

# Extreme temperature events alter demographic rates, relative fitness, and community structure

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## Abstract

The frequency and magnitude of extreme events are predicted to increase under future climate change. Despite recent advancements, we still lack a detailed understanding of how changes in the frequency and amplitude of extreme climate events are linked to the temporal and spatial structure of natural communities. To answer this question, we used a combination of laboratory experiments, field experiments, and analysis of multi-year field observations to reveal the effects of extreme high temperature events on the demographic rates and relative dominance of three co-occurrence aphid species which differ in their transmission efficiency of different agricultural pathogens. We then linked the geographical shift in their relative dominance to frequent extreme high temperatures through a meta-analysis. We found that both frequency and amplitude of extreme high temperatures altered demographic rates of species. However, these effects were species-specific. Increasing the frequency and amplitude of extreme temperature events altered which species had the highest fitness. Importantly, this change in relative fitness of species was consistent with significant changes in the relative dominance of species in natural communities in a 1 year long field heating experiment and 6 year long field survey of natural populations. Finally, at a global spatial scale, we found the same relationship between relative abundance of species and frequency of extreme temperatures. Together, our results indicate that changes in frequency and amplitude of extreme high temperatures can alter the temporal and spatial structure of natural communities, and that these changes are driven by asymmetric effects of high temperatures on the demographic rates and fitness of species. They also highlight the importance of understanding how extreme events affect the life-history of species for predicting the impacts of climate change at the individual and community level, and emphasize the importance of using a broad range of approaches when studying climate change.

**Keywords:** climate change, community structure, extreme climatic event, heat stress, heat waves, insects, relative dominance, temperature extremes

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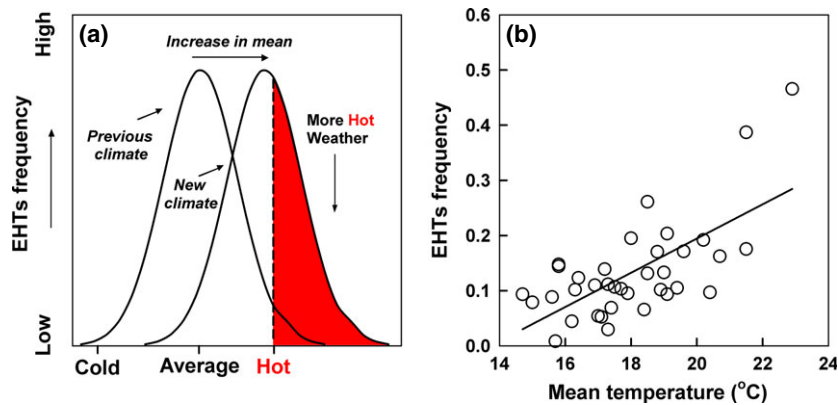
## Introduction

The increase in frequency and severity of extreme climate events (heat waves, cold snaps, droughts, floods, etc.) has become an important topic for the global change agenda and ecological research. Observations and climate projections indicate a continuing increase in average surface temperatures (IPCC, 2013). Importantly, even small changes in average temperature can dramatically increase the frequency and magnitude of extreme high temperature events (EHTs) (Fig. 1). Such EHTs have already caused a series of severe social, economic, and ecological problems (Easterling *et al.*, 2000; Parmesan *et al.*, 2000; Jiguet *et al.*, 2011) and are expected to increase in intensity and in frequency with the continuation of climate warming (Easterling *et al.*,

2000; Meehl & Tebaldi, 2004; Hansen *et al.*, 2012; IPCC, 2013). Yet, previous studies have largely focused on how changes in mean temperature affect populations and community structure while neglecting changes in EHTs (reviewed in Easterling *et al.*, 2000; Jiguet *et al.*, 2011; Smith, 2011a; Lloret *et al.*, 2012; Reyer *et al.*, 2013). Consequently, we still have a poor understanding of when EHTs influence the structure of natural communities and what the underlying mechanisms are.

