Influences of extreme weather, climate and pesticide use on invertebrates in cereal fields over 42 years

JULIE A. EWALD[1], CHRISTOPHER J. WHEATLEY[1], NICHOLAS J. AEBISCHER[1], STEPHEN J. MOREBY[1], SIMON J. DUFFIELD[2], HUMPHREY Q. P. CRICK[3] and MICHAEL B. MORECROFT[2]

[1]*Game & Wildlife Conservation Trust, Fordingbridge Hampshire SP6 1EF, UK*, [2]*Natural England, Cromwell House, Andover Road, Winchester SO23 7BT, UK*, [3]*Natural England, Eastbrook, Shaftesbury Road, Cambridge CB2 8DR, UK*

Abstract

Cereal fields are central to balancing food production and environmental health in the face of climate change. Within them, invertebrates provide key ecosystem services. Using 42 years of monitoring data collected in southern England, we investigated the sensitivity and resilience of invertebrates in cereal fields to extreme weather events and examined the effect of long-term changes in temperature, rainfall and pesticide use on invertebrate abundance. Of the 26 invertebrate groups examined, eleven proved sensitive to extreme weather events. Average abundance increased in hot/dry years and decreased in cold/wet years for Araneae, Cicadellidae, adult Heteroptera, Thysanoptera, Braconidae, *Enicmus* and Lathridiidae. The average abundance of Delphacidae, Cryptophagidae and Mycetophilidae increased in both hot/dry and cold/wet years relative to other years. The abundance of all 10 groups usually returned to their long-term trend within a year after the extreme event. For five of them, sensitivity to cold/wet events was lowest (translating into higher abundances) at locations with a westerly aspect. Some long-term trends in invertebrate abundance correlated with temperature and rainfall, indicating that climate change may affect them. However, pesticide use was more important in explaining the trends, suggesting that reduced pesticide use would mitigate the effects of climate change.

Keywords: agri-environment, agricultural intensification, drought, farmland, long-term study, rainfall, Sussex study, temperature

Received 2 March 2015; revised version received 22 May 2015 and accepted 17 June 2015

Introduction

Invertebrates on farmland provide key ecosystem services (Millennium Ecosystem Assessment, 2005) such as pollination (Pimentel *et al.*, 1997; Ricketts *et al.*, 2008), pest control (Bianchi *et al.*, 2006) and nutrient recycling (Losey & Vaughan, 2006). They are a key link in the food chain supporting farmland mammals (Hof & Bright, 2010), and declines in the abundance of in-field invertebrates are linked to declines in farmland birds (Potts, 1986; Brickle *et al.*, 2000; Hart *et al.*, 2006). Lastly, farmland invertebrates are of biodiversity interest in their own right (Dover, 1991; Carvell *et al.*, 2007).

The major challenges to invertebrates in arable systems are climate change, operating both through an increased frequency of extreme weather events and more gradual changes in temperature and patterns of rainfall (Mossman *et al.*, 2013; Ma *et al.*, 2014; Bell *et al.*, 2015), and agricultural intensification, operating through changes in crop rotations and management particularly the use of pesticides (Aebischer, 1991; Benton *et al.*, 2002; Eglington & Pearce-Higgins, 2012). Many climate models predict changes to the patterns of

extreme weather events (Klein Tank & Können, 2003), including increased frequency (Mearns *et al.*, 1984; Easterling *et al.*, 2000; Peterson *et al.*, 2012), as well as increased magnitude of these events (Meehl *et al.*, 2000; Jentsch *et al.*, 2007). Some effects of extreme weather events on arable invertebrates have been investigated in model systems (Zaller *et al.*, 2014), but little is known from field situations. 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). Understanding how vulnerable farmland invertebrates are to extreme weather events could prove to be important when developing models of climate change impacts, as well as when planning and targeting conservation measures to mitigate against climate change (Parmesan *et al.*, 2000).

Climate change (particularly changes in the long-term trends in temperature, rainfall) and rising CO_2 concentrations affect invertebrate abundance and phenology in an agricultural situation (Newman, 2005; Musolin, 2007; Stige *et al.*, 2007; Villalpando *et al.*, 2009; Robinet & Roques, 2010; Bell *et al.*, 2015), through expansion or contraction of species ranges (Mair *et al.*, 2012), increased risks from invasive species (Robinet &

Correspondence: J. A. Ewald, tel. 01425 651 005, fax 01425 655848, e-mail:jewald@gwct.org.uk

Roques, 2010) and increased abundance of pest species (Cannon, 1998; Mossman *et al.*, 2013; Bell *et al.*, 2015). A large body of scientific work already demonstrates the impact of agricultural intensification (measured through increases in chemical inputs, change in cultivation, etc.) on the abundance of invertebrates on farmland (Potts, 1986; Aebischer, 1991; Benton *et al.*, 2002; Donald *et al.*, 2006), but little research has compared the effects of agricultural intensification and changes in long-term trends in weather, often because measurements of both these processes at the same scale are lacking (Bell *et al.*, 2015).

Planning mitigation measures to counteract the effects of ongoing climate change requires some knowledge of the resilience of taxa affected by climate change. Developing a greater understanding of factors that confer resilience will help to bridge the gap between ecological theory and practical land management (Morecroft *et al.*, 2012). In semi-natural habitats, summer droughts are capable of causing a range of changes to butterflies, moth and carabid beetle communities (Morecroft *et al.*, 2002), although the impact of these events was readily reversed. Landscape factors such as elevation, aspect and slope can play an important role in creating microclimates (Bennie *et al.*, 2008), creating refugia for invertebrates and plants against the effects of climate change (Ashcroft *et al.*, 2009; Oliver *et al.*, 2010). The wide array of invertebrate taxa that exist within arable ecosystems mean that they are likely to show differing responses under climate change scenarios and have different abilities to recover.

We present here analysis on the effects of both climate change (extreme events and long-term changes) and agricultural intensification from a continuous 42-year time series of invertebrate taxa collected within cereal fields from a landscape-scale study in southern England that includes information on pesticide use (Aebischer, 1991; Ewald & Aebischer, 2000; Potts *et al.*, 2010). We determined the sensitivity of a range of individual invertebrate taxa to extreme weather events and also investigated how long-term trends in weather and agricultural intensification affected trends in invertebrate abundance. We investigated what habitats, such as field boundaries, surrounding semi-natural habitat, patch interconnectedness, altitude and aspect, and management practices such as cropping and pesticide use, were associated with invertebrate resilience to extreme events.

Materials and methods

Study area

From 1970 to the present day, The Game & Wildlife Conservation Trust has collected data on the invertebrate, flora and avian components of the cereal ecosystem, as well as on cereal crop management, from 32 km² of farmland on the Sussex Downs in southern England (Potts, 1986, 2012; Aebischer, 1991; Ewald & Aebischer, 1999, 2000; Potts *et al.*, 2010). The study area is situated between the rivers Adur and Arun, and the dominant soils are chalk rendzinas with abundant flint, isolated caps of clay on higher parts and postglacial deposits along the lower parts of a series of 'dry valleys'. The cropping consists of a mix of cereals (winter wheat, spring barley and winter barley) with break crops (oilseed rape, linseed and peas) and some grass leys (established through direct sowing or undersowing). As the study began, cereal cropping over the study area has moved from primarily spring barley to a system dominated by winter wheat (Potts *et al.*, 2010).

Invertebrate data

Information on the abundance of invertebrates in cereals was obtained by sampling approximately 100 cereal fields per year from 1970 to 2011 in the third week of June using a Dietrick vacuum suction trap (D-Vac, Dietrick, 1961). Efforts were made to sample every cereal field across the study area each year. Invertebrates were identified at least to family level using a binocular microscope. Although there are over 500 individual taxa recorded in the data set, analysis has been restricted to long-term trends at the genus, family and class level to ensure identification consistency over time, although this may obscure trends at lower taxonomic levels (Aebischer, 1991).

One thing that should be borne in mind with this approach is that other researchers have found that changes in weather, particularly increases in temperature, have led, in some cases, to changes in abundance at the species level, but no overall change in abundance measured at higher taxonomic levels (e.g. Collembola – Bokhorst *et al.*, 2012; Braconidae – Fernandez-Triana *et al.*, 2011; Aphididae – Ma *et al.*, 2014). Some studies have even revealed changes within species reflected in DNA-level changes over time (Drosophila – Umina *et al.*, 2005).

Statistical analysis. We selected for analysis those taxa that were most commonly identified over time (occurred in an average of 50% of the fields over the years where data were available) and where the calculated change in abundance (change index) was normally distributed. To obtain the annual change indices, the invertebrate data were analysed using a generalized linear model (GLM) with a Poisson error distribution and logarithmic link function, with field and year as factors. Fields with only 1 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 differences between successive years were computed and the distribution of these differences was compared to a normal distribution (Shapiro–Wilk test, *W* statistic, Shapiro & Wilk,

1965). Taxa where the differences were not normally distributed were excluded from further analysis.

Invertebrate taxa selected for further analysis

In total, 26 individual taxa/age groups were selected for analysis: Araneae (spiders); Collembola (springtails); Aphididae (aphids); Cicadellidae (leafhoppers); Delphacidae (planthoppers); Heteroptera (bugs), including all stages combined, adults and young separately; Thysanoptera (thrips); Braconidae (braconid wasps); Chalcididae (chalcid wasps); Carabidae (ground beetles); *Tachyporus* (Staphylinidae: rove beetles), including all stages combined, adults and young; *Enicmus* (Lathridiidae: mould beetles) and Lathridiidae; *Atomaria* (Cryptophagidae: silken fungus beetles) and Cryptophagidae; Cecidomyiidae (gall midges); Mycetophilidae (fungus gnats); Empididae (dance flies); Lonchopteridae (spear-winged flies); Agromyzidae (leaf-miner flies); Opomyzidae (grass flies); and Drosophilidae (fruit flies).

Invertebrate long-term trends

Statistical analysis. Confidence limits (95%) around the index values of each taxon were obtained by bootstrapping at the field level. For each of 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 (original plus bootstrapped outcomes). To obtain the long-term trends in invertebrate abundance, a generalized additive model (GAM) was fitted to the abundance indices with one degree of freedom per decade or part-decade. The 95% confidence limits around the trendline were obtained by fitting GAMs to each bootstrap sample and selecting the lower and upper 95th percentiles of each set of 200 annual values that resulted. A decline was determined to have occurred when the upper 95% confidence limit fell below one, while an increase occurred when the lower 95% confidence limit was above one.

Invertebrate extreme events

Statistical analysis. The changes in annual invertebrate indices were used to identify extreme events. For a given taxon/age group, extreme event years were identified as such if interannual change deviated by at least two standard deviations from the mean change.

Extreme weather events

The type of weather events that are commonly associated with changes in invertebrate abundance is either droughts (low precipitation) or temperature anomalies (Frampton *et al.*, 2000; Morecroft *et al.*, 2002; Morsello *et al.*, 2010; Zhou *et al.*, 2011). Consequently, we used monthly mean temperature and total monthly precipitation in the analysis. The months of April, May and June were selected, as this was considered to be the

time period of the greatest importance to invertebrate development prior to our invertebrate sampling. Together with the average over this period, this meant that a total of eight weather variables were used to identify extreme weather events.

Statistical analysis. Data for each of the weather variables were identified from the UK 5 × 5-km gridded climate data set provided by the Meteorological Office (Perry & Hollis, 2005). A total of eight 5 × 5-km grid squares contained at least some part of the Sussex Study Area, so an average value was calculated for each of the annual weather variables across these eight grid squares. An extreme weather event was defined to be where a climatic variable deviated from the mean by more than two standard deviations. This approach identified an extreme weather event once every 20 years on average, 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 were suitable for identifying extreme events using this definition. Precipitation events were normally distributed after a square root transformation. The extreme events were grouped into two categories for ease of interpretation: cold and wet (low mean monthly temperature and high monthly precipitation) and hot and dry (high mean monthly temperature and low monthly precipitation).

Landscape variables

The Sussex Study data set includes a Geographic Information System database (ARCGIS 10.1; ESRI, Redlands, CA, USA) 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). We extracted habitat variables pertaining to 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 (see analysis section below). Around each of the invertebrate sampling locations, a circular buffer of radius 100 m was used to calculate the number of patches of habitat and the length of field boundaries in the vicinity. This resulted in two variables describing the sampling location:

1 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.
2 Field boundary density – the density of field boundaries (m ha^{-1}).

Other descriptive variables concerning the sampling location and extracted from the GIS database were as follows:

1 Crop – the crop in which the sample was taken (spring cereal, winter wheat, winter barley/oats).
2 Field area – the area (ha) of the field in which the sample was taken, ln-transformed.

Additionally, the GIS database includes a Land-form Panorama Digital Terrain Model, and the elevation, aspect and slope of each sampling location were determined. Aspect was categorized into north (315°–45°), east (45°–135°), south (135°–225°) and west (225°–315°).

Pesticide use

Field-by-field information on pesticide use was available from 1970 to 2004 and included the number and type of herbicide, foliar fungicide and insecticide applications made per year (Ewald & Aebischer, 2000). The yearly intensity of pesticide use 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 was transformed to percentage spray area by dividing by cropped area and multiplying by 100. We used principal component analysis to combine the trends in herbicide, fungicide and insecticide use intensity into one variable (Pesticide PC1) to represent the annual variation in overall pesticide use intensity.

Sensitivity to weather events

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.

Statistical analysis. Analysis of variance, weighted by the reciprocal of the variance of the annual indices, was used to compare the average annual change in indices between the hot/dry event years, the cold/wet ones and the remaining nonevent years (including the years identified as invertebrate extreme events). When significant differences were found between the three types of events, they were compared using least significant difference tests. 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 as described above, excluding years in which an extreme weather event was identified (to limit the influence that extreme weather events may have had on the overall trend). Any years in which invertebrate extreme events were identified for a taxon were also excluded before trend estimation.

Statistical analysis. 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 GAM spline fitted to the data. 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.

Event years were included in the analysis of recovery time only if no other extreme weather event occurred in the 3 years following, to remove any influence of other events on observed recovery times. Recovery time was calculated for all taxa, regardless of the results from the sensitivity analysis.

Influence of habitat and landscape on sensitivity and resilience

Statistical analysis. To investigate the factors influencing sensitivity and resilience, we related the ln-transformed change in abundance between the event year and the year following the event at all sampling locations to the variables describing landscape, habitat and pesticide use using linear mixed modelling. We restricted the extreme weather events to exclude any occurring in consecutive years to limit compounding effects and undertook one analysis of all hot/dry events and one of all cold/wet ones. Sampling location was entered as a random effect; all potential explanatory variables were entered as fixed effects and tested for significance using Wald statistics. Year was entered as a categorical fixed effect to avoid confounding temporal effects with habitat and landscape ones. 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.

Invertebrate abundance and long-term trends in weather

Statistical analysis. To test for linear relationships between invertebrate abundances and weather, we calculated Pearson correlation coefficients between the annual abundance index of each taxon and each of the eight weather variables.

Spectral and coherence analysis. Standardized (zero mean, unit variance) series of abundance indices and their 5-year running means for each taxon, as well as for temperature and rainfall, 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 4-year cycle but where the cyclical peaks and troughs of the second series lag behind those of the first series by 1 year, will exhibit a peak in coherence at 0.25 and a phase of $-(\pi/2)$ radians equal to $-90°$, that is one-quarter of the cycle length.

Spectra were calculated according to Barrodale & Erickson (1980), and coherences were calculated according to Strand (1977), both with a filter length of 4. Significance of peaks was determined by comparison with results calculated from 1000 randomly generated time series for both spectral densities and coherence of trends in invertebrate indices with trends in weather.

Invertebrate abundance, long-term trends in weather and changes in pesticide use

Statistical analysis. The relative importance of weather and pesticide use on the indices of invertebrate abundance was 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.

All statistical analysis was carried out in GENSTAT RELEASE 15.0 for Windows (VSN International Ltd, Hemel Hempstead, UK).

Results

Temporal trends

The long-term trends in the invertebrate annual indices of abundance follow four broad patterns (Fig. 1). Several taxa showed an increase at some point over the 40 years of the study (pattern i). Cicadellidae and Delphacidae both increased in the last few years, and Chalcididae increased between 1980 and the mid-2000s, before beginning to decline again in the latter part of the decade. Collembola decreased between 1980 and 2000, before increasing in the last 10 years to abundances similar to those seen at the start of the study. Decreases in indices of abundance (pattern ii) were noted for Araneae, Aphididae, Braconidae, Carabidae, *Tachyporus*, *Enicmus*, Lathridiidae, *Atomaria*, Cryptophagidae, Lonchopteridae, Agromyzidae and Drosophilidae.

More complex changes (pattern iii) were seen in the trends for Heteroptera, Empididae and Opomyzidae,
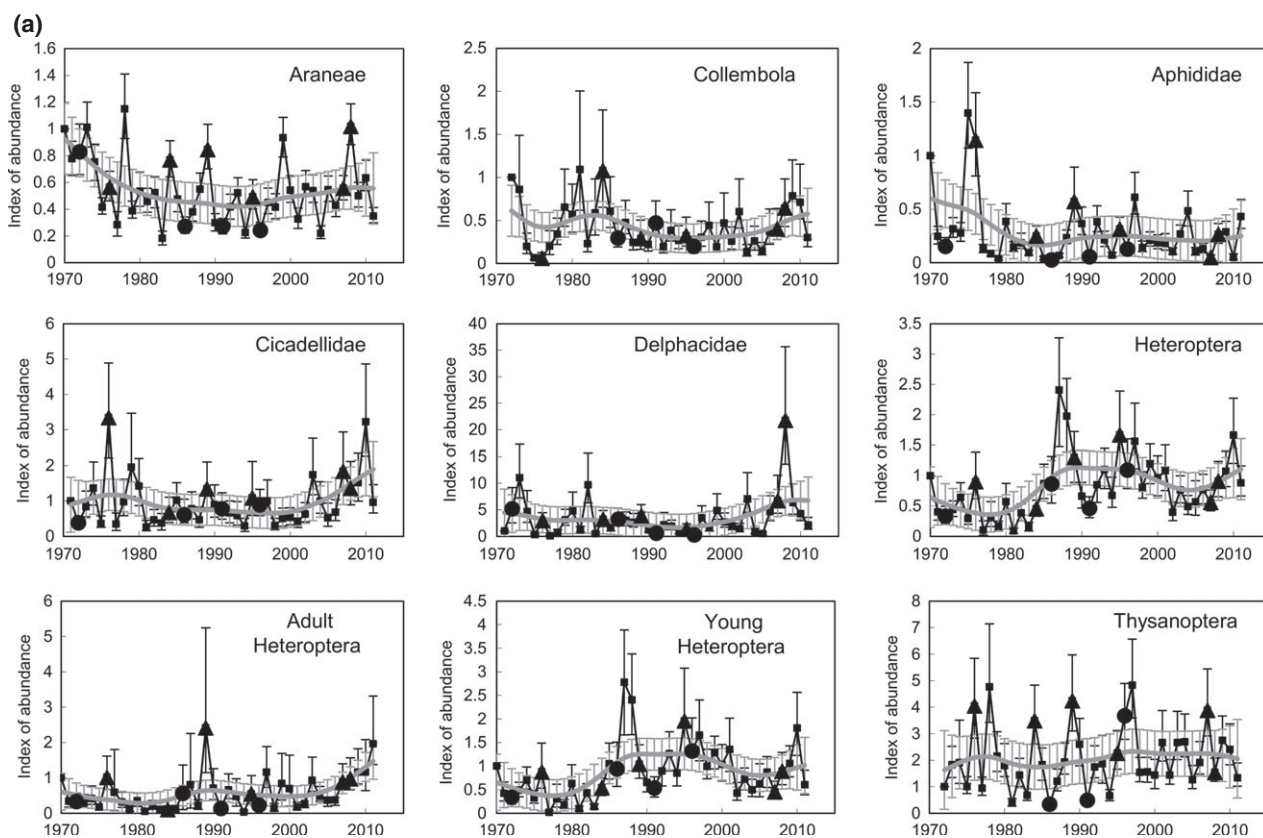
Fig. 1 (a–c). Long-term trends in invertebrate indices of abundance and 95% confidence intervals, from 1970 to 2011. The grey line and 95% confidence intervals represent the long-term smoothed trend. Cold/wet event years are represented by large dots and hot/dry events by triangles.

(b)

Fig. 1 (continued)

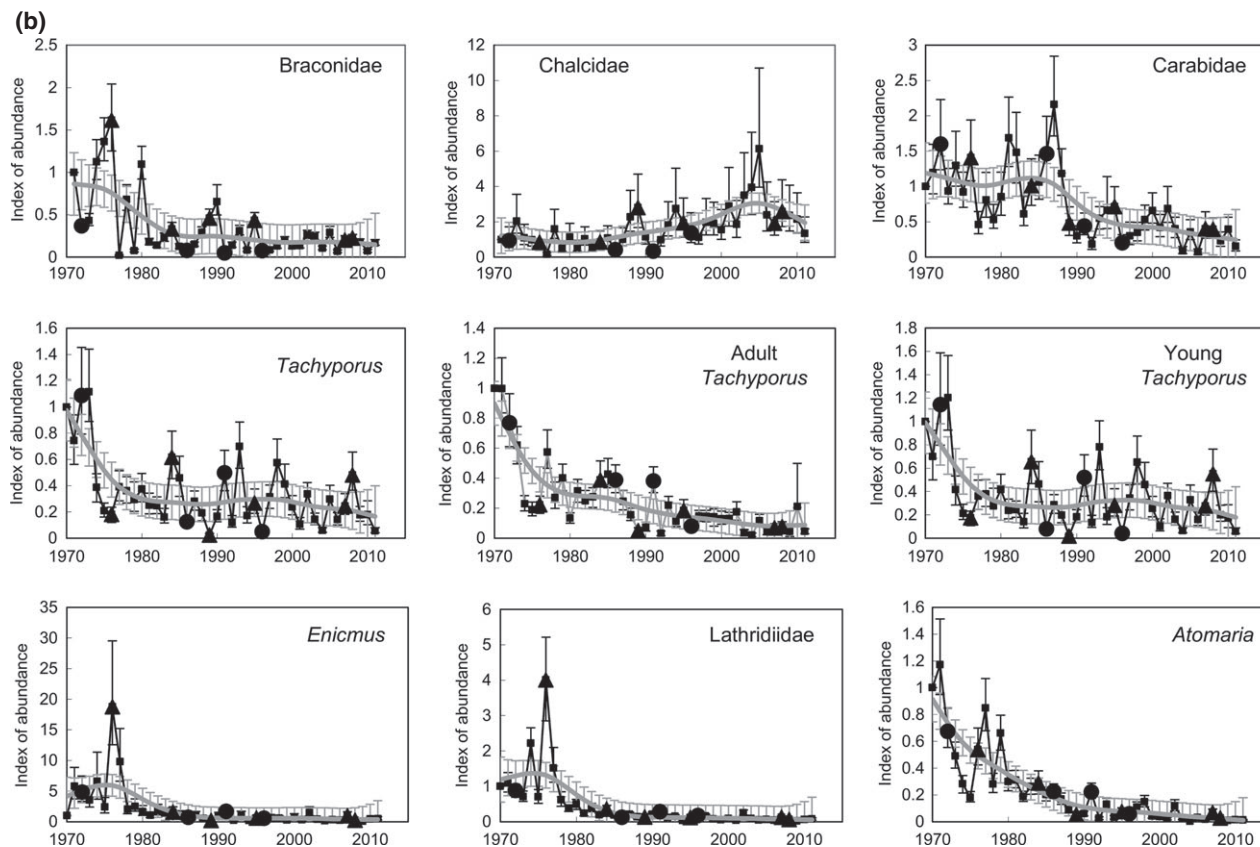with early declines, recovering to initial abundances in the 1980s. Heteroptera have recently exceeded the abundance of early years, but Empididae and Opomyzidae have returned to the low levels of the early 1980s. Three taxa showed no change in abundance (pattern iv – Thysanoptera, Cecidomyiidae and Mycetophilidae).

Temperature, measured as the average of April, May and June, showed a long-term increase, while there was no long-term trend in precipitation over the same time period (Fig. 2).

Pesticide use has increased throughout the time of the Sussex Study, with big increases noted in the late 1980s to early 1990s (Fig. 3). Pesticide use was significantly positively correlated ($r_{34} = 0.438$, $P = 0.002$) with increases in temperature.

Extreme events

A total of 12 extreme weather events were identified: four low-precipitation events, one high-precipitation event, four high-temperature events and three low-temperature events (Table 1). Some overlap in years among these 12 extreme weather events left a total of 10 event

years for use in the analysis. The years identified in each category are as follows:

1 Cold/wet: 1972, 1986, 1991, 1996
2 Hot/dry: 1976, 1984, 1989, 1995, 2007, 2008

Overall 35 extreme events in the invertebrate series were identified, of which 11 (31%) coincided with extreme weather events and five with the drought of 1976 (Table 1). There were also seven invertebrate extreme events the year after the 1976 drought, six of which were negative, followed by a further six positive invertebrate extreme events in 1977. This accounts for 18 of the 35 invertebrate extreme events (51%) in a 3-year period.

Eleven (42%) of the 26 taxa examined were sensitive to extreme weather events, namely Araneae, Cicadellidae, Delphacidae, adult Heteroptera, Thysanoptera, Braconidae, *Enicmus*, Lathridiidae, Cryptophagidae and Mycetophilidae (Table 2). For Araneae, Cicadellidae, adult Heteroptera, Thysanoptera and Braconidae, differences between year categories followed a linear pattern, whereby hot/dry events resulted in an increase in the abundance index, which was higher than nonevent years, which in turn was higher than for the cold/wet

(c)
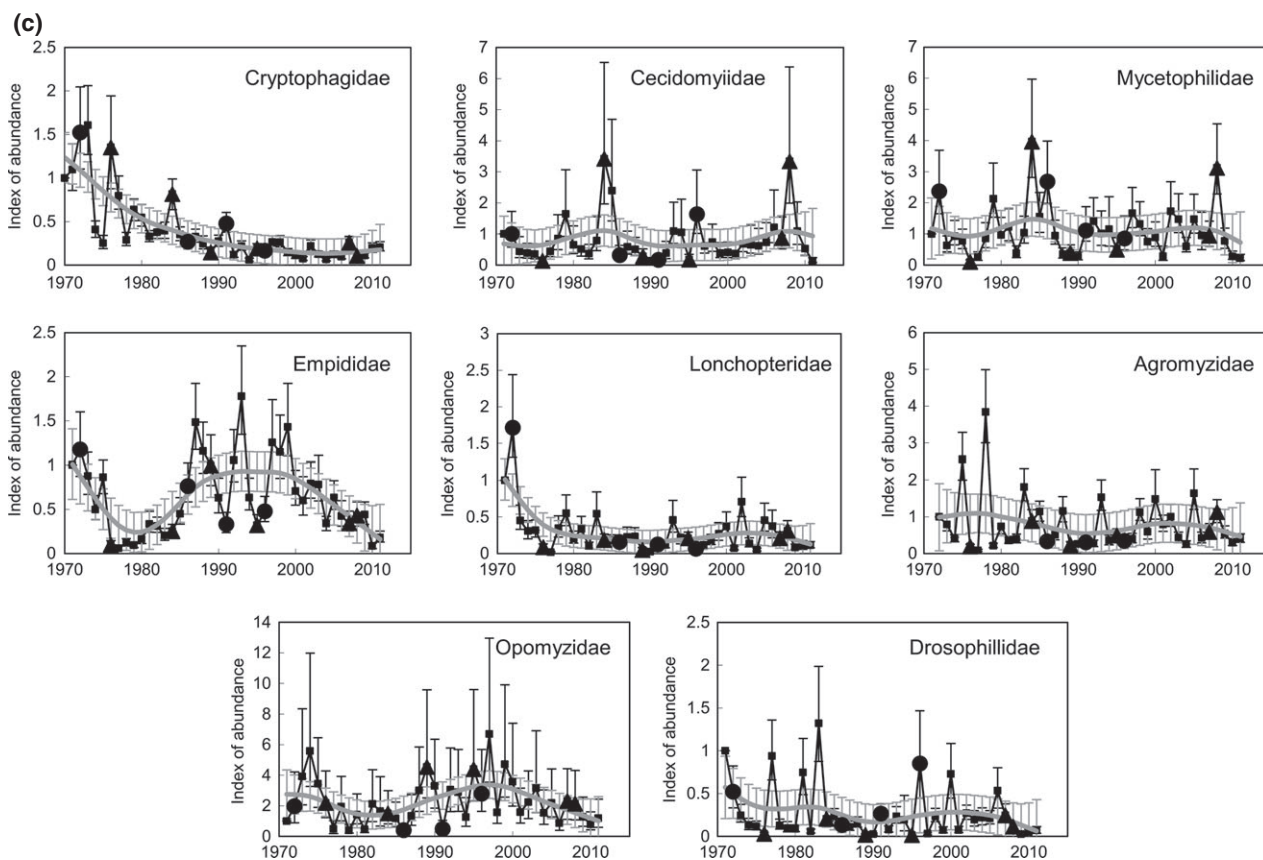
Fig. 1 (continued)
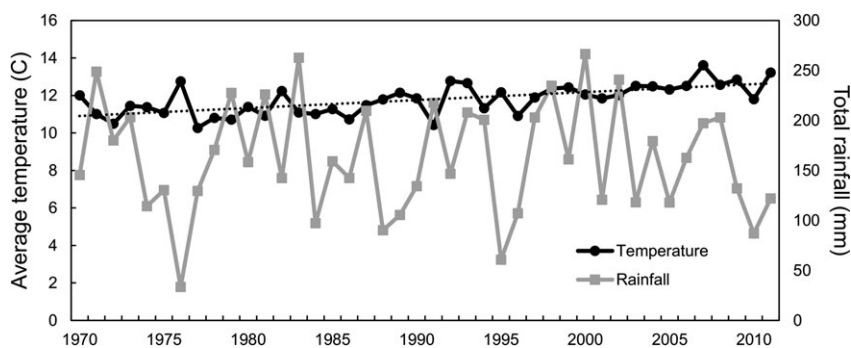
Fig. 2 Long-term trend in temperature (average April, May and June) and total rainfall (April, May and June) from 1970 to 2011. Temperature showed a significant linear increase over the 42 years of the Sussex Study ($F_{1,40} = 26.10$, $P < 0.001$), while there was no trend in total rainfall ($F_{1,40} = 0.07$, $P = 0.799$).

years. For the remaining taxa, the average change in abundance indices was lowest in nonevent years.

Only five (two hot/dry and three cold/wet) 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 3 years. Mean recovery time in the case of extreme weather events was a year or less for the majority of the 26 taxa (Table 3). Only two taxa (Cecidomyiidae and Myce-

tophilidae) took longer than a year to recover from hot/dry events, and again only two taxa (Thysanoptera and *Tachyporus* young) took longer than a year to recover from cold/wet events. For the 24 extreme events identified in the invertebrate series that did not coincide with an extreme weather event, the time to recovery was also an average of 1 year. Only two taxa took longer than a year to recover from these events, Delphacidae and Heteroptera.
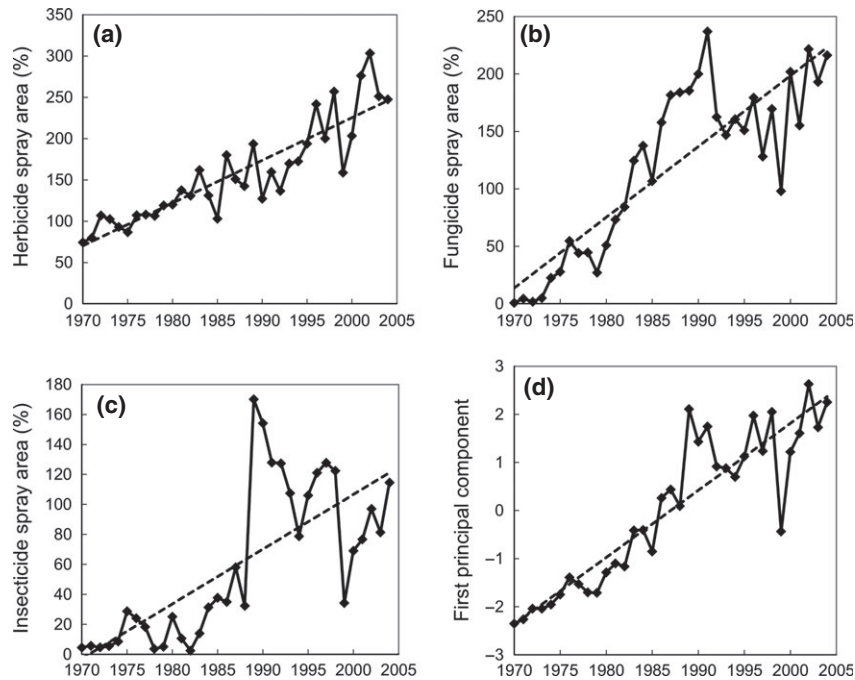
Fig. 3 Long-term trends in intensity of pesticide use measures as percentage spray area from 1970 to 2004. Herbicide (a, $F_{1,33} = 122.5$, $P < 0.001$), fungicide (b, $F_{1,33} = 92.0$, $P < 0.001$) and insecticide (c, $F_{1,33} = 37.3$, $P < 0.001$) use increased in intensity. This is reflected in the trend through time of the first principal component of the three series (d, $F_{1,33} = 164.5$, $P < 0.001$).

There were few significant findings in the effect of habitat and landscape on either the sensitivity or resilience of invertebrate taxa (Tables 4 and 5, respectively). The only one of note was for aspect in relation to sensitivity to cold, wet years. Changes in the abundance of five of the ten taxa examined (Araneae, Cicadellidae, Thysanoptera, Cryptophagidae and Mycetophilidae) showed a significant effect of aspect (Table 4b), such that an increase in abundance was mainly associated with west-facing slopes and a decrease in abundance with east-facing slopes (Table 6). The large variation in the samples from north-facing slopes was due to small sample size within the study area. In the case of Cicadellidae, abundance in samples on north-facing slopes declined significantly more than those in samples on other slopes.

Invertebrate abundance and weather

Of the 26 taxa, 14 showed a significant correlation between their annual index of abundance (Fig. 1) and at least one measure of temperature for the April–May–June period (Table 7). There were positive correlations between temperature and the abundance of Hemiptera (Aphididae, Delphacidae and Heteroptera) and Chalcididae. The opposite was true of four of the Coleopteran taxa tested (Carabidae, *Tachyporus*, *Atomaria* and Cryptophagidae). The abundance of Drosophilidae was also

negatively correlated with two measures of temperature. Seventeen taxa showed a significant correlation between their annual index of abundance and at least one measure of precipitation for the April–May–June period. Precipitation was negatively correlated with the abundance of Aphididae, Cicadellidae, Heteroptera, Thysanoptera and Lathridiidae. Positive correlations for precipitation were found for Collembola, several Coleoptera taxa (*Tachyporus*, *Enicmus* and *Atomaria*) as well as five of the seven Diptera taxa.

Comparing the results for temperature and precipitation, in general if the abundance of a taxon increased with temperature, it declined with precipitation and vice versa. Of the 26 taxa examined, only three taxa showed no significant correlations with at least one of the weather variables: Araneae, Agromyzidae and Opomyzidae (Table 7).

Periodicities in invertebrate abundance and weather

Most spectral densities varied from random frequencies relating to long timescales – 20–100 years (Table 8; Fig. S1). Significant periodicity at long timescales was identified for temperature and thirteen of the taxa/age groups examined (Collembola, Heteroptera adults, Heteroptera young, Braconidae, Chalcididae, Carabidae, *Tachyporus* adults, *Enicmus*, Lathridiidae, *Atomaria*, Cryptophagidae, Empididae and Opomyzidae). Significant

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

Year	Araneae	Collembola	Aphididae	Cicadellidae	Delphacidae	Heteroptera	Heteroptera (adults)	Heteroptera (nymphs)	Thysanoptera	Braconidae	Chalcididae	Carabidae	Tachyporus	Tachyporus (adults)	Tachyporus (young)	Enicmus	Lathrididae	Atomaria	Cryptophagidae	Cecidomyiidae	Mycetophilidae	Empididae	Lonchopteridae	Agromyzidae	Opomyzidae	Drosophillidae	Weather event
1970																											
1971																											
1972																											Low June temp
1973																											
1974																											
1975																											
1976			+														+		+		−	−					Low average rainfall and high June temp
1977			−	−	−			−	−	−														+			
1978	+						+		+	+												+	+				
1979																								−			
1980																											
1981								−																			
1982		−																									
1983																											
1984	+																										Low April rain
1985																											
1986																				−							Low April temp
1987																											
1988																											
1989																											Low May rain
1990																											
1991																											High June rain
1992																				−							
1993																											
1994								−																			
1995									+																		Low average rain
1996																				+						+	Low May temp
1997																											
1998																											
1999																											
2000																											
2001																											
2002												+					+										
2003																											
2004												−															
2005												+															
2006									−																		
2007												+															High April and average temp
2008																											High May temp
2009																											
2010																				−							
2011																											

shorter periodicity was identified for rainfall and only two taxa (Braconidae and Drosophilidae). Three taxa show periodicity at medium frequencies: Thysanoptera, Mycetophilidae and Agromyzidae, which did not reflect periodicity in the weather variables examined.

The coherence analysis between temperature and changes in invertebrate indices revealed a general pattern of significant similarities at two timescales (Table 9; Fig. S2). These are at long timescales 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 timescales, centring around 2 years. The nine taxa/age groups with coherence with temperature at long timescale

Table 2 Annual changes in invertebrate abundance in cereals in hot/dry, cold/wet and nonevent years (±standard error). Significant differences indicate sensitivity to weather events. The data for taxa identified as being sensitive to extreme weather events are shown in bold

Taxa	Years	F	Hot/dry	Nonevent	Cold/wet
Araneae	40	$F_{2,37} = 4.30^*$	**0.549 ± 0.221[a]**	**−0.141 ± 0.096[b]**	**−0.225 ± 0.290[b]**
Collembola	38	$F_{2,35} = 1.18$	0.327 ± 0.256	−0.083 ± 0.118	−0.196 ± 0.354
Aphididae	40	$F_{2,37} = 1.06$	0.191 ± 0.347	−0.028 ± 0.196	−0.919 ± 0.679
Cicadellidae	39	$F_{2,36} = 3.52^*$	**0.761 ± 0.318[a]**	**−0.078 ± 0.143[b]**	**−0.409 ± 0.401[c]**
Delphacidae	39	$F_{2,36} = 4.38$	**0.906 ± 0.377[a]**	**−0.282 ± 0.190[b]**	**0.640 ± 0.719[a]**
Heteroptera	40	$F_{2,37} = 1.01$	0.288 ± 0.256	0.003 ± 0.110	−0.267 ± 0.300
Heteroptera adults	40	$F_{2,37} = 3.27^*$	**0.884 ± 0.369[a]**	**−0.105 ± 0.158[b]**	**−0.365 ± 0.577[b]**
Heteroptera nymphs	40	$F_{2,37} = 0.56$	0.179 ± 0.286	0.031 ± 0.118	−0.257 ± 0.311
Thysanoptera	38	$F_{2,35} = 2.54$	**0.622 ± 0.306[a]**	**−0.112 ± 0.141[b]**	**−0.306 ± 0.528[b]**
Braconidae	39	$F_{2,36} = 4.22^*$	**0.321 ± 0.268[a]**	**0.130 ± 0.163[a]**	**−1.238 ± 0.480[b]**
Chalcididae	39	$F_{2,36} = 0.97$	0.018 ± 0.220	0.027 ± 0.102	−0.516 ± 0.378
Carabidae	40	$F_{2,37} = 0.72$	0.186 ± 0.238	−0.072 ± 0.101	0.153 ± 0.264
Tachyporus	40	$F_{2,37} = 2.17$	0.517 ± 0.360	−0.219 ± 0.129	0.152 ± 0.337
Tachyporus adult	40	$F_{2,37} = 0.49$	0.188 ± 0.318	−0.146 ± 0.115	−0.089 ± 0.251
Tachyporus young	40	$F_{2,37} = 2.37$	0.548 ± 0.379	−0.234 ± 0.136	0.238 ± 0.368
Enicmus	40	$F_{2,37} = 8.50^{**}$	**1.400 ± 0.368[a]**	**−0.247 ± 0.155[b]**	**−0.073 ± 0.399[ab]**
Lathridiidae	40	$F_{2,37} = 11.16^{***}$	**1.360 ± 0.320[a]**	**−0.282 ± 0.136[b]**	**−0.083 ± 0.381[ab]**
Atomaria	40	$F_{2,37} = 2.38$	0.527 ± 0.311	−0.163 ± 0.111	−0.260 ± 0.261
Cryptophagidae	40	$F_{2,37} = 7.23^{**}$	**0.836 ± 0.280[a]**	**−0.247 ± 0.110[c]**	**0.234 ± 0.260[b]**
Cecidomyiidae	39	$F_{2,36} = 2.39$	0.570 ± 0.313	−0.174 ± 0.148	−0.248 ± 0.497
Mycetophilidae	39	$F_{2,36} = 5.18^*$	**0.562 ± 0.334[a]**	**−0.276 ± 0.142[b]**	**0.730 ± 0.369[a]**
Empididae	39	$F_{2,36} = 0.72$	−0.309 ± 0.274	0.006 ± 0.104	0.133 ± 0.300
Lonchopteridae	39	$F_{2,36} = 1.35$	−0.527 ± 0.387	−0.189 ± 0.169	0.347 ± 0.380
Agromyzidae	38	$F_{2,35} = 0.89$	−0.423 ± 0.438	0.091 ± 0.202	−0.629 ± 0.760
Opomyzidae	39	$F_{2,36} = 0.80$	0.186 ± 0.293	−0.005 ± 0.138	−0.499 ± 0.456
Drosophilidae	39	$F_{2,36} = 2.56$	−1.300 ± 0.501	−0.049 ± 0.234	−0.319 ± 0.531

Means with the same letter are not significantly different ($P < 0.05$).
$^*P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$.

were as follows: Cicadellidae, Braconidae, Chalcididae, Carabidae, *Tachyporus* adults, Lathridiidae, *Atomaria*, Cryptophagidae and Empididae. There were twelve taxa/age groups that showed coherence with temperature at shorter timescales (Aphididae, Cicadellidae, Heteroptera, Heteroptera adults, Heteroptera nymphs, Thysanoptera, Braconidae, Carabidae, Lathridiidae, *Atomaria*, Opomyzidae and Drosophilidae). These short timescale events are not confined to taxa found to be sensitive to extreme weather events, although the timescales involved reflect the recovery rates identified for extreme weather events.

The results of the comparison between rainfall and changes in invertebrate indices (Table 9b; Fig. 3) produced fewer significant similarities, with the general trend of most significant coherences being at a timescale of between 5 and 10 years, as was the case for Delphacidae, Thysanoptera, *Tachyporus*, *Tachyporus* young, *Atomaria* and Lonchopteridae. Coherence between rainfall and Collembola and Drosophilidae were significant at shorter timescales (2 years).

Invertebrate abundance and multivariate relationships

A multiple regression involving temperature, rainfall and pesticide use was significant in 22 of 26 cases (Table 10). In five cases, only pesticide use was significant (Araneae, Carabidae, *Enicmus*, *Atomaria* and Cryptophagidae), in seven only weather variables (Collembola, Aphididae, Cicadellidae, Empididae, Lonchopteridae, Opomyzidae and Drosophilidae) and for the remaining 10 a combination of both was significant.

Considering all the Coleoptera (Carabidae, *Tachyporus*, *Enicmus*, Lathridiidae, *Atomaria* and Cryptophagidae), abundance declined with increasing pesticide use, with a few instances of weather also having an effect. For Diptera, changes in abundance more closely reflected long-term trends in weather than those in pesticide use, if a relationship was present. The abundance of Araneae was negatively related to pesticide use, while Collembola abundance was positively related to rainfall. The abundance of Braconidae and Chalcididae was related to both weather and pesticide use, but Bra-

Table 3 Average number of years (±standard error) taken to recover following an extreme weather event and invertebrate extreme events for invertebrates in cereals. The data for taxa identified as being sensitive to extreme weather events are shown in bold

Taxa	Hot/dry events	Cold/wet events	Invertebrate extreme events
Araneae	**0.5 ± 0.5**	**0.3 ± 0.3**	**1.0**
Collembola	1.0 ± 1.0	0.0 ± 0.0	1.0
Aphididae	0.5 ± 0.5	0.3 ± 0.3	
Cicadellidae	**0.5 ± 0.5**	**0.3 ± 0.3**	**1.0**
Delphacidae	**1.0 ± 1.0**	**0.3 ± 0.3**	**2.0**
Heteroptera	0.5 ± 0.5	0.3 ± 0.3	2.5
Heteroptera adults	**1.0 ± 1.0**	**0.7 ± 0.3**	**1.0**
Heteroptera nymphs	0.5 ± 0.5	0.7 ± 0.7	0.5
Thysanoptera	**0.5 ± 0.5**	**1.5 ± 0.5**	
Braconidae	**0.5 ± 0.5**	**0.7 ± 0.7**	0.5
Chalcididae	0.0 ± 0.0	0.3 ± 0.3	1.0
Carabidae	0.5 ± 0.5	0.7 ± 0.3	1.0
Tachyporus	1.0 ± 0.0	1.3 ± 0.3	
Tachyporus adult	0.5 ± 0.5	0.3 ± 0.3	
Tachyporus young	1.0 ± 0.0	1.3 ± 0.3	
Enicmus	**1.0 ± 1.0**	**0.0 ± 0.0**	
Lathridiidae	**1.0 ± 1.0**	**0.0 ± 0.0**	**1.0**
Atomaria	0.0 ± 0.0	0.0 ± 0.0	0.7
Cryptophagidae	**1.0 ± 1.0**	**1.0 ± 0.6**	
Cecidomyiidae	1.5 ± 0.5	0.7 ± 0.3	
Mycetophilidae	**1.5 ± 0.5**	**0.3 ± 0.3**	
Empididae	1.0 ± 1.0	1.0 ± 0.0	1.0
Lonchopteridae	1.0 ± 1.0	0.7 ± 0.3	0.5
Agromyzidae	1.0 ± 1.0	0.0 ± 0.0	1.0
Opomyzidae	0.0 ± 0.0	0.3 ± 0.3	
Drosophilidae	0.5 ± 0.5	0.3 ± 0.3	1.0

conidae abundance was negatively related to rainfall and pesticide use, while Chalcididae abundance was positively related to temperature and pesticide use.

Discussion

Extreme weather events

We were able to identify several extreme weather events that occurred during the course of the Sussex Study and found that several invertebrate taxa in cereals were sensitive to these events. However, the invertebrates we considered were also quick to recover, with only two taxa taking longer than a year to return to pre-event trends. Morley & Lewis (2014) reported similar responses and quick recoveries when reviewing host–pathogen responses to one of the extreme weather events considered here, the 1976 drought. The invertebrate taxa that we examined can exhibit great

interannual variability in their abundance (Fig. 1). The 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. This favours species with an ability to cope with a highly variable environment. Farming intensification, with the associated increase in pesticide use, will have increased selection for taxa that are able to recolonize fields after pesticide treatment (but see Ewald & Aebischer, 1999 for evidence of a 'carry-over' effect of pesticide use on some invertebrate groups). Beddington (2009) postulated that, for arable agriculture, one of the consequences of climate change (both globally and nationally) may be increased use of pesticides in response to pest outbreaks. The main effect of climate change on invertebrates in cereal fields may be this intensification.

The only consistent trend to emerge from the analysis of habitat and landscape features on the sensitivity 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 compared to the preceding year on west-facing slopes, whereas it tended to decrease compared to the preceding year on other slopes, especially east-facing ones. This may indicate potential microclimate refugia to extreme weather events on these slopes in arable systems (Suggitt *et al.*, 2014).

Aspect has been highlighted as a potentially key landscape component in influencing climatic conditions at a small, localized 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 *et al.*, 1994), to bird species (Calladine & Bray, 2012). Explanations for the influence of aspect 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 *et al.*, 1994) and increased exposure to warm dry NW winds (Ashcroft *et al.*, 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 microclimatic level leading to conditions more suitable for invertebrates on those west-facing slopes is likely to be occurring. 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). The lack of any

Table 4 Sensitivity. Wald statistics testing for effects of habitat and landscape factors on sensitivity to (a) hot/dry events and (b) cold/wet events. Results are from linear mixed modelling of changes in invertebrate abundance in cereals in the event year relative to the pre-event year for 10 taxa shown to be sensitive to extreme weather events, with an overall sample size of 210 fields

	Degrees of freedom	Araneae	Cicadellidae	Delphacidae	Heteroptera adults	Thysanoptera	Braconidae	Enicmus	Lathridiidae	Cryptophagidae	Mycetophilidae
(a) Hot/dry											
Year	3	8.70*	4.33	1.56	3.85	1.47	1.48	10.19*	4.45	14.38**	0.82
Crop	2	1.94	1.78	0.24	0.58	2.52	2.86	0.01	0.05	0.61	2.68
Aspect	3	2.13	4.66	1.79	0.38	3.10	0.92	0.62	0.40	1.53	1.92
Field boundary density	1	0.03	0.51	0.04	0.99	0.98	0.01	0.04	1.50	0.32	0.01
Slope	1	1.31	0.20	2.12	1.99	0.20	0.10	0.01	0.60	0.23	0.95
Elevation	1	2.46	0.12	1.52	0.66	0.03	0.01	0.30	0.32	0.04	0.05
Patch density (log)	1	1.61	0.01	0.05	1.54	0.14	0.35	0.22	1.30	0.01	0.01
Field area (log)	1	0.57	1.05	1.15	0.38	1.33	2.27	3.95*	2.49	3.27	0.01
(b) Cold/wet											
Year	3	14.46**	9.50*	1.48	12.58**	2.40	1.58	3.29	2.08	2.47	11.26*
Crop	2	2.88	0.41	1.01	0.51	2.11	0.83	0.28	2.22	1.44	2.09
Aspect	3	8.79*	10.50*	2.70	5.32	12.21**	3.22	6.51	3.68	9.35*	11.75*
Field boundary density	1	0.43	2.43	0.01	1.37	1.22	0.33	0.34	0.48	0.88	2.48
Slope	1	0.37	0.28	0.01	0.02	3.61	0.35	1.82	1.29	1.39	1.64
Elevation	1	0.50	0.60	0.01	0.18	0.48	3.28	3.70	3.23	4.22*	1.44
Patch density (log)	1	0.02	0.14	0.01	1.25	2.93	0.69	0.18	1.12	0.27	1.57
Field area (log)	1	0.83	0.58	0.01	1.19	0.13	0.26	3.65	0.55	0.24	5.19*

*$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$.

Table 5 Resilience. Wald statistics testing for effects of habitat and landscape factors on resilience to (a) hot/dry events and (b) cold/wet events. Results are from linear mixed modelling of changes in invertebrate abundance in the event year relative to the pre-event year for 10 taxa shown to be sensitive to extreme weather events, with an overall sample size of 210 fields

	Degrees of freedom	Araneae	Cicadellidae	Delphacidae	Heteroptera adults	Thysanoptera	Braconidae	Enicmus	Lathridiidae	Cryptophagidae	Mycetophilidae
(a) Hot/dry											
Year	3	0.89	10.51*	0.58	4.53	2.53	11.05*	2.14	2.65	3.34	0.64
Crop	2	0.50	0.03	2.75	2.72	2.20	0.10	3.93	1.71	4.77	0.82
Aspect	3	3.49	2.22	4.51	3.89	2.41	1.51	2.46	2.77	4.37	3.69
Field boundary density	1	1.35	0.08	0.47	0.01	0.38	0.05	0.12	0.05	1.68	0.59
Slope	1	1.35	0.43	0.69	0.20	0.38	0.20	0.03	0.90	0.02	0.20
Elevation	1	0.22	0.04	0.11	2.17	0.49	0.65	14.60***	8.58**	3.70	0.30
Patch density (log)	1	2.51	4.96*	0.01	0.53	0.72	0.49	0.15	2.02	4.51*	1.45
Field area (log)	1	0.03	3.83	2.19	2.24	0.29	0.29	0.88	1.88	2.67	2.16
(b) Cold/wet											
Year	3	1.48	4.04	2.16	2.54	2.41	5.03	1.69	3.83	1.89	2.25
Crop	2	2.00	2.65	2.70	0.48	0.03	2.23	1.72	1.43	4.65	0.28
Aspect	3	7.42	1.85	8.86*	2.06	0.92	1.19	4.60	2.55	2.43	5.65
Field boundary density	1	0.44	0.01	0.18	1.03	0.01	0.01	0.64	1.05	0.84	2.19
Slope	1	0.74	0.03	2.61	0.24	2.13	0.19	0.02	0.03	0.74	2.89
Elevation	1	0.04	0.08	0.02	0.01	3.48	0.01	1.97	0.21	0.13	1.60
Patch density (log)	1	0.05	2.31	0.01	2.19	0.26	0.47	3.39	5.18*	1.36	1.79
Field area (log)	1	0.14	1.31	0.23	5.03*	0.46	1.77	1.41	0.28	4.41*	1.34

*$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$.

Table 6 Mean change (±standard error) in abundance of invertebrates in cereals in relation to aspect of sampling location, for five taxa sensitive to cold/wet extreme events that showed a significant result for aspect (Table 4). 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	Cryptophagidae	Mycetophilidae
North	-0.254 ± 0.376 ab	-1.038 ± 0.346 a	-0.633 ± 0.56 ab	0.349 ± 0.448 ab	0.570 ± 0.418 bc
East	-0.235 ± 0.223 a	-0.151 ± 0.206 b	-0.827 ± 0.323 a	-0.258 ± 0.259 ab	-0.385 ± 0.244 a
South	-0.013 ± 0.125 a	0.006 ± 0.115 b	0.122 ± 0.180 b	-0.377 ± 0.145 a	-0.190 ± 0.137 ab
West	0.464 ± 0.166 b	0.165 ± 0.154 b	0.439 ± 0.234 b	0.254 ± 0.189 b	0.392 ± 0.179 c

Table 7 Pearson's correlation coefficients and associated significance for correlation between each weather variable and annual abundance index for each of the 26 invertebrate taxa

		Mean temperature				Total precipitation			
	Years	April	May	June	April–June	April	May	June	April–June
Araneae	40	−0.035	0.266	−0.001	0.113	−0.137	0.047	0.052	−0.036
Collembola	38	0.025	−0.174	−0.216	−0.178	0.004	0.498**	0.183	0.383*
Aphididae	40	−0.091	0.116	0.331*	0.175	−0.195	−0.321*	−0.250	−0.415**
Cicadellidae	39	0.237	0.042	0.425**	0.317*	−0.423**	−0.188	−0.034	−0.398*
Delphacidae	39	0.194	0.377*	0.249	0.380*	−0.092	0.226	0.053	0.102
Heteroptera	40	0.306	0.235	0.190	0.339*	−0.047	−0.383*	−0.108	−0.308
Heteroptera (adults)	40	0.181	0.476**	0.339*	0.469**	−0.089	−0.364*	−0.035	−0.259
Heteroptera (nymphs)	40	0.288	0.165	0.139	0.274	−0.032	−0.346*	−0.116	−0.289
Thysanoptera	38	0.150	0.173	0.316	0.292	−0.426**	−0.183	−0.084	−0.361*
Braconidae	39	−0.117	−0.043	0.157	0.002	−0.369*	−0.327*	−0.114	−0.455**
Chalcididae	39	0.287	0.373*	0.458**	0.524***	0.172	−0.049	−0.305	−0.133
Carabidae	40	−0.197	−0.349*	−0.293	−0.393*	−0.182	0.023	0.127	−0.043
Tachyporus	40	−0.059	−0.104	−0.414**	−0.271	0.010	0.171	0.374*	0.315*
Tachyporus (adults)	40	−0.390*	−0.417**	−0.571***	−0.642***	−0.030	0.156	0.311	0.216
Tachyporus (young)	40	−0.012	−0.056	−0.375*	−0.209	0.015	0.165	0.366*	0.314*
Enicmus	40	−0.237	−0.129	0.015	−0.158	−0.358*	−0.178	−0.041	−0.356*
Lathridiidae	40	−0.221	−0.126	0.062	−0.127	−0.410**	−0.221	−0.053	−0.407**
Atomaria	40	−0.391*	−0.345*	−0.475**	−0.562***	−0.112	0.092	0.286	0.129
Cryptophagidae	40	−0.281	−0.297	−0.263	−0.391*	−0.246	0.032	0.158	−0.045
Cecidomyiidae	39	0.066	−0.077	−0.024	−0.027	−0.076	0.440**	−0.163	0.124
Mycetophilidae	39	−0.096	−0.161	−0.139	−0.19	−0.011	0.423**	−0.029	0.258
Empididae	39	0.178	0.292	−0.057	0.202	0.351*	−0.182	0.146	0.203
Lonchopteridae	39	0.007	−0.196	−0.348*	−0.255	0.243	0.375*	0.037	0.334*
Agromyzidae	38	0.010	−0.072	−0.200	−0.124	−0.138	0.003	0.150	0.035
Opomyzidae	39	0.132	0.293	0.172	0.287	−0.196	−0.253	0.060	−0.179
Drosophilidae	39	−0.227	−0.337*	−0.242	−0.380*	0.249	0.458**	−0.047	0.350*

*$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$.

other clear-cut associations between landscape/habitat and either sensitivity or resilience supports results from our analysis of recovery time.

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

The measures of weather that we considered had both significant positive and negative correlations with invertebrate taxa over the duration of the study. This may indicate that long-term changes in weather – con-

sistent with climate change – have been altering invertebrate abundance over the time of the Sussex Study. Any landscape-scale change in weather will also be confounded with other landscape-scale changes taking place in the Sussex Study area, for instance the background intensification of farming.

Our time series comparisons of invertebrate abundance with temperature showed coherence at two time periods, one of a relatively short time frame (~2 years) and the other acting over long timescales (10 + years). The shorter time frame may represent the impact of

Table 8 Spectral analysis of invertebrate abundance indices, temperature and rainfall. Grey rectangles indicate where spectral densities are significantly higher than expected

The table plots Frequency (0.01–0.50) across the top and Periodicity (years) (100.00 down to 2.00) across the bottom. Grey rectangles mark the frequency ranges where spectral densities are significantly higher than expected:

Taxon	Frequency range of significant spectral density (grey rectangle)
Araneae	—
Collembola	~0.04–0.10
Aphididae	—
Cicadellidae	—
Delphacidae	—
Heteroptera	—
Heteroptera (adults)	—
Heteroptera (nymphs)	~0.01–0.11
Thysanoptera	~0.16–0.20
Braconidae	~0.49–0.50
Chalcididae	~0.01–0.07
Carabidae	~0.03–0.09
Tachyporus	—
Tachyporus (adults)	~0.01–0.09
Tachyporus (young)	—
Enicmus	—
Lathridiidae	~0.01–0.09
Atomaria	—
Cryptophagidae	~0.01–0.04
Cecidomyiidae	—
Mycetophilidae	~0.10–0.14
Empididae	—
Lonchopteridae	~0.01–0.09
Agromyzidae	—
Opomyzidae	~0.33–0.39
Drosophillidae	~0.03–0.08
Temperature	~0.44–0.50
Rainfall	~0.01–0.05

Frequency scale: 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

Periodicity (years) scale: 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

direct weather events that, owing to the quick recovery of invertebrates in cereals, 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 matches the correlations between temperature and abundance across the taxa examined.

Our multivariate analysis of invertebrate abundance in relation to weather and pesticide use suggests that the long-term trends in some higher-level taxa in Sussex (Araneae and Coleoptera, for example, both predominately predatory arthropod groups and both important components of integrated pest management – IPM) are driven by increasing use of pesticide applications. Others (Collembola, Aphididae, Cicadellidae, Lonchopteridae, Opomyzidae and Drosophilidae, groups that are either herbivorous or that feed on rotting plant material at some stage in their life cycle) appear to be related more to changes in weather over the long term. One driving force behind changes in some groups may be a change in 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), related in part to the uptake of

agri-environmental options, in particular conservation headlands (Ewald *et al.*, 2012).

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 direct effects of increased temperature and CO_2 have been varied and are species specific (Newman *et al.*, 2003). The interaction of temperature and CO_2 may result in little change in abundance (Hoover & Newman, 2004); models that have applied this experimental work on a regional basis have found the same (Newman, 2005). Monitoring across Europe suggests an increase in the number of aphid species recorded and changes in timing of first or last flights (Hullé *et al.*, 2010; Bell *et al.*, 2015), but no change in overall abundance due perhaps to changes in the relative abundance of different species (Ma *et al.*, 2014). 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; Diehl *et al.*, 2013), and changes to the abundance and composition of these naturally occurring biocontrol agents may explain why there has been no long-term increase in the abundance of Aphididae in Sussex, although several of the poly-

Table 9 Coherence analysis of invertebrate abundance indices against (a) temperature and (b) rainfall. Grey rectangles indicate where spectral frequencies of taxa were significantly similar to weather variable frequencies

(a) Temperature.

Taxon	Grey-shaded frequency range(s)
Araneae	—
Collembola	—
Aphididae	0.13–0.22; 0.30–0.44
Cicadellidae	0.05–0.09; 0.31–0.45
Delphacidae	—
Heteroptera	0.44–0.50
Heteroptera (adults)	0.18–0.30; 0.42–0.43
Heteroptera (nymphs)	—
Thysanoptera	0.30–0.44; 0.42–0.50
Braconidae	0.01–0.03
Chalcididae	0.01–0.08
Carabidae	—
Tachyporus	—
Tachyporus (adults)	0.09–0.18
Tachyporus (young)	—
Enicmus	—
Lathridiidae	0.01
Atomaria	0.30–0.31; 0.40–0.50
Cryptophagidae	0.04–0.09
Cecidomyiidae	0.02–0.03
Mycetophilidae	—
Empididae	0.11–0.18
Lonchopteridae	—
Agromyzidae	—
Opomyzidae	—
Drosophillidae	0.30–0.50

Frequency axis: 0.01 … 0.50; Periodicity (years): 100.00 … 2.00

(b) Rainfall.

Taxon	Grey-shaded frequency range(s)
Araneae	—
Collembola	0.41–0.50
Aphididae	—
Cicadellidae	—
Delphacidae	0.12–0.18
Heteroptera	—
Heteroptera (adults)	—
Heteroptera (nymphs)	—
Thysanoptera	0.12–0.17
Braconidae	—
Chalcididae	—
Carabidae	—
Tachyporus	0.12–0.19
Tachyporus (adults)	—
Tachyporus (young)	0.12–0.19
Enicmus	—
Lathridiidae	—
Atomaria	0.13–0.14
Cryptophagidae	—
Cecidomyiidae	—
Mycetophilidae	—
Empididae	—
Lonchopteridae	0.12–0.18
Agromyzidae	—
Opomyzidae	—
Drosophillidae	—

Frequency axis: 0.01 … 0.50; Periodicity (years): 100.00 … 2.00

phagous predator groups that we looked at have declined (Araneae, Carabidae, *Tachyporus*). If this regulation of abundance ceased, aphid pest outbreaks may increase if temperature rises as projected under climate change models.

In line with our results, other researchers have noted the negative effect of agricultural intensification (including pesticide use) on the diversity of spiders in arable landscapes (Dormann *et al.*, 2008), with the effect of reducing pesticides theorized 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 *et al.*, 2000). 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), although this may be offset through

Table 10 Multiple regression of abundance indices against temperature, rainfall and pesticide use for each of 26 invertebrate taxa in cereals

Taxa/age groups	Test statistic	Regression coefficients		
		Temperature	Rainfall	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
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*
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
Drosophilidae	$F_{3,29} = 3.40$*	−0.169*	0.060	0.015

*$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$.

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 Carabidae of either climate, land-use intensity or landscape variables (Dormann *et al.*, 2008).

We note that most other data sets cover shorter time periods and often begin between the mid-1980s to the 1990s, substantially after many of the changes in fungi-cide and insecticide use that we have observed in the Sussex Study data set (Ewald & Aebischer, 1999, 2000). The first hot, dry extreme event identified here (1976) is correlated with the first indications of large-scale insecticide use within Sussex. 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 has had more of an effect on long-term changes in invertebrate abundance for some of the taxa we investigated (particularly Araneae, Carabidae and *Tachyporus*) than did temperature change. Changes in the abundance of farmland birds across the United Kingdom have been linked more closely to increases in agricultural intensification than climate change (Eglington & Pearce-Higgins, 2012). Both of these findings suggest that the main driver of change in an agricultural ecosystem is the anthropogenic management undertaken within this system, which in turn will be influenced by a changing climate.

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 of invertebrates in cereal fields to extreme weather events. Methods to mitigate the effect of farming intensification are well known, and many are currently funded in England through agri-environment schemes (beetle banks, conservation headlands, unharvested cereal margins, low-input cereals). 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).

Several of the long-term effects of climate change may lead to increases in some taxa (Rosenzweig *et al.*, 2001; Shaw *et al.*, 2008; Finlay & Luck, 2011), some 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 invertebrate taxa. This appears to be the most likely long-term negative effect of climate change on invertebrate numbers in cereal fields based both on our results here and in other analyses of the effects of pesticide use (Potts, 1986; Aebischer, 1990, 1991; Sotherton, 1991; Ewald & Aebischer, 1999; Benton *et al.*, 2002; Geiger *et al.*, 2010). The utilization of conservation headlands (Sotherton, 1991) together with beetle banks, as part of an agri-environmental package for the conservation of farmland birds, will counteract this and reap benefits for the conservation of invertebrates in cereal fields (Winspear *et al.*, 2010).

Acknowledgements

References

Aebischer NJ (1990) Assessing pesticide effects on non-target invertebrates using long-term monitoring and time-series modelling. *Functional Ecology*, **4**, 369–373.

Aebischer NJ (1991) Twenty years of monitoring invertebrates and weeds in cereal fields. In: *The Ecology of Temperate Cereal Fields* (eds Firbank LG, Carter N, Derbyshire JF, Potts GR), pp. 305–331. Blackwell Scientific Publications, Oxford.

Aebischer NJ, Coulson JC, Colebrook JM (1990) Parallel long-term trends across four trophic levels and weather. *Nature*, **347**, 753–755.

Amano T, Kusumoto Y, Okamura H, Baba YG, Hamasaki K, Tanaka K, Yamamoto S (2011) A macro-scale perspective on within-farm management: how climate and topography alter the effect of farming practices. *Ecology Letters*, **14**, 1263–1272.

Ashcroft MB, Chisholm LA, French KO (2009) Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. *Global Change Biology*, **15**, 656–667.

Barrodale I, Erickson RE (1980) Algorithms for least-squares linear prediction and maximum entropy spectral analysis – Part II: Fortran program. *Geophysics*, **45**, 433–446.

Beddington J (2009) *Food, energy, water and the climate: a perfect storm of global events?* In Conference presentation given to the Sustainable Development UK Annual Conference, QEII Conference Centre, London, 19 March 2009. See http://webarchive.nationalarchives.gov.uk/20121212135622/http://www.bis.gov.uk/assets/go-science/docs/p/perfect-storm-paper.pdf (accessed 24 February 2015).

Bell JR, Alderson L, Izera D *et al.* (2015) Long-term phenological trends, species accumulation rates, aphid traits and climate: five decades of change in migrating aphids. *Journal of Animal Ecology*, **84**, 21–34.

Bennie J, Huntley B, Wiltshire A, Hill MO, Baxter R (2008) Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling*, **216**, 47–59.

Bennie JJ, Wiltshire AJ, Joyce AN *et al.* (2010) Characterising inter-annual variation in the spatial pattern of thermal microclimate in a UK upland using a combined empirical-physical model. *Agricultural and Forest Meteorology*, **150**, 12–19.

Benton TG, Bryant DM, Cole L, Crick HQP (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology*, **39**, 673–687.

Bianchi FJJA, Booij CJH, Tscharntke T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 1715–1727.

Bokhorst S, Phoenix GK, Bjerke JW, Callaghan TV, Huyer-Brugman F, Berg MP (2012) Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. *Global Change Biology*, **18**, 1152–1162.

Brickle NW, Harper DGC, Aebischer NJ, Cockayne SH (2000) Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. *Journal of Applied Ecology*, **37**, 742–755.

Brooks DR, Bater JE, Clark SJ *et al.* (2012) Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *Journal of Applied Ecology*, **49**, 1009–1019.

Calladine J, Bray J (2012) The importance of altitude and aspect for breeding whinchats *Saxicola rubetra* in the uplands: limitations of the uplands as a refuge for a declining, formerly widespread species? *Bird Study*, **59**, 43–51.

Cannon RJC (1998) The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology*, **4**, 785–796.

Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, **44**, 29–40.

Denis D, Pierre JS, Van Baaren J, van Alphen JJM (2011) How temperature and habitat quality affect parasitoid lifetime reproductive success: a simulation study. *Ecological Modelling*, **222**, 1604–1613.

Denis D, Pierre JS, Van Baaren J, van Alphen JJM (2012) Physiological adaptations to climate change in pro-ovigenic parasitoids. *Journal of Theoretical Biology*, **309**, 67–77.

Dennis P, Thomas MB, Sotherton NW (1994) Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators. *Journal of Applied Ecology*, **31**, 361–370.

Diehl E, Sereda E, Wolters V, Birkhofer K (2013) Effects of predator specialization, host plant and climate on biological control of aphids by natural enemies: a meta-analysis. *Journal of Applied Ecology*, **50**, 262–270.

Dietrick EJ (1961) An improved backpack motorised fan for suction sampling of insects. *Journal of Economic Entomology*, **54**, 394–395.

Donald PF, Sanderson FJ, Burfield IJ, Van Bommel FPJ (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. *Agriculture, Ecosystems & Environment*, **116**, 189–196.

Dormann CF, Schweiger O, Arens P *et al.* (2008) Prediction uncertainty of environmental change effects on temperate European biodiversity. *Ecology Letters*, **11**, 235–244.

Dover JW (1991) The conservation of insects on arable farmland. In: *The Conservation of Insects and Their Habitats* (eds Collins NW, Thomas J), pp. 293–317, Royal Entomological Society of London, Symposium 15. Academic Press, London.

Duffield SJ, Aebischer NJ (1994) The effect of spatial scale of treatment with dimetho- ate on invertebrate population recovery in winter wheat. *Journal of Applied Ecology*, **31**, 263–281.

Easterling DR, Evans JL, Groisman PY, Karl TR, Kunkel KE, Ambenje P (2000) Ob- served variability and trends in extreme climate events: a brief review. *Bulletin of the American Meteorological Society*, **81**, 417–425.

Eglington SM, Pearce-Higgins JW (2012) Disentangling the relative importance of changes in climate and land-use Intensity in driving recent bird population trends. *PLoS One*, **7**, e30407.

Ewald JA, Aebischer NJ (1999) *Pesticide use, avian food resources and bird densities in Sussex*, Report number 296, pp. 1–111. Joint Nature Conservation Committee, Peterborough.

Ewald JA, Aebischer NJ (2000) Trends in pesticide use and efficacy during 26 years of changing agriculture in southern England. *Environmental Monitoring and Assess- ment*, **64**, 493–529.

Ewald JA, Potts GR, Aebischer NJ (2012) Restoration of a wild grey partridge shoot: a major development in the Sussex study, UK. *Animal Biodiversity and Conservation*, **35**, 363–369.

Fernandez-Triana J, Smith MA, Boudreault C, Goulet H, Hebert PDN, Smith AC, Roughley R (2011) A poorly known high-latitude parasitoid wasp community: unexpected diversity and dramatic changes through time. *PLoS One*, **6**, e23179.

Finlay KJ, Luck JE (2011) Response of the bird cherry-oat aphid (*Rhopalosiphum padi*) to climate change in relation to its pest status, vectoring potential and function in a crop-vector-virus pathosystem. *Agriculture, Ecosystems & Environment*, **144**, 405– 421.

Frampton GK, Van Den Brink PJ, Gould PJL (2000) Effects of spring drought and irri- gation on farmland arthropods in southern Britain. *Journal of Applied Ecology*, **37**, 865–883.

Geiger F, Bengtsson J, Berendse F *et al.* (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, **11**, 97–105.

Hart JD, Milsom TP, Fisher G, Wilkins V, Moreby SJ, Murray AWA, Robertson PA (2006) The relationship between yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. *Journal of Applied Ecol- ogy*, **43**, 81–91.

Hof AR, Bright PW (2010) The value of agri-environment schemes for macro-inverte- brate feeders: hedgehogs on arable farms in Britain. *Animal Conservation*, **13**, 467– 473.

Hoover JK, Newman JA (2004) Tritrophic interactions in the context of climate change: a model of grasses, cereal Aphids and their parasitoids. *Global Change Biol- ogy*, **10**, 1197–1208.

Hullé M, d'Acier AC, Bankhead-Dronnet S, Harrington R (2010) Aphids in the face of global changes. *Comptes Rendus Biologies*, **333**, 497–503.

Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*, **5**, 365– 374.

Klein Tank AMG, Können GP (2003) Trends in indices of daily temperature and pre- cipitation extremes in Europe, 1946-99. *Journal of Climate*, **16**, 3665–3680.

Legrand MA, Colinet H, Vernon P, Hance T (2004) Autumn, winter and spring dynamics of aphid *Sitobion avenae* and parasitoid *Aphidius rhopalosiphi* interactions. *Annals of Applied Biology*, **145**, 139–144.

Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. *BioScience*, **56**, 311–323.

Ma G, Rudolf VHW, Ma C-S (2014) Extreme temperature events alter demographic rates, relative fitness, and community structure. *Global Change Biology*, **21**, 1794– 1808.

Mair L, Thomas CD, Anderson BJ, Fox R, Botham M, Hill JK (2012) Temporal varia- tion in responses of species to four decades of climate warming. *Global Change Biol- ogy*, **18**, 2439–2447.

Mearns LO, Katz RW, Schneider SH (1984) Extreme high-temperature events: changes in their probabilities with changes in mean temperature. *Journal of Climate and Applied Meteorology*, **23**, 1601–1613.

Meehl GA, Karl T, Easterling DR *et al.* (2000) An introduction to trends in extreme weather and climate events: observations, socioeconomic impacts, terrestrial eco- logical impacts, and model projections. *Bulletin of the American Meteorological Soci- ety*, **81**, 413–416.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Biodiver- sity Synthesis*, pp. 1–56. World Resources Institute, Washington, DC.

Morecroft MD, Bealey CE, Howells O, Rennie S, Woiwod IP (2002) Effects of drought on contrasting insect and plant species in the UK in the mid-1990s. *Global Ecology and Biogeography*, **11**, 7–22.

Morecroft MD, Bealey CE, Beaumont DA *et al.* (2009) The UK Environmental Change Network: emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation*, **142**, 2814–2832.

Morecroft MD, Crick HQP, Duffield SJ, Macgregor NA (2012) Resilience to climate change: translating principles into practice. *Journal of Applied Ecology*, **49**, 547–551.

Morley NJ, Lewis JW (2014) Extreme climatic events and host–pathogen interactions: the impact of the 1976 drought in the UK. *Ecological Complexity*, **17**, 1–19.

Morsello SC, Beaudoin ALP, Groves RL, Nault BA, Kennedy GG (2010) The influence of temperature and precipitation on spring dispersal of *Frankliniella fusca* changes as the season progresses. *Entomologia Experimentalis et Applicata*, **134**, 260–271.

Mossman HL, Franco AMA, Dolman PM (2013) Implications of climate change for UK invertebrates (excluding butterflies and moths). In: *Terrestrial Biodiversity Cli- mate Change Impacts* (eds Morecroft MD, Speakman L), pp. 1–28. University of East Anglia, Norwich.

Musolin DL (2007) Insects in a warmer world: ecological, physiological and life-his- tory responses of true bugs (Heteroptera) to climate change. *Global Change Biology*, **13**, 1565–1585.

Newman JA (2005) Climate change and the fate of cereal aphids in Southern Britain. *Global Change Biology*, **11**, 940–944.

Newman JA, Gibson DJ, Parsons AJ, Thornley JHM (2003) How predictable are aphid population responses to elevated CO2? *Journal of Animal Ecology*, **72**, 556–566.

Oliver T, Roy DB, Hill JK, Brereton T, Thomas CD (2010) Heterogeneous landscapes promote population stability. *Ecology Letters*, **13**, 473–484.

Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, **81**, 443–450.

Perry M, Hollis D (2005) The generation of monthly gridded datasets for a range of climatic variables over the UK. *International Journal of Climatology*, **25**, 1041–1054.

Peterson TC, Stott PA, Herring S (2012) Explaining extreme events of 2011 from a cli- mate perspective. *Bulletin of the American Meteorological Society*, **93**, 1041–1067.

Pimentel D, Wilson C, McCullum C *et al.* (1997) Economic and environmental bene- fits of biodiversity. *BioScience*, **47**, 747–757.

Potts GR (1986) *The Partridge: Pesticides, Predation and Conservation*, pp. 1–274. Collins, London.

Potts GR (2012) *Partridges. Countryside Barometer*, pp. 1–465. HarperCollins Publishers Limited, London.

Potts GR, Ewald JA, Aebischer NJ (2010) Long-term changes in the flora of the cereal ecosystem on the Sussex Downs, England, focusing on the years 1968-2005. *Journal of Applied Ecology*, **47**, 215–226.

Ricketts TH, Regetz J, Steffan-Dewenter I *et al.* (2008) Landscape effects on crop polli- nation services: are there general patterns? *Ecology Letters*, **11**, 499–515.

Robinet C, Roques A (2010) Direct impacts of recent climate warming on insect popu- lations. *Integrative Zoology*, **5**, 132–142.

Rosenzweig C, Iglesias A, Yang XB, Epstein PR, Chivian E (2001) Climate change and extreme weather events – implications for food production, plant diseases and pests. *Global Change & Human Health*, **2**, 90–104.

Scheffer M, Carpenter S (2003) Catastrophic regime shifts in ecosystems: linking the- ory to observation. *Trends in Ecology & Evolution*, **18**, 648–656.

Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete sam- ples). *Biometrika*, **52**, 591–611.

Shaw MW, Bearchell SJ, Fitt BDL, Fraaije BA (2008) Long-term relationships between environment and abundance in wheat of *Phaeosphaeria nodorum* and *Mycosphaerella graminicola*. *New Phytologist*, **177**, 229–238.

Sotherton NW (1991) Conservation headlands: a practical combination of intensive cereal farming and conservation. In: *The Ecology of Temperate Cereal Fields* (eds Fir- bank LG, Carter N, Derbyshire JF, Potts GR), pp. 373–397. Blackwell Scientific Publications, Oxford.

Stige LC, Chan KS, Zhang ZB, Frank D, Stenseth NC (2007) Thousand-year-long Chinese time series reveals climatic forcing of decadal locust dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 16188–16193.

Stireman JO, Dyer LA, Janzen DH *et al.* (2005) Climatic unpredictability and para- sitism of caterpillars: implications of global warming. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 17384–17387.

Strand O (1977) Multichannel complex maximum entropy (autoregressive) spectral analysis. *IEEE Transactions on Automatic Control*, **22**, 634–640.

Suggitt J, Wilson RJ, August TA *et al.* (2014) *Climate change refugia for the flora and fauna of England*, 202 pp., Natural England Commissioned Reports NECR162. Natural England, York.

Umina PA, Weeks AR, Kearney MR, McKechnie SW, Hoffmann AA (2005) A rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science*, **308**, 691–693.

Villalpando SN, Williams RS, Norby RJ (2009) Elevated air temperature alters an old-field insect community in a multifactor climate change experiment. *Global Change Biology*, **15**, 930–942.

Weiss SB, Murphy DD, Ehrlich PR, Metzler CF (1993) Adult emergence phenology in checkerspot butterflies: the effects of macroclimate, topoclimate, and population history. *Oecologia*, **96**, 261–270.

Western AW, Grayson RB, Blöschl G, Willgoose GR, McMahon TA (1999) Observed spatial organization of soil moisture and its relation to terrain indices. *Water Resources Research*, **35**, 797–810.

Winspear R, Grice P, Peach W *et al.* (2010) The development of farmland bird packages for arable farmers in England. *Aspects of Applied Biology*, **100**, 347–352.

Zaller JG, Simmer L, Santer N *et al.* (2014) Future rainfall variations reduce abundances of aboveground arthropods in model agroecosystems with different soil types. *Frontiers in Environmental Science*, **2**, 44.

Zhou ZS, Guo JY, Min L, Wan FH (2011) Effect of short-term high temperature stress on the development and fecundity of *Ophraella communa* (Coleoptera: Chrysomelidae). *Biocontrol Science and Technology*, **21**, 809–819.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. (a) Spectral density curves (logarithms) vs. frequency (year^{-1}) for temperature and invertebrate abundance. (b) Spectral density curves (logarithms) vs. frequency (year^{-1}) for rainfall and invertebrate abundance.
Figure S2. (a–c) Coherence and phase spectra for temperature paired with invertebrate abundance.
Figure S3. (a–c) Coherence and phase spectra for rainfall paired with invertebrate abundance.