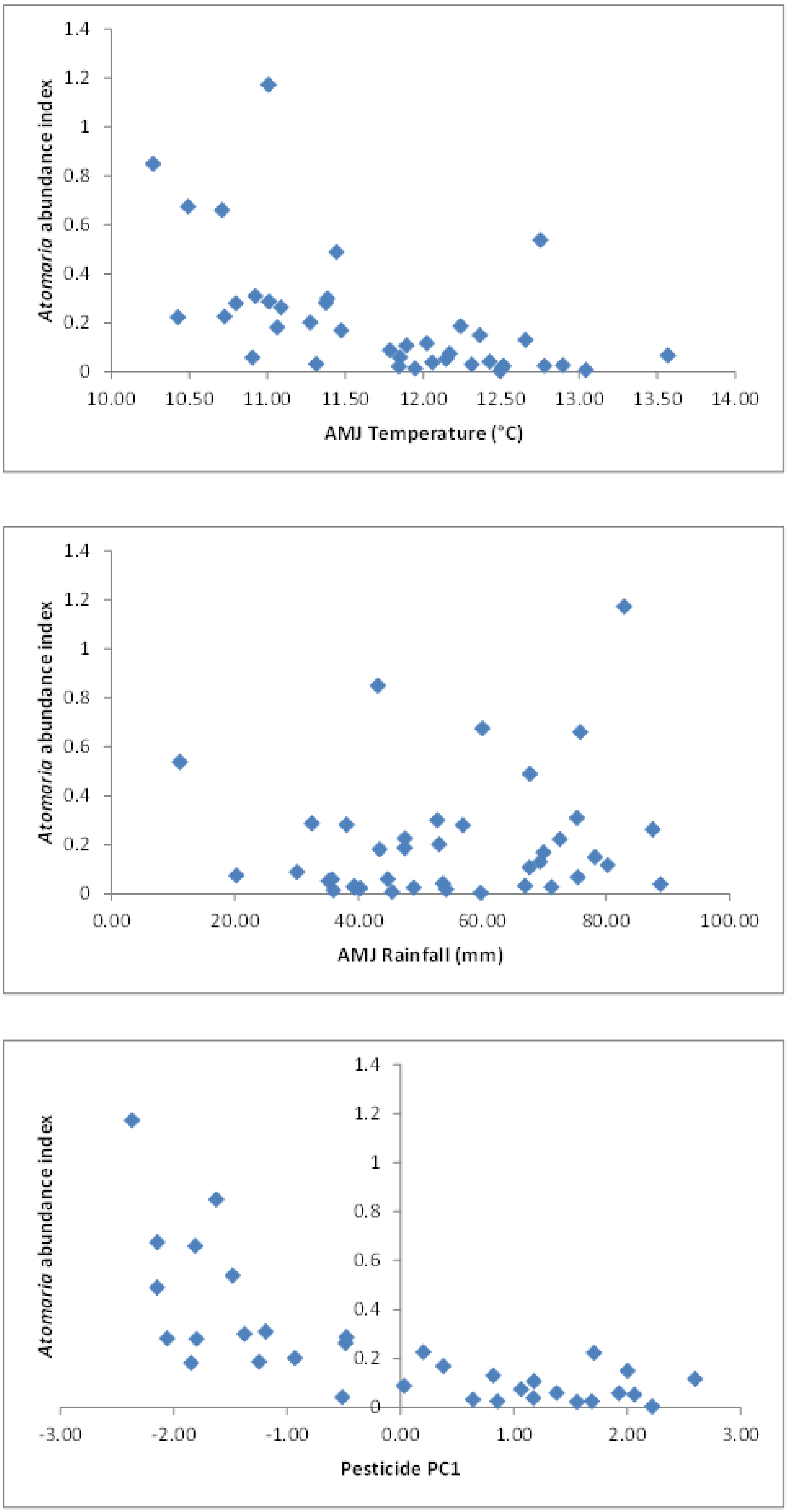


Figure 20. Correlation between *Atomaria* abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

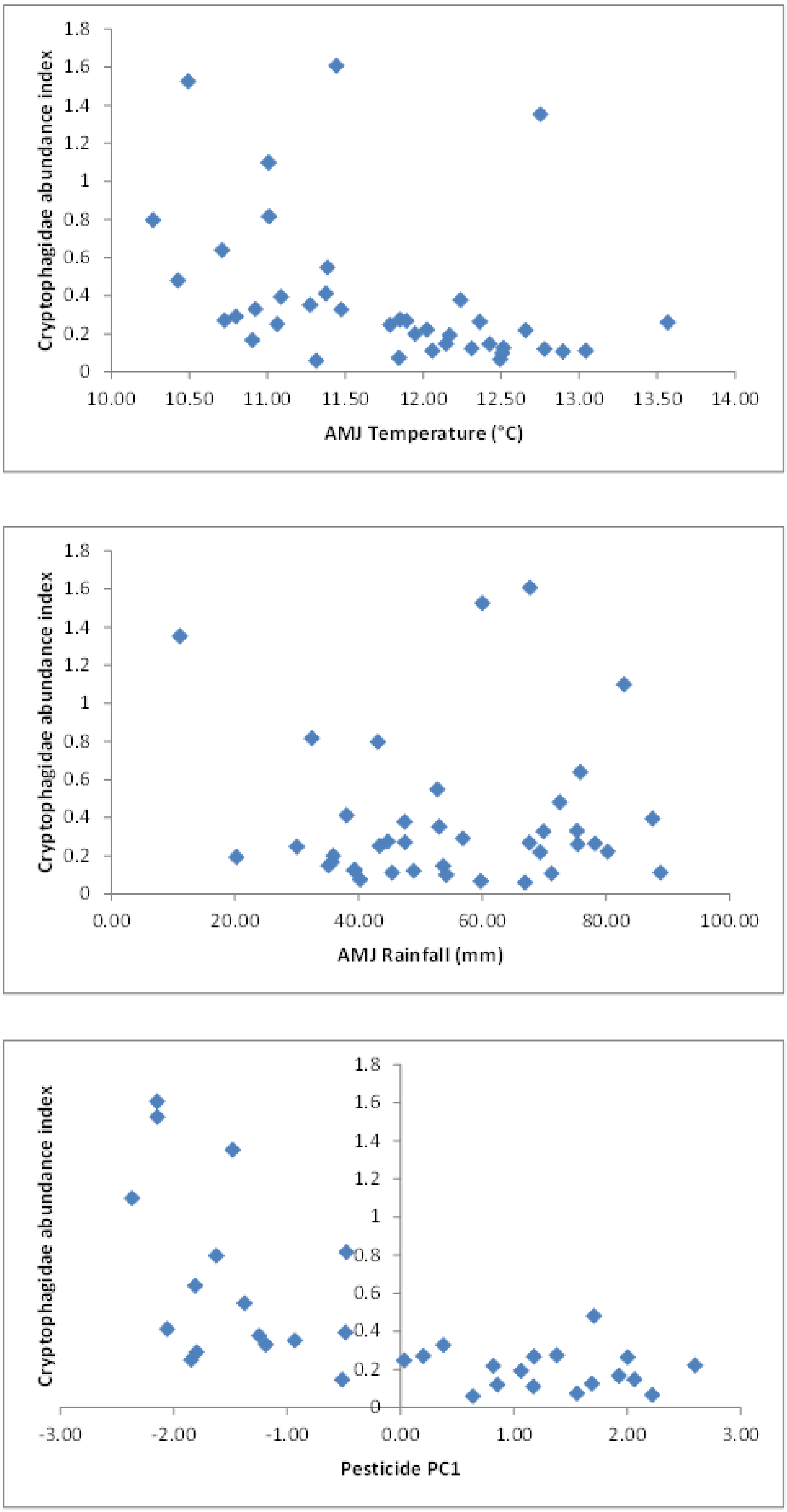


Figure 21. Correlation between Cryptophagidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

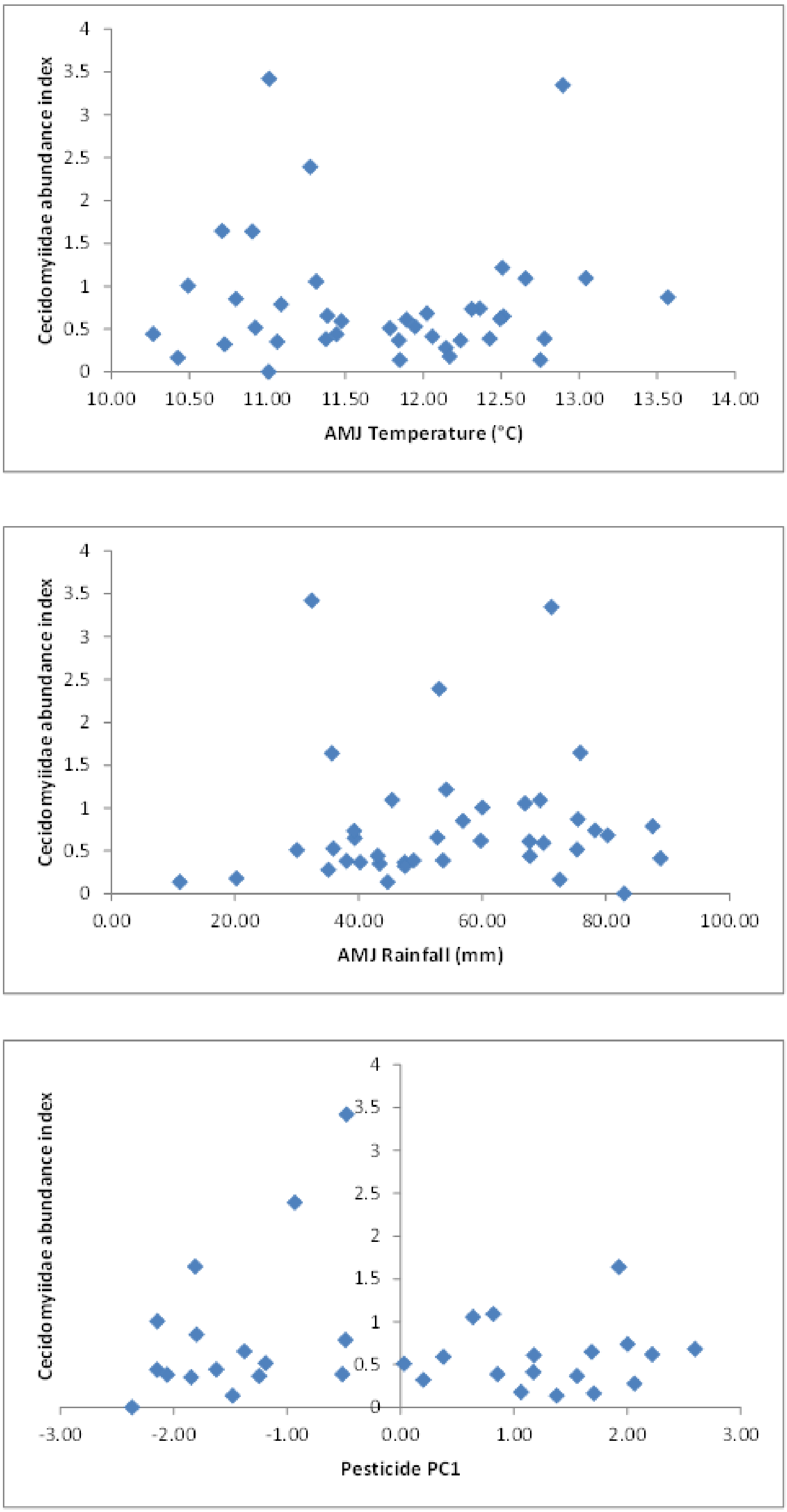


Figure 22. Correlation between Cecidomyiidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

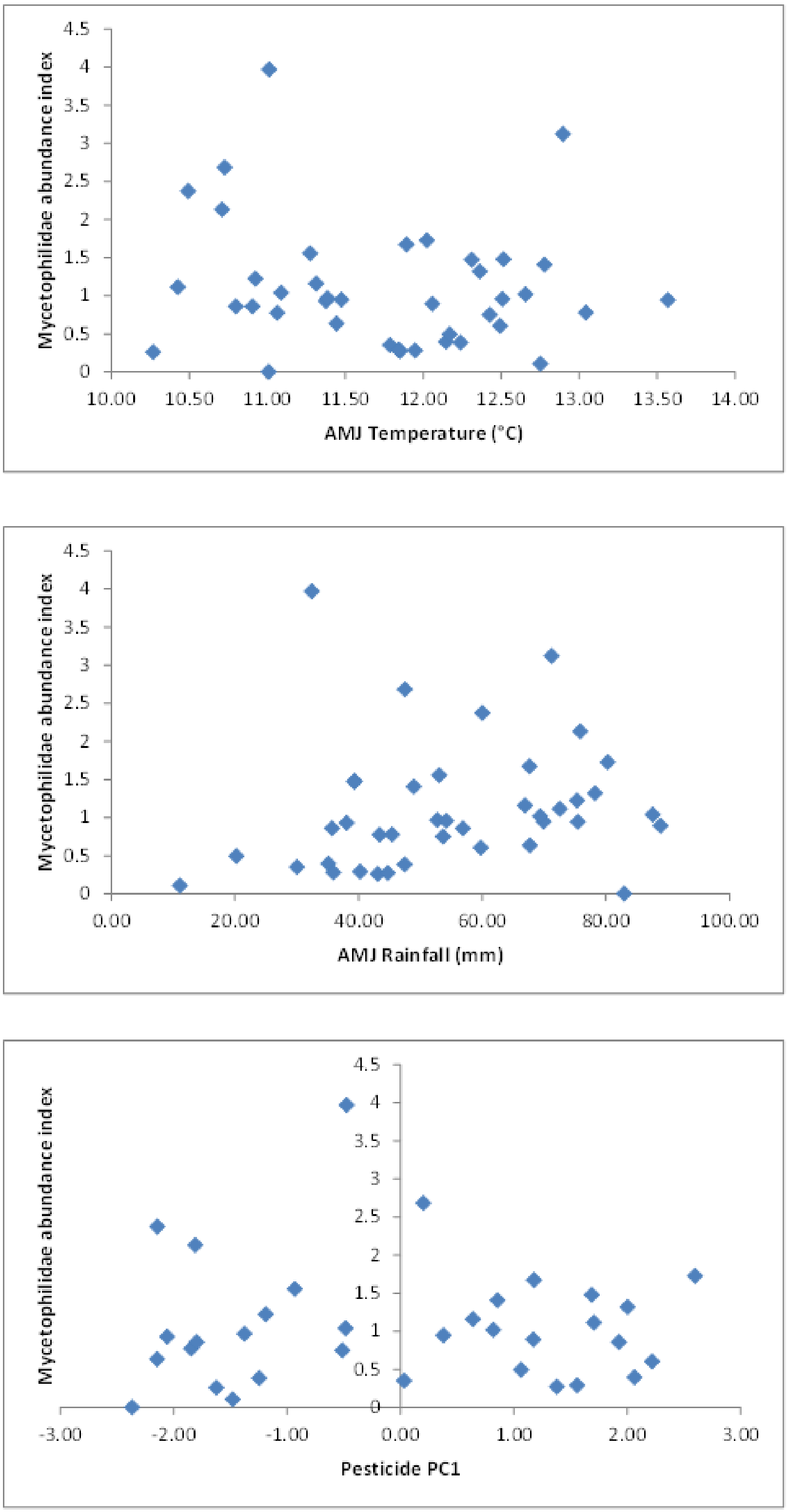


Figure 23. Correlation between Mycetophilidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

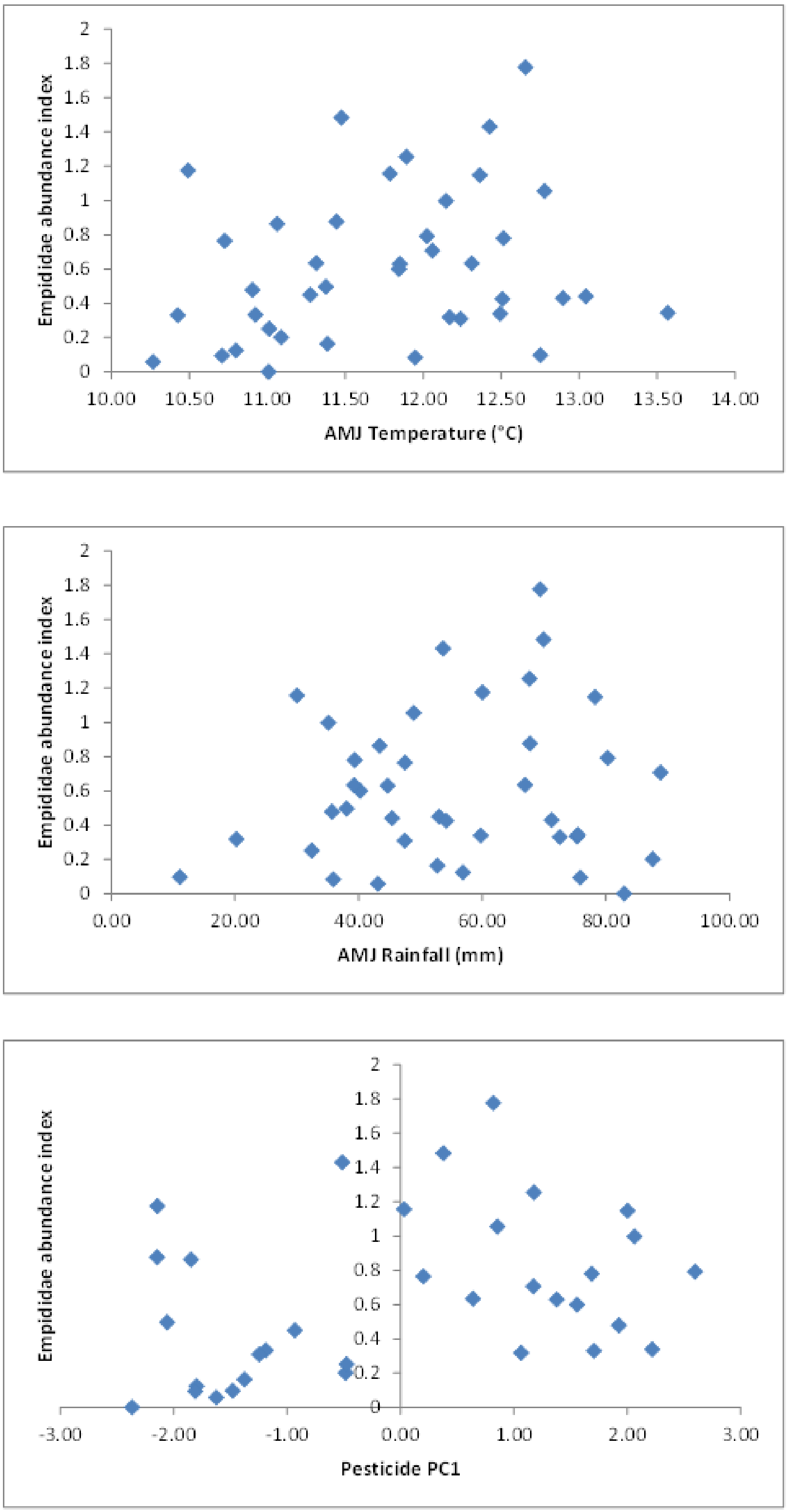


Figure 24. Correlation between Empididae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

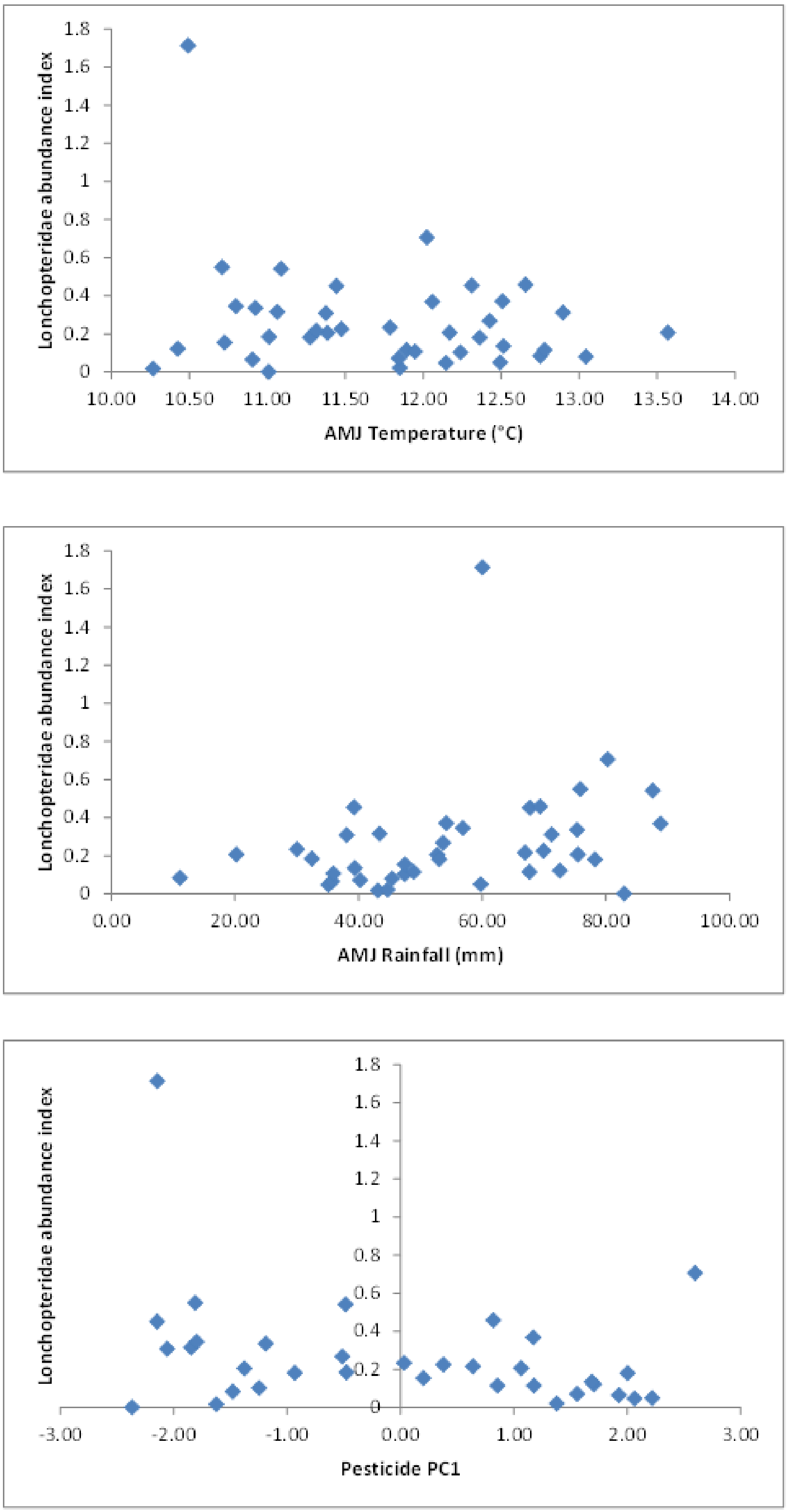


Figure 25. Correlation between Lonchopteridae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

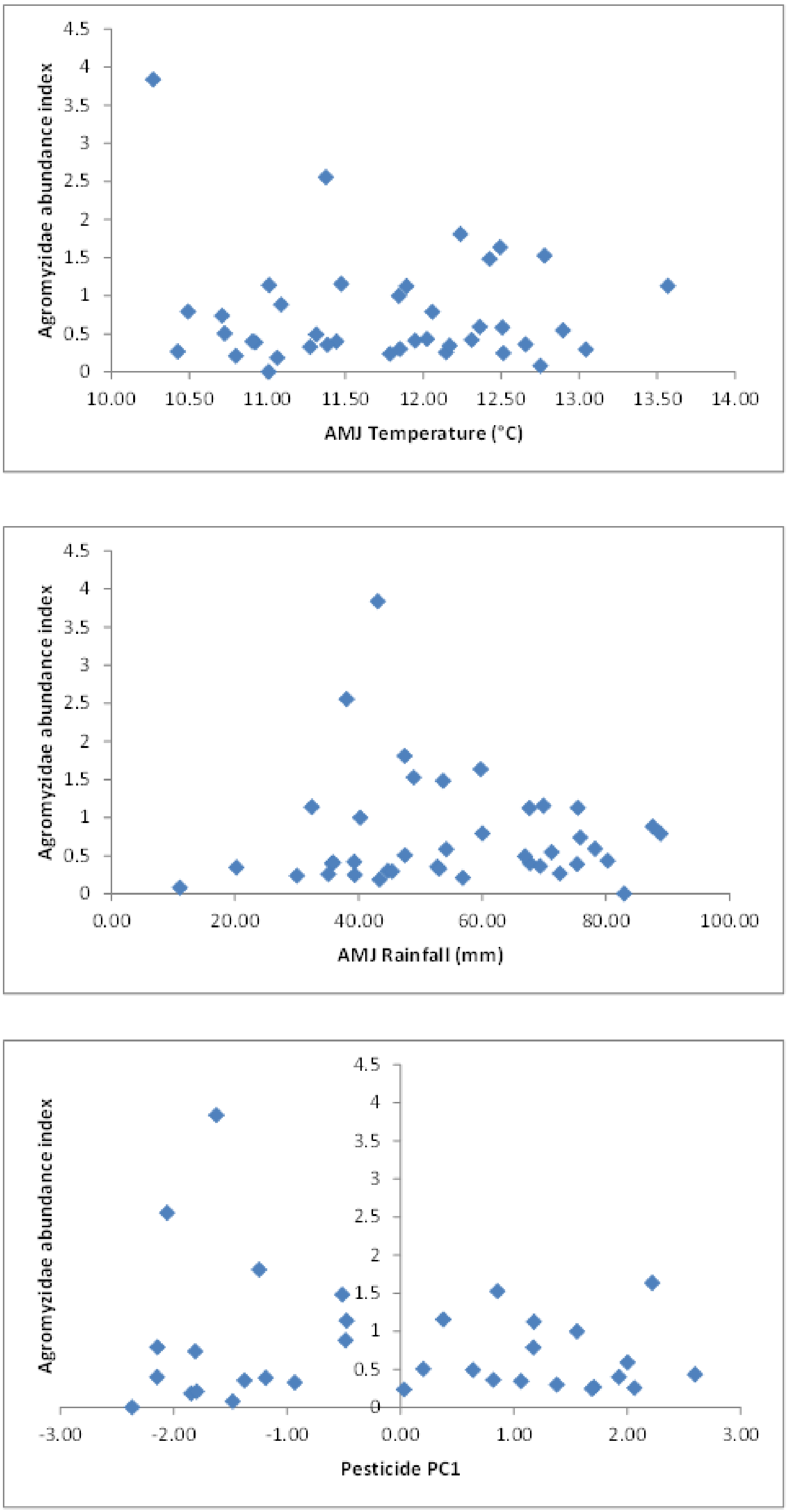


Figure 26. Correlation between Agromyzidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

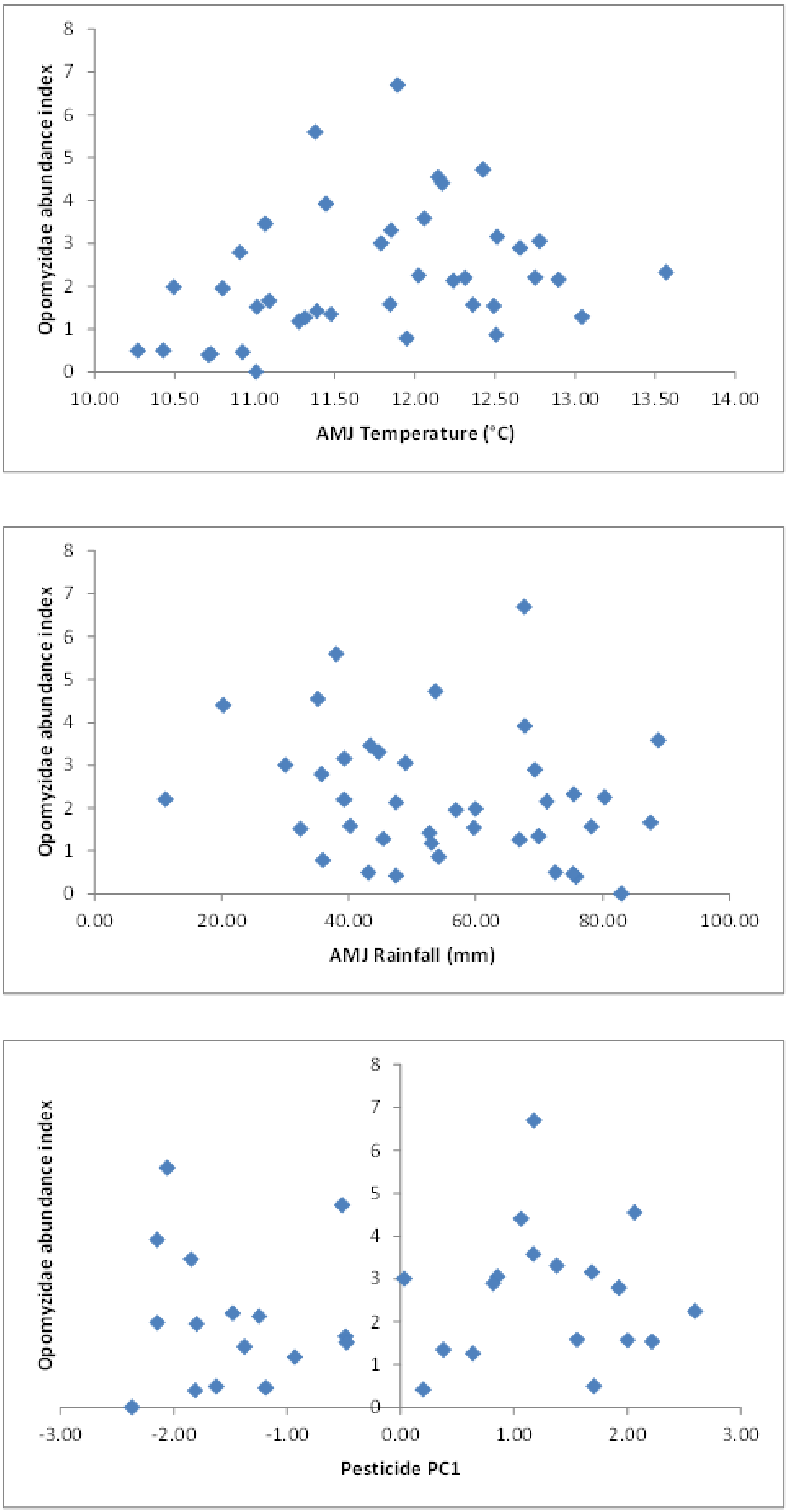


Figure 27. Correlation between Opomyzidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

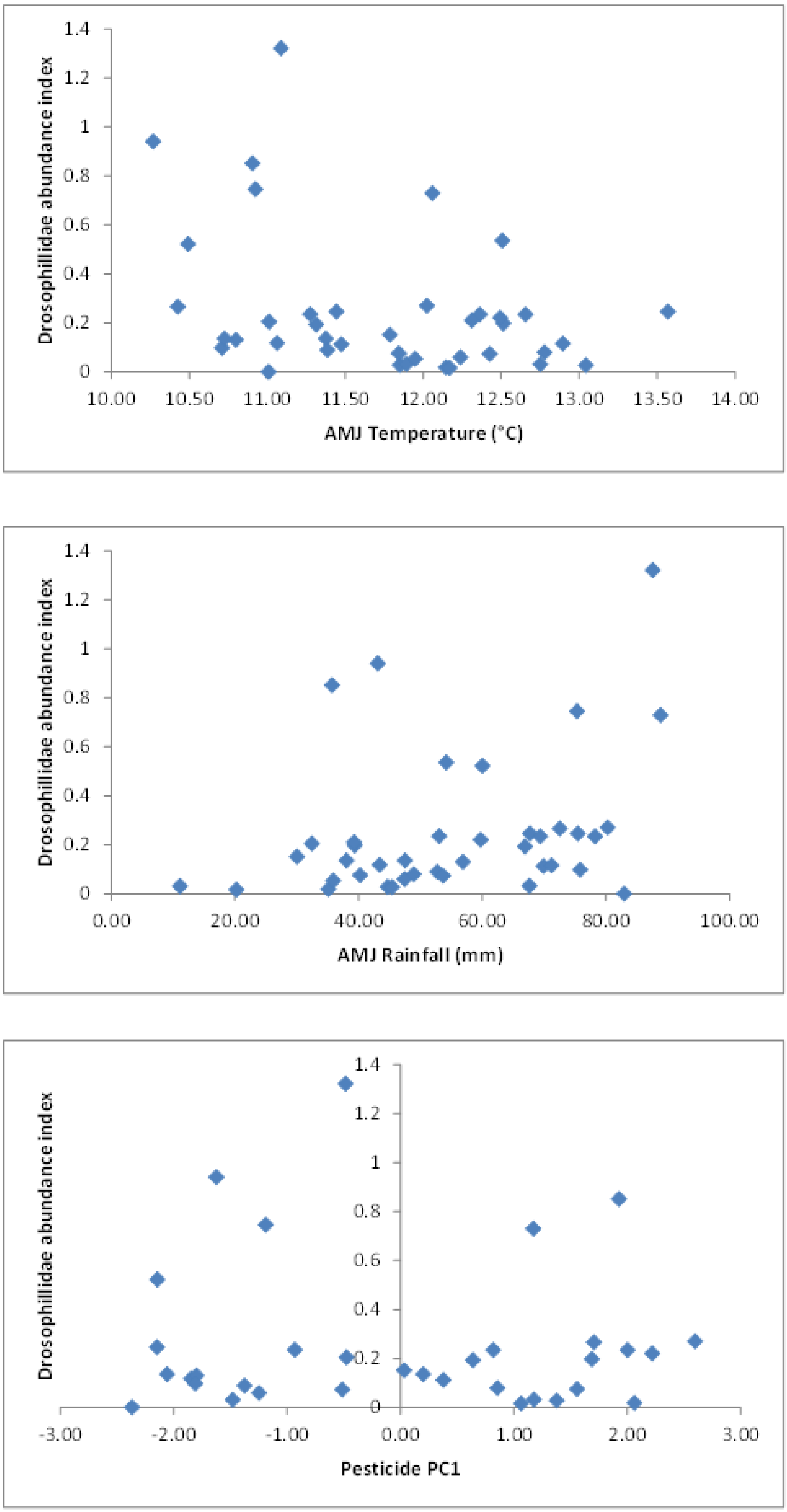


Figure 28. Correlation between Drosophilidae abundance index and: (A.) AMJ temperature, (B.) AMJ rainfall, and (C). the first principle component of pesticide use.

Appendix 11

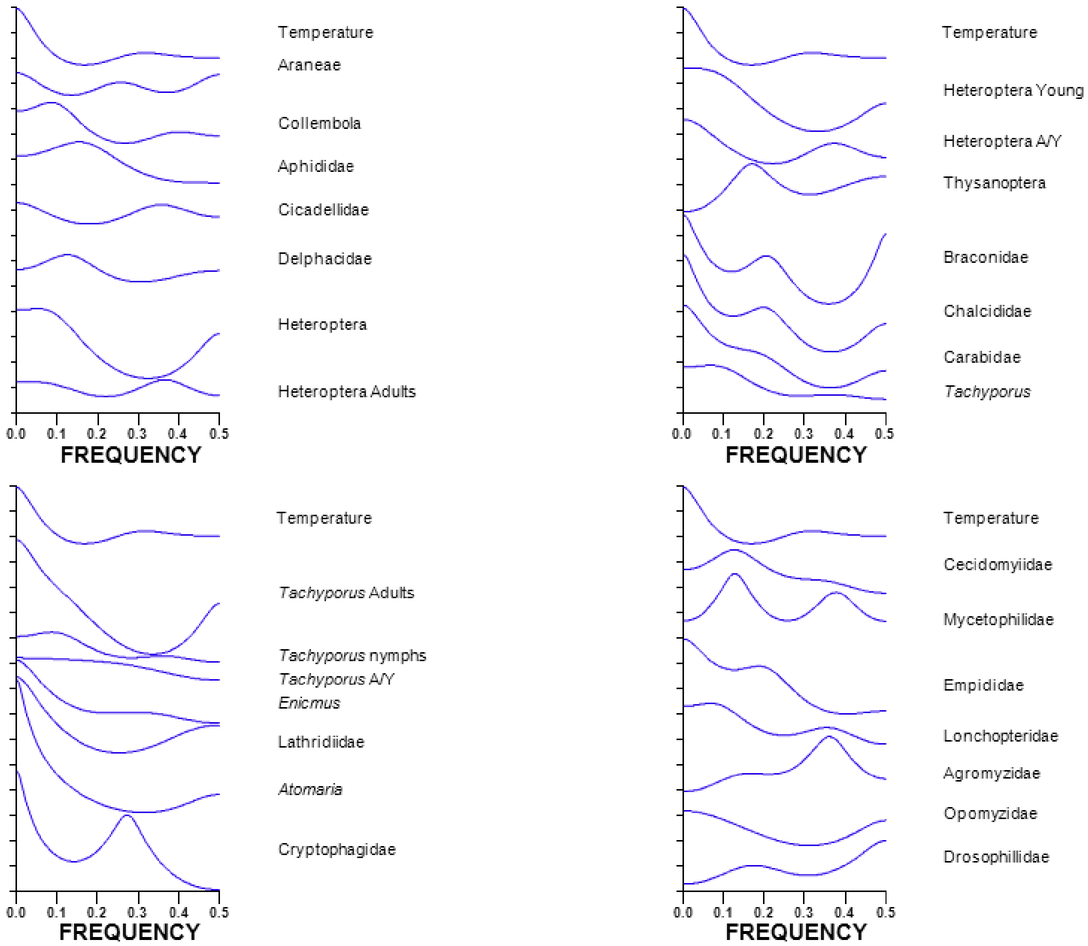


Figure 1a. Spectral density curves (logarithms) versus frequency (yr^{-1}) for time series of temperature and the invertebrate taxa considered. Spectra calculated according to Barrowdale and Erickson with filter length of four.

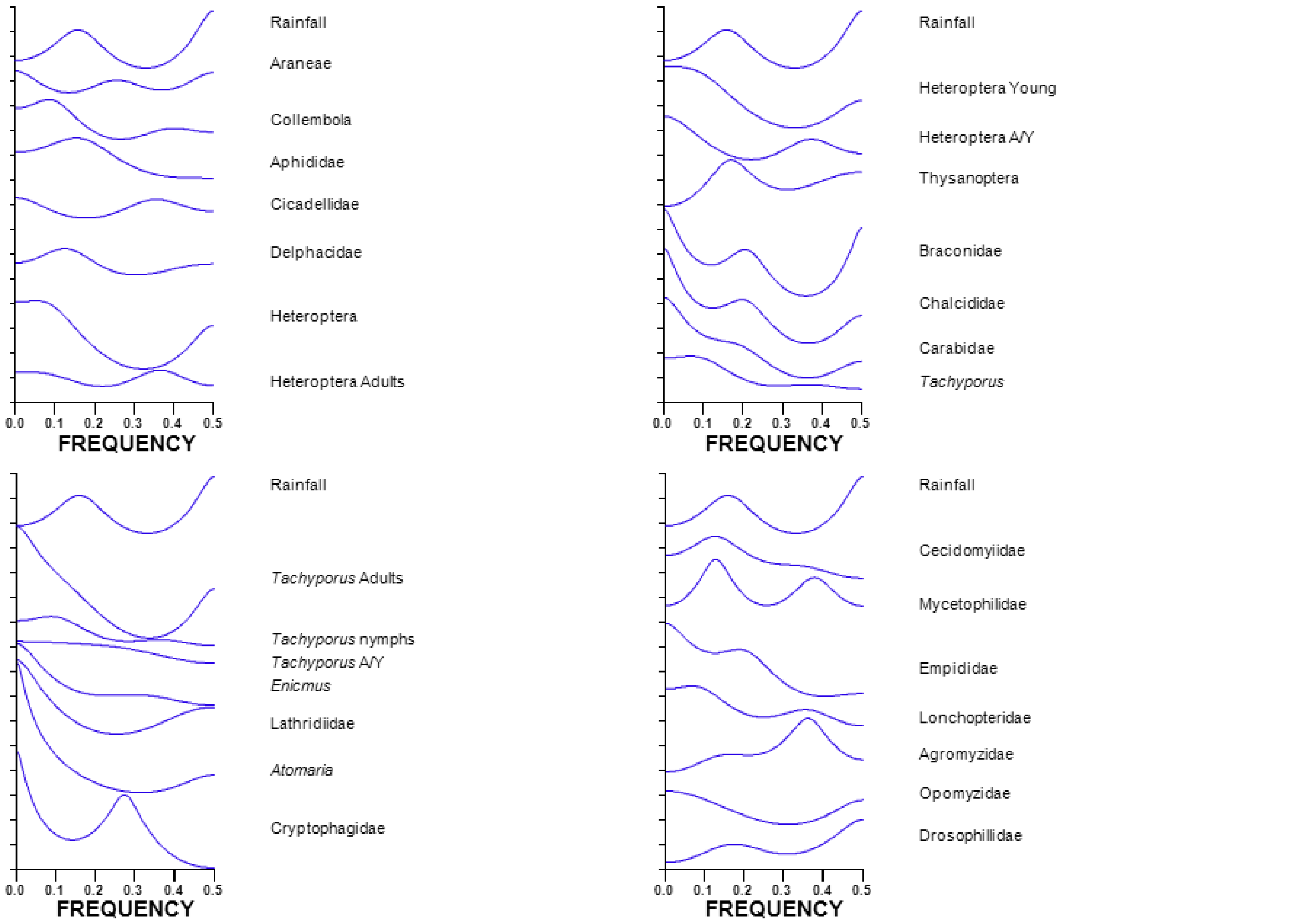


Figure 1b. Spectral density curves (logarithms) versus frequency (yr^{-1}) for time series of temperature and the invertebrate taxa considered. Spectra calculated according to Barrowdale and Erickson with filter length of four.

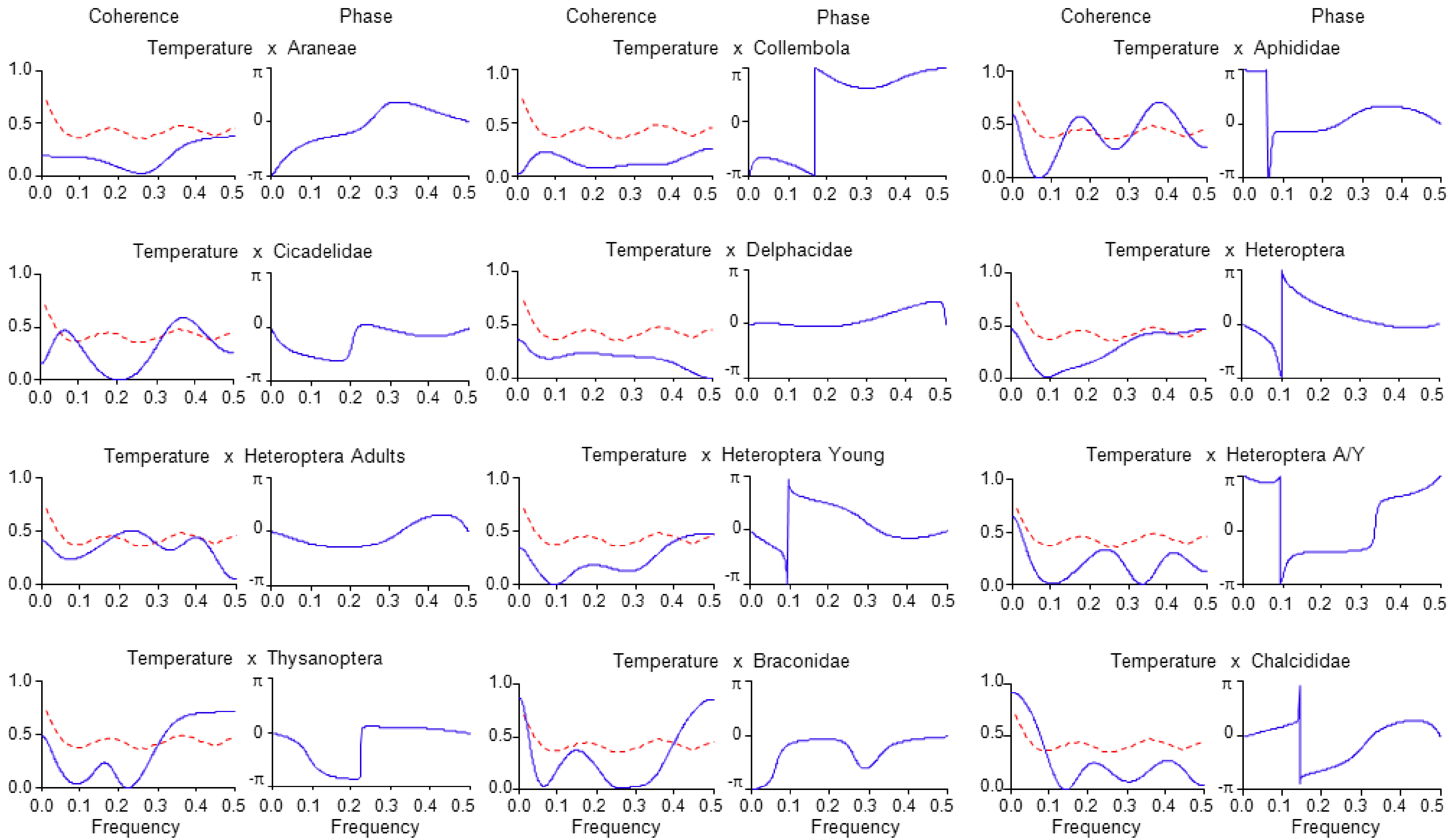


Figure 2. Coherence and phase spectra for temperature paired with each of the taxa examined. The red dotted line is the coherence level to exceed for significance at P < 0.05, obtained from the coherence spectra of 1000 pairs comprising the principal component of weather and one randomly generated time-series.

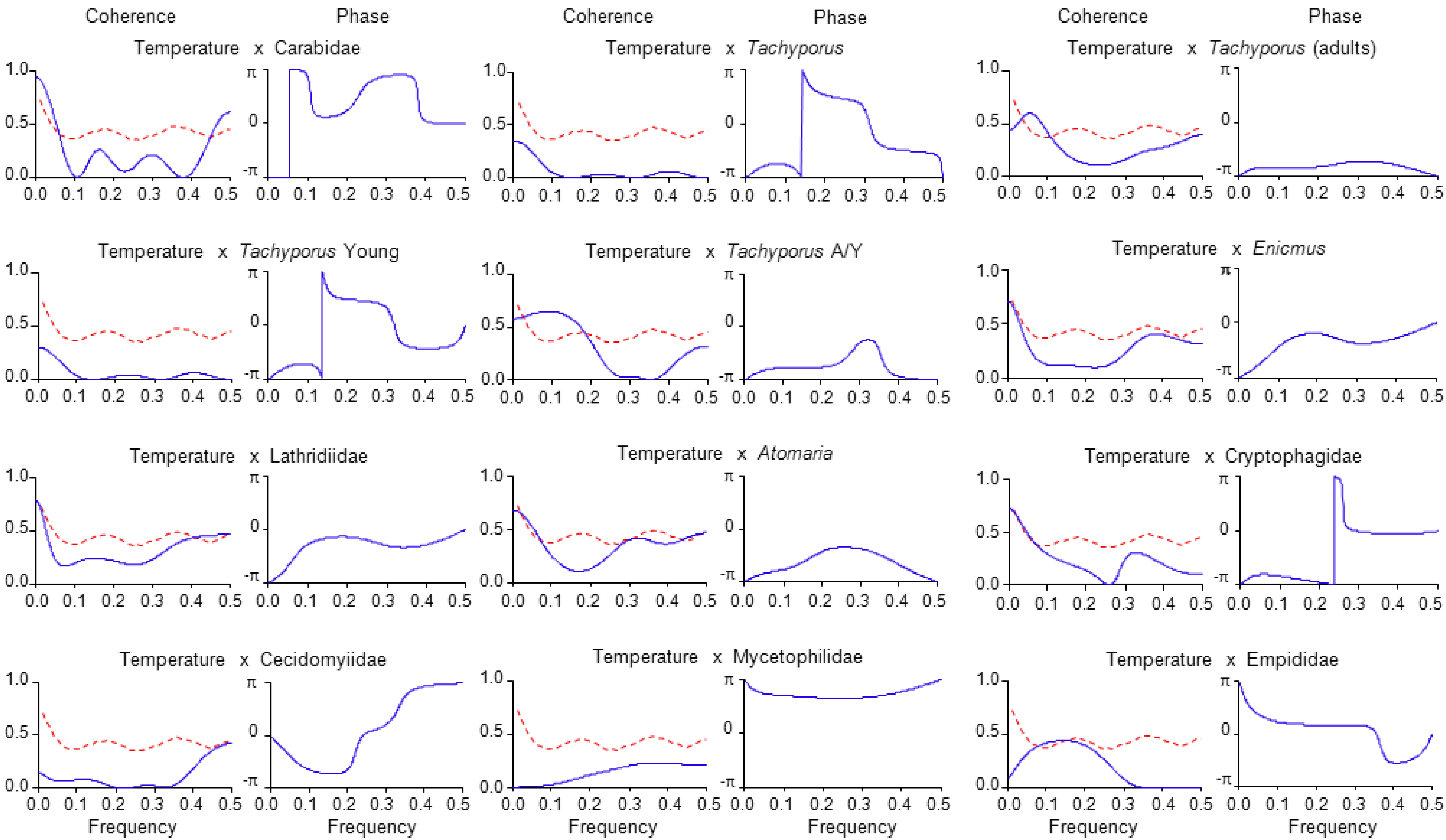


Figure 2 (continued).

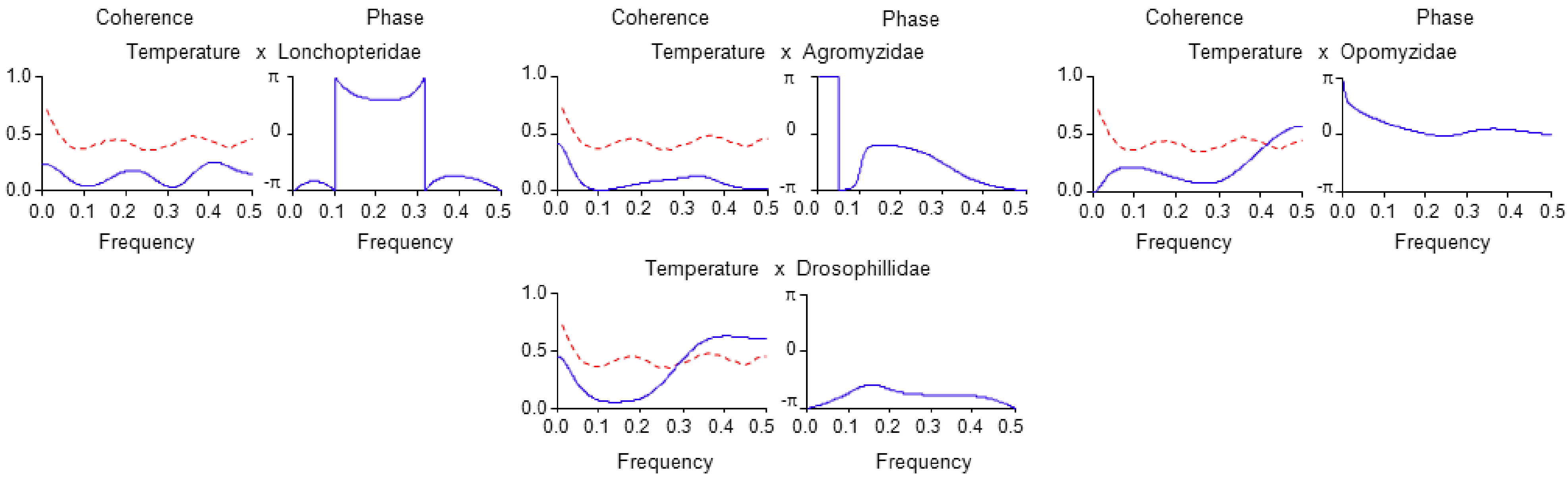


Figure 2 (continued).

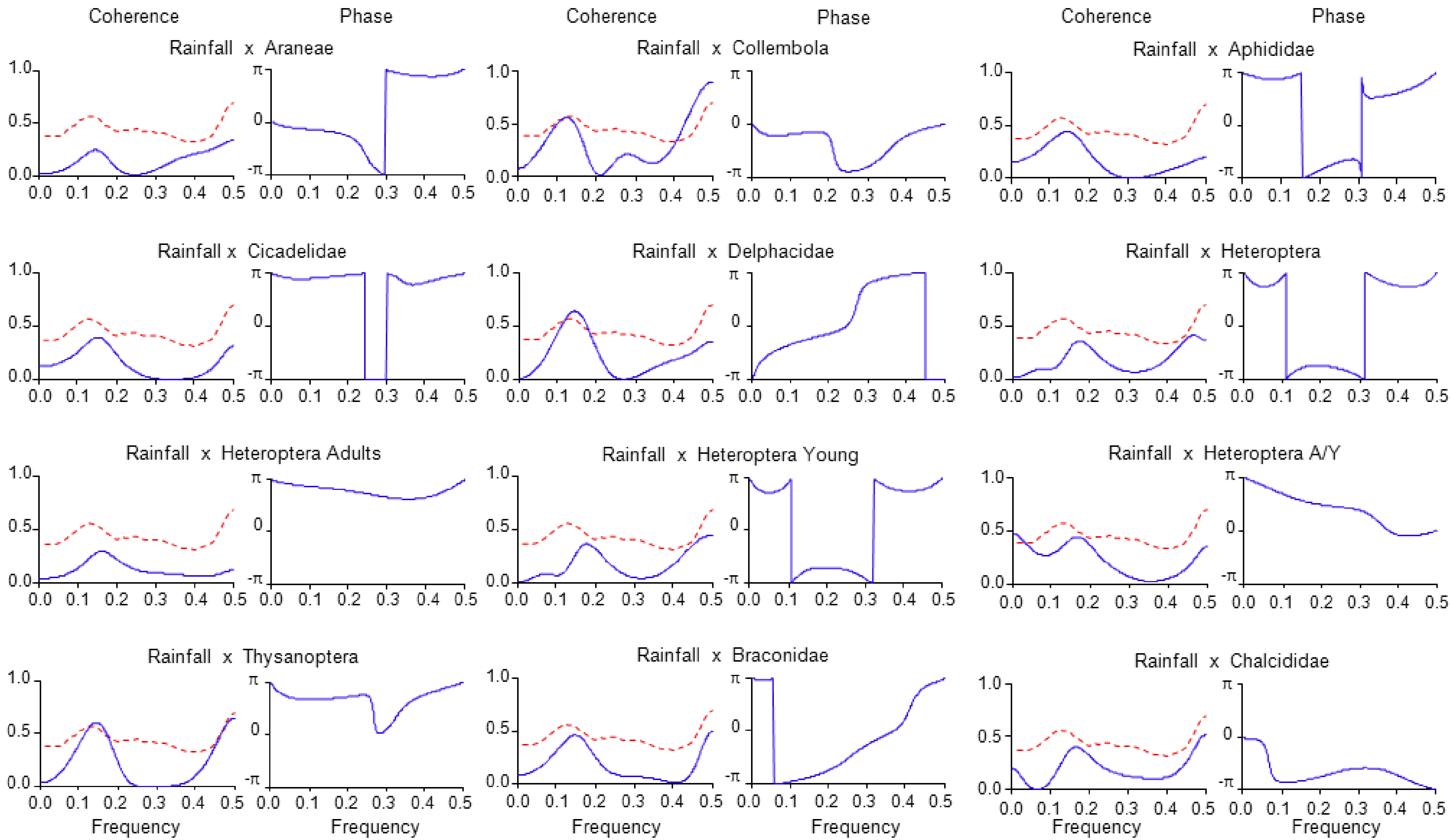


Figure 3. Coherence and phase spectra for rainfall paired with each of the taxa examined. The red dotted line is the coherence level to exceed for significance at P < 0.05, obtained from the coherence spectra of 1000 pairs comprising the principal component of weather and one randomly generated time-series.

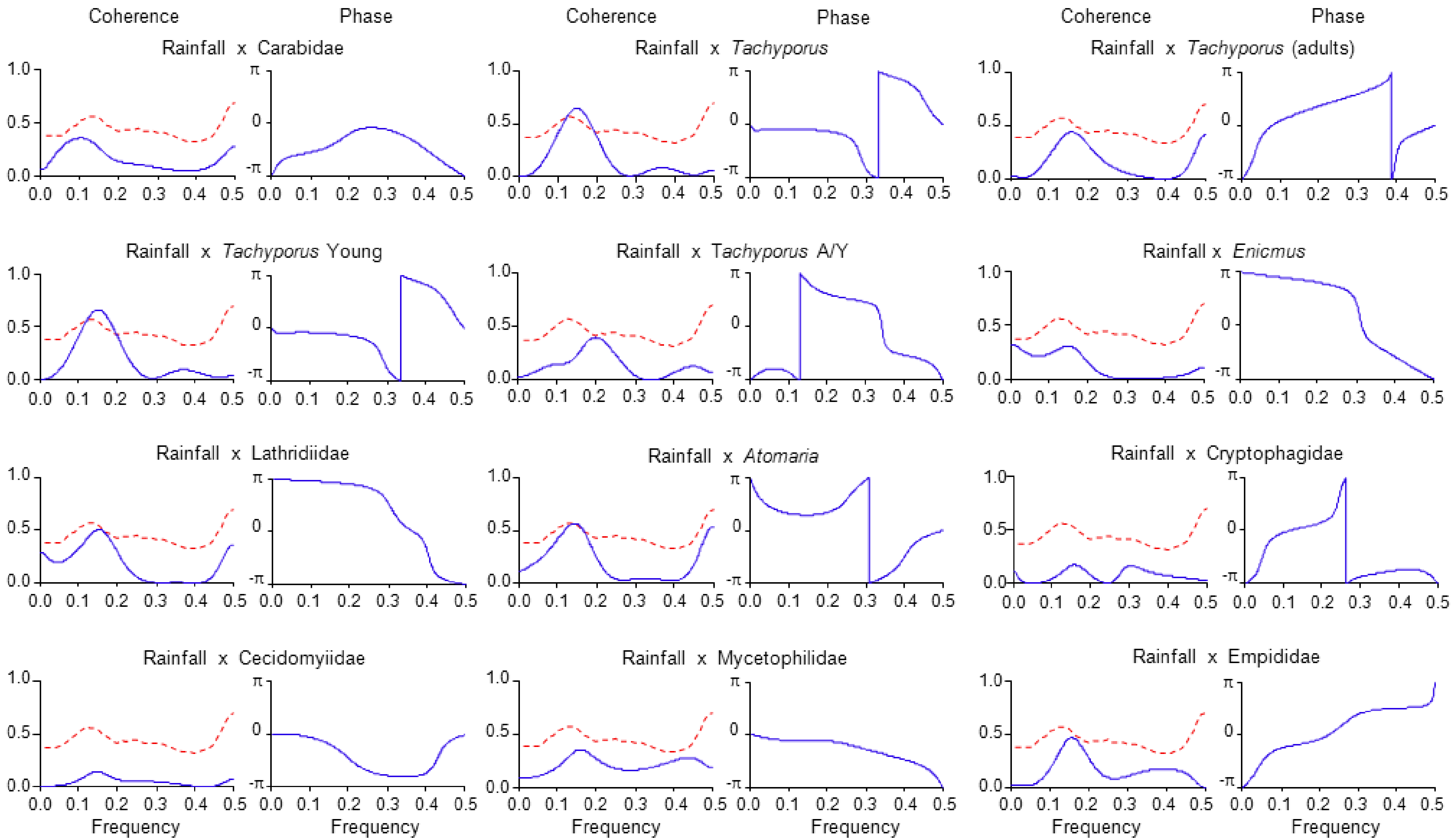


Figure 3 (continued).

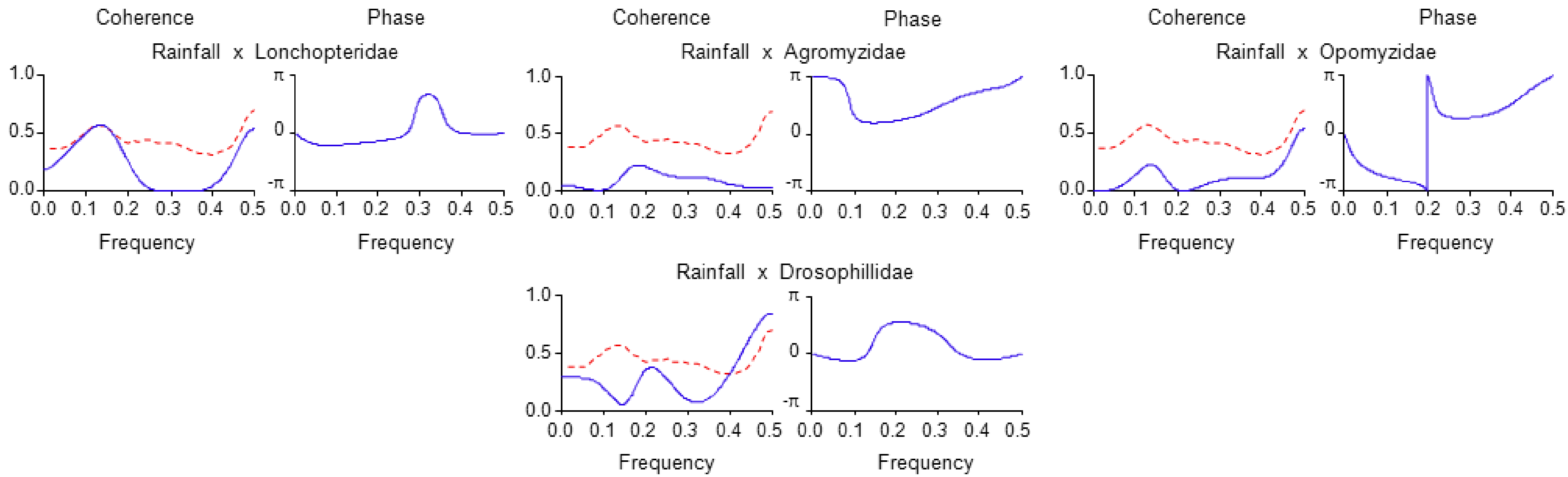


Figure 3 (continued).