Recent theory and empirical work suggest that extreme temperatures are often more important for fitness and demographic rates of species than mean temperature. For instance, important fitness components such as critical thermal maximum and thermal optimum are more closely related to the variation in temperature than to the mean (Clusella-Trullas *et al.*, 2011). As a consequence, studies based on constant temperatures often overestimate optimal temperature, thermal

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**Fig. 1** (a) Theoretical relationship between the frequency of extreme high temperatures (EHTs) and the increases in mean temperature assuming a normal temperature distribution [Source: adapted from IPCC (2013)]. (b) The relationship between the mean temperature and EHTs frequency (number of days with maximum temperatures  $>30^{\circ}\text{C}$  during  $\sim 2$  months before winter wheat harvest) across global areas where cereal aphids infest [Linear regression (solid line):  $y = -0.43 - 0.03x$ ,  $R^2 = 0.448$ ,  $P < 0.001$ ]. Data collected from Table 1.

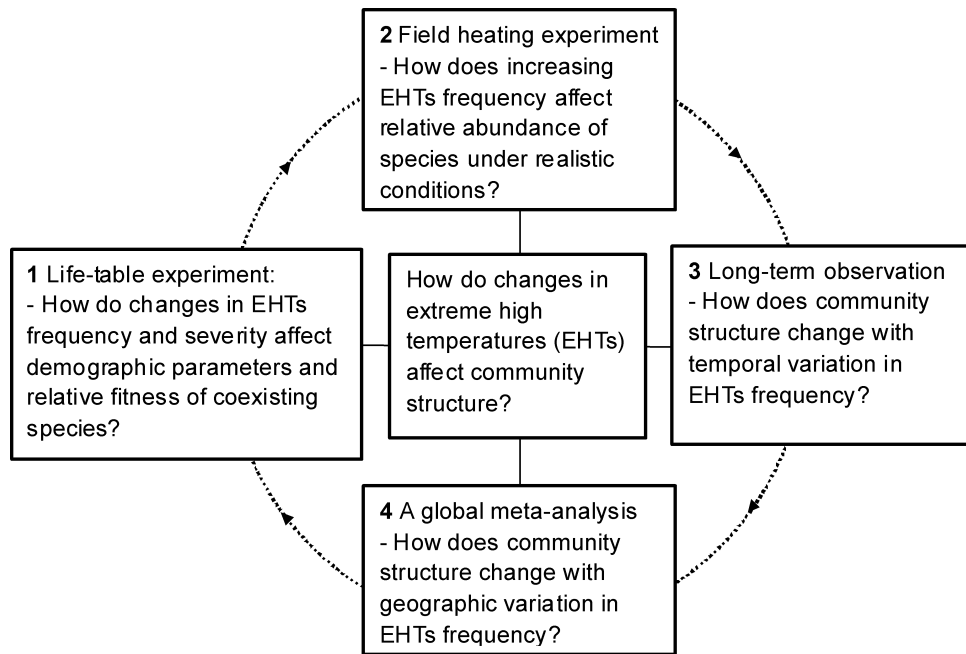
safety margins (Clusella-Trullas *et al.*, 2011), and temperature-dependent fitness in animals (Ragland & Kingsolver, 2008; Paaijmans *et al.*, 2010; Clusella-Trullas *et al.*, 2011; Lyons *et al.*, 2013) and plants (reviewed in Reyer *et al.*, 2013). EHTs could therefore have significant negative impacts on the fitness of species even if the mean temperature is still within a suitable (or even optimal) temperature range.

While these studies suggest that EHTs can influence the fitness of species, EHTs will only affect the structure of communities (i.e. relative abundances of species) when they differentially affect the fitness of coexisting species. Such species-specific responses require that organisms differ in how their demographic rates and fitness are affected by high temperatures and that EHTs push the temperature above a threshold level at which these differences become significant. Hence, variation in the amplitude of EHTs should determine when and how EHTs alter community structure. In addition, these EHT episodes have to be frequent enough for fitness differences to manifest. For instance, exposing the aphid *Metopolophium dirhodum* to an extreme high temperature for a single day had no consequences, but its performances were greatly decreased when this treatment was repeated for several successive days (Ma *et al.*, 2004a,b). Thus, when and how EHTs alter community structure should depend on the interactive effects of their frequency and amplitude on the relative fitness of coexisting species.

While increasing evidence indicates that EHTs have the potential to alter animal and plant communities (Smith, 2011b; Reyer *et al.*, 2013; Wernberg *et al.*, 2013), studies examining the effects of changes in the frequency and amplitude of EHTs are rare (Kreyling & Beier, 2013). The few existing studies that manipulated

the frequency and amplitude of EHTs clearly demonstrate that variation in the frequency and amplitude of EHTs has the potential to alter communities, but they were restricted to laboratory systems and did not measure which demographic rates were affected and whether these effects were species-specific (Gillespie *et al.*, 2012; Sentis *et al.*, 2013). Thus, we still lack a detailed mechanistic understanding of how relative differences in demographic rates and fitness of coexisting species are linked to changes in EHTs and the temporal and spatial structure of natural communities.

To address this conceptual gap, we used a combination of laboratory and field experiments, analysis of field observations, and a meta-analysis to determine how the frequency and severity of EHTs influence the structure of natural communities (Fig. 2). In particular, we used a guild of aphid species to test the hypothesis that changes in the amplitude and frequency of EHTs differentially affect demographic rates (and thus population growth rates) of coexisting species and thereby alter relative abundances of species across temporal and spatial scales. First, we used a laboratory experiment to test how intensity and frequency of EHTs affected demographic rates and relative fitness of species. Second, we conducted a field study, a 6 year field investigation, and a meta-analysis to determine how EHT frequency is correlated with changes in the relative dominance of these species across time and space in complex natural communities and whether this corresponds to observed changes in relative fitness across species. This combination of controlled experiments and field observations overcomes limitations of previous approaches (Kreyling & Beier, 2013; Reyer *et al.*, 2013) and allowed us to explicitly link fitness differences among species to variation in the frequency



**Fig. 2** Four complementary approaches used in this study to determine how changes in extreme temperature events (EHTs) will affect structure of natural communities.

and amplitude of EHTs and the structure of natural communities.

## Materials and methods

### Study system

To examine the effects of EHTs on natural communities, we used a guild of three coexisting aphid species as a model system: *Sitobion avenae*, *Schizaphis graminum*, and *Rhopalosiphum padi*. These species coexist in our local study site where they face extreme summer temperatures during the growing season in their natural habitat, and these temperature extremes are predicted to increase in both intensity and frequency in this geographic region (Liu *et al.*, 2004; Zhang *et al.*, 2008). The species have short life-cycles and are consequently highly vulnerable to the changes in short-term EHTs (Danks, 2006). Their field population dynamics and outbreaks are known to be temperature-dependent (Acreman & Dixon, 1989; De Barro & Maelzer, 1993; Ma, 2000; Asin & Pons, 2001). Importantly, the three focal species tolerate different constant high temperatures (Asin & Pons, 2001; Merrill *et al.*, 2009; Tofangsazi *et al.*, 2010), suggesting that changes in EHTs could alter their relative abundance in the community. Finally, while all these aphid species are important pest species causing severe yield losses, they differ in their preferred infestation site on cereals (Dean, 1974; Dixon, 1977; Qureshi & Michaud, 2005a) and their ability to transmit Barley Yellow Dwarf Virus (BYDV) (Zhang *et al.*, 1983; Seabloom *et al.*, 2009, 2013), one of the most widely distributed viral disease of cereals. Thus, changes in the relative abundances of these species are likely to have important, ecosystem wide consequences.

### Effects of EHTs on demographic rates and fitness: laboratory experiment

**Experimental design.** We used a factorial design that independently manipulated the frequency and amplitude (peak temperature) of EHTs in conjunction with a modified life-table experiment to test how the frequency and intensity of EHTs affect demographic parameters and population growth of the three aphid species. The resulting four EHT regimes were: LL: low intensity-low frequency with one peak of 34 °C every 2 days, LH: low intensity-high frequency with one peak of 34 °C daily, HL: high intensity-low frequency with one peak of 38 °C every 2 days, and HH: high intensity-high frequency with one peak of 38 °C daily (Figure S1). We selected these treatments for several reasons. 34 °C was a frequently recorded high temperature in our study region (see Figure S2). The maximum temperature observed during aphid infestation in our study area in 2013 was 37.5 °C (see Figure S3), and climate models for our study site region predict that the extreme maximum temperature will increase by 1.27 °C by the end of this century (Liu *et al.*, 2004). Thus, 38 °C is an extreme temperature that naturally occurs in our field sites and is expected to be more frequent in the future. Finally, we used our two frequency treatments for EHTs (0.5 and 1.0 EHT per day) based on climate change models which also predict that the frequency of extreme heat events in China will increase by more than five times in the future (2071–2100) (Zhang *et al.*, 2008). Based on current frequencies of EHTs (see Table S1), this would result in an average frequency of EHTs exceeding 0.5 in our study region. Thus, our design follows previous studies (Gillespie *et al.*, 2012; Sentis *et al.*, 2013) by using two typical intensities and two frequencies of EHTs in our

experiment which represent possible future climate conditions in our study area.

Temperature was kept constant at 22 °C on days without a peak. On days including a peak, temperature started to increase linearly at 08:00 hours, reached and stayed at the maximum (34 or 38 °C) from 12:00 to 13:00 hours, and then decreased to 22 °C by 16:00 hours. Temperature was kept constant at 22 °C for the rest of the day. While this inevitably lead to small differences in daily mean temperatures of the four regimes (23.3, 24.4, 23.6, and 25.3 °C respectively), keeping minimum temperatures constant eliminated the confounding effects of different minimum temperatures that occur in our study system (Zhao *et al.*, 2014). In addition, these differences were very small and daily means were below the range of upper critical mean temperatures for population growth [intrinsic rate of increase ( $r_m$ ) > 0] recorded for all three aphid species in different regions, i.e. 25–26.5 °C for *S. avenae*, 25–27 °C for *S. graminum* and 27–28.5 °C for *R. padi* (Table S2). The small differences in mean temperatures we used are therefore unlikely to alter the relative abundance of these species, while changing other aspects of the temperature regime (e.g., reducing minimum temperatures) are known to alter life-history traits and thereby lead to confounding effects of EHT treatments (see Discussion).

**Experimental manipulation.** We ran the life-table experiment for one generation in climatic chambers (PQX, Laifu Ltd., Ningbo, China; accuracy: 1 °C). The three species were tested separately to eliminate possible direct or indirect interspecific competition. For each species, 30 newborn aphids (0–6 h old) were tested for their whole life from birth to death. All aphids were obtained from stock colonies reared on 5–20 cm high winter wheat seedlings (CA0045) in screen cages (60 × 60 × 60 cm) at a constant temperature of 20 °C at 50–70% relative humidity and 16 : 8 light : dark photoperiod. These aphids were placed into six translucent clip-cages (diameter = 35 mm, with two window screens for ventilation) in groups of five. The aphids in each clip-cage were fed on one fresh leaf (clamped by the clip-cage) of wheat seedlings. Nymphal development and survival were checked twice per day at 07:00 and 19:00 hours, respectively. Different instar nymphs were determined by their exuvia and exuvia and any dead nymphs were removed from the clip-cage. Reproduction and survival of adults were observed once a day at 19:00 hours, and dead adults and new offspring were removed. After each observation, the focal aphids from a clip-cage were placed into a new one and returned to climatic chambers. The aphids were transferred to new seedlings weekly. Within each chamber, photoperiod was 16L: 8D, with light from 06:00 to 22:00 and darkness from 22:00 to 06:00, and relative humidity was the same to their rearing condition.

**Response variables.** Proportional survival, developmental rate, lifetime fecundity, adult longevity, and lifespan were used as demographic variables, and the intrinsic rate of increase,  $r_m$ , was used as a measure of relative fitness and population growth. For each variable, we calculated cage means by averaging across all five individuals within a cage. Proportional survival was the number of alive nymphs that developed into

adult stage. Developmental rate was given by the number of days until nymphs reached the adult stage. Lifetime fecundity (no. offspring/female) and adult longevity were calculated as the total number of offspring and days from adult emergence until death respectively. Lifespan was given by the number of days from newborn to death.  $r_m$  was calculated from the life-table with Pop Tools 3.2.5 according to Hood (2011).

**Statistical analysis.** The effects of changes in EHTs on each response variable were analyzed using a 2 × 2 × 3 factorial design, with frequency and amplitude of EHTs and species identity as fixed factors. The effects on developmental rate, lifetime fecundity, adult longevity, lifespan and  $r_m$  of different species were analyzed with ANOVAs and normally distributed errors using the GLM procedure in SAS V8. Proportional survival was analyzed with a generalized linear mixed model (GLM) with binomial error distribution using the GENMOD procedure. For each variable, the levels of significant differences between different species under the four regimes were compared using planned contrasts based on least-square means.

#### *Effects of EHTs on the structure of natural communities: field experiment*

**Experimental design.** To reveal the effects of different EHT frequency on the population dynamics and relative dominance of the three species under natural climate conditions and species interactions (e.g., competition, predation, parasitism), a field study was conducted in winter wheat fields (ZM9023) in Wuhan (30°28' N, 114°25' E), Hubei province, China, from April 1 to May 31, 2013. Each of five randomly selected plots was divided into two 2 × 2 m paired subplots and one subplot was exposed to warming and the other to a control (ambient) treatment. In the warming treatment, we followed previous studies (Dollery *et al.*, 2006; Fujimura *et al.*, 2008; Villalpando *et al.*, 2009) by using open-top chambers (height: 1.0 m; area: 3.5 m<sup>2</sup>) to simulate an increase in average surface temperature ( $\approx$  ambient + 1.5 ± 0.5 °C across years). Natural enemies were frequently observed to enter (and reproduce in) the open-top chambers as well as the ambient treatment. As expected (Fig. 1a), the warming treatment elevated daily maximum temperatures (Figure S2a) and thereby increased EHT frequency (the number of days with daily maximum temperatures > 30 °C during aphid infestation) by ~ 60% (Figure S2b). Thus, the ambient and warming treatments represented low EHT frequency (0.361) and high EHT frequency (0.508) conditions, respectively. The 30 °C was selected as the threshold temperature because field aphid populations of *S. avenae* typically collapse when daily maximum temperatures exceed this value (Castanera, 1986). Temperatures within the ambient and warming treatments were recorded every 20 min (Hobo Pro Ltd., Bourne, MA, USA; accuracy: 0.1 °C). Importantly, differences in mean temperatures between the ambient and warming treatments were small (20.0 ± 4.6 °C vs. 21.5 ± 4.7 °C, respectively) and well below the upper critical mean temperatures for population growth of all species (Table S2).

**Experimental manipulation.** The winter wheat was sown in late October 2012. When the winter wheat revived from overwintering (early March), it was naturally colonized by alate (winged) aphid morphs. After this colonization period, we placed the open-top chambers on the subplots in warming (high frequency) treatment. In both ambient and warming treatments, the aphids came just from natural colonization and subsequent reproduction, and no aphid was added. The original abundances (adults per tiller) of *S. avenae*, *S. graminum* and *R. padi* were 0.32, 0.04, 0.12 (ambient), and 0.04, 0.0, 0.14 (warming), respectively. Within each subplot, number of individuals per tiller of each of the three aphid species was recorded on 10 tillers (belonging to ten different wheat plants) every 3–4 days from April 1st to May 31st (~5–8 generations for each species).

**Statistical analysis.** We first examined the effect of EHT frequency on the relative dominance of each species using a multivariate permutation test PERMANOVA (Anderson, 2001) with the average proportional abundance of the three species as dependent variable and ambient (low frequency) and warming (high frequency) conditions as fixed effect and plot as random effect. The community matrix was based on proportional abundances of species to account for any potential differences in total abundance across plots. The analysis was based on Bray–Curtis dissimilarity index and 9 999 permutations. Average proportional abundance was based on all observations in a subplot during April–May where at least one individual of a species was observed. To gain further insight into the patterns driving shifts in community structure, we examined species-specific responses to EHT frequency using a one-way ANOVA with species as fixed effect, the difference in average proportional abundance (high frequency–low frequency) between subplots as dependent variable and plot as random effect. This allowed us to determine whether the relative abundance of a species changed significantly with treatments, and whether this change was species-specific.

#### *Effect of EHTs on the structure of natural communities: field observation*

**Experimental design.** To reveal how variation in EHT frequency between years would affect the relative dominance of the three species in natural communities, a 6 year field observation was conducted in the same location during 2008–2013. Five monitoring plots (2 × 2 m) were randomly selected in each year. Within each plot, we recorded the number of aphids on each of 10 tillers every 3–4 days, using the same method described in the field study (see above). For each species, we calculated aphid abundance and proportional abundance per year as the mean aphid number (cumulative per tiller) and their proportion within each of the five plots. Daily mean and maximum temperatures were recorded (Hobo Pro Ltd.; accuracy: 0.1 °C) during the growing season of winter wheat. Here, a hot day was again defined as a day where the maximum day temperature exceeded 30 °C. We focused on frequency of a much lower threshold (30 °C) than in the laboratory experiment (34 and

38 °C) because the air temperatures (which we recorded in field) were found to be much lower than the temperatures on wheat plant (Pararajasingham & Hunt, 1991; Asin & Pons, 2001; Inagaki & Nachit, 2008). The number of hot days during April and May were used for calculating EHT frequency because the aphids mainly infested fields during this period. During 2008–2013, the EHT frequency ranged from 0.066 to 0.164 and the average temperatures from 18.6 °C to 21.1 °C (Table S1).

**Statistical analysis.** To determine whether changes in EHT frequency influence community structure, we used PERMANOVA with frequency of EHT events within a year as fixed effect. The community matrix was again based on proportional abundances of species to account for any potential differences in total abundance across years and plots. Statistics are based on Bray–Curtis distances and 9 999 permutations. We then determined the effect of EHT frequency on proportional abundance of each species using GLM with binomial distributed error terms with the GENMOD procedure in SAS.

#### *Linking EHT frequency and community structure on a global scale: a meta-analysis*

**Relative dominance.** We used a meta-analysis to reveal whether and how the frequency of EHTs affects the relative dominance of the three aphid species at a large geographical scale. Data for their relative dominance worldwide were collected by using the following search engines: Google, CAB Abstract, and Web of Knowledge, with the scientific names of at least two species (because not all areas have all three species) as key words. Previous studies indicate that, although the relative abundances of the three species could vary in some years, their relative dominance is typically stable over long time periods for a given area (Carter *et al.*, 1982; Huang *et al.*, 1996; Leslie *et al.*, 2009). Therefore, we only included studies based only on long-term observations that fulfilled at least one of the following criteria: (i) successive observations, including field investigations (≥4 successive growing seasons), literature reviews or the data on official websites of extension services and research institutes; (ii) nonsuccessive observations, including at least four different growing-season observations in the same areas where each observation showed the same relative dominances of the three species. Data collected from cold areas, such as Sweden and Finland, were excluded because the presence of the primary host (*Prunus padus*) for overwintering of *R. padi* may lead to more overwintering survival in this species and consequently higher abundance (relative dominance) than the others in these areas (Rautapaa, 1976; Chiverton, 1986). Studies on the aphid abundance only based on migration data (suction, water, sticky traps, etc.) or autumn/overwintering number were also excluded because these data might not represent the aphid density in spring and early summer. We then determined the relative dominance of the three species for each area using three groups: 3 = dominant, 2 = subdominant, 1 = least dominant (no record or restrict distributed according to the Distribution Maps of Plant Pests, CABI). We only used one randomly selected

representative location to represent the relative dominance of the three species in each area to avoid pseudo replication.

**Frequency of EHTs.** For each location, we determined the mean temperature and number of hot days with daytime maximum temperature  $>30$  °C during main aphid infestation time period to calculate the frequency of EHTs. Data for daily maximum and mean temperatures for each location were collected from China Meteorological Data Sharing Service System (CMDS) (<http://cdc.cma.gov.cn>). Overall, each meteorological data point was chosen to be as close as possible to the study site (no more than  $1^\circ$  latitude  $\times$  longitude). For each location, the data for 10 years before the latest literatures were used for calculating the frequency of EHTs and mean temperatures. The 10 years were selected as the typical climatic conditions because the data for relative dominance in most locations were within this time scale. For some locations (9/36 of the total sites) where temperature data could not be obtained from CMDS, data for daily maximum and mean temperatures were collected from Weather Underground (<http://www.wunderground.com>). In field conditions, the aphid density of all three species increased rapidly before wheat maturity. Therefore, the 2 months before wheat harvest were selected as the main time period for aphid infestation. The wheat harvest time for each location was determined according to World Wheat Harvesting Calendar (International Wheat Council), Usual Planting and Harvesting Dates for U.S. Field Crops (USDA) and Australian Wheat (AWB). The relative dominance of the three aphid species in different areas with various latitude, frequency of EHTs, and mean temperatures were shown in Table 1.

**Statistical analysis.** We analyzed the relationships between relative dominance of the three species and the frequency of EHTs for various areas using ordinal regression. Because EHT frequency and mean temperature are closely correlated (Fig. 1), we included mean temperature in the full model to separate the effects of EHT frequency from change in mean temperature. Significance of mean temperature and EHT effects were determined with likelihood ratio test and we only report partial coefficients and significance values that control for the other main effect. We used the package 'ordinal' in R, with probit-link function and flexible thresholds. All assumptions of the model were met.

## Results

### *Effects of EHTs on demographic rates and fitness: laboratory experiment*

The results of ANOVAs and GENMOD analyses for the effects of intensity, frequency and species on proportional survival, developmental rate, lifetime fecundity, adult longevity, lifespan and  $r_m$  of the aphids were given in Table 2. Overall, intensity and frequency had significant effects on almost all demographic rates and fitness of species, but the significant interactions with species indicated that these effects were typically spe-

cies specific. These interactions were generally driven by a switch in the relative ranking of fitness and demographic rates of *S. graminum* and *R. padi* with changing in EHT intensity. In low intensity–low frequency treatments, the three species had little difference in nymphal survival ( $\chi^2_{2, 15} = 1.12$ ,  $P = 0.5718$ ) and adult longevity ( $F_{2,17} = 2.06$ ,  $P = 0.1618$ ), but *S. graminum* had significant higher developmental rate ( $F_{2,17} = 43.67$ ,  $P < 0.0001$ ) and lifetime fecundity ( $F_{2,17} = 9.45$ ,  $P = 0.0022$ ) than *S. avenae* and *R. padi*. Although *S. graminum* had the shortest lifespan ( $F_{2,17} = 3.09$ ,  $P = 0.0754$ ), it still had a significant higher fitness (i.e. intrinsic rate of increase,  $r_m$ ) ( $F_{2,17} = 25.18$ ,  $P < 0.0001$ ) than the other species (Fig. 3). In the low intensity–high frequency treatment, there was no significant difference between these species on nymphal survival ( $\chi^2 = 0.63$ ,  $df = 2$ ,  $15$ ;  $P = 0.7289$ ), lifetime fecundity ( $F_{2,17} = 2.23$ ,  $P = 0.1419$ ), and lifespan ( $F_{2,17} = 2.93$ ,  $P = 0.0841$ ). *S. graminum* had significant higher developmental rate ( $F_{2,17} = 27.26$ ,  $P < 0.0001$ ). Despite *R. padi* having the longest adult longevity ( $F_{2,17} = 5.15$ ,  $P = 0.0198$ ), *S. graminum* still had the highest fitness ( $r_m$ ) ( $F_{2,17} = 5.55$ ,  $P = 0.0157$ ).

However, the pattern changed dramatically in the high intensity–low frequency treatment. Now, *R. padi* had a significant higher developmental rate ( $F_{2,17} = 30.81$ ,  $P < 0.0001$ ), lifetime fecundity ( $F_{2,17} = 8.17$ ,  $P = 0.0040$ ), nymphal survival ( $\chi^2 = 4.89$ ,  $df = 2$ ,  $15$ ;  $P = 0.0866$ ), and adult longevity ( $F_{2,17} = 5.38$ ,  $P = 0.0173$ ) than *S. avenae* and *S. graminum*, but there was no significant difference for lifespan between these species ( $F_{2,17} = 2.15$ ,  $P = 0.1507$ ). Consequently, *R. padi* had also the highest fitness ( $r_m$ ) ( $F_{2,16} = 7.87$ ,  $P = 0.0051$ ), reversing the relative fitness difference observed in both low intensity treatments (Fig. 3).

A similar pattern was observed in high intensity–high frequency treatment. *R. padi* had again significant higher lifetime fecundity ( $F_{2,14} = 29.5$ ,  $P < 0.0001$ ), adult longevity ( $F_{2,14} = 31.09$ ,  $P < 0.0001$ ), nymphal survival ( $\chi^2 = 8.29$ ,  $df = 2$ ,  $15$ ;  $P = 0.0159$ ), and developmental rate ( $F_{2,14} = 15.96$ ,  $P = 0.0004$ ) than the other two species, but now it also had the highest lifespan ( $F_{2,17} = 2.91$ ,  $P = 0.0858$ ). Thus, *R. padi* had even higher relative fitness ( $r_m$ ) ( $F_{2,11} = 15.98$ ,  $P = 0.0011$ ) compared to the other two species (Fig. 3).

### *Effect of EHTs on the structure of natural communities: field experiment*

The aphid community structure differed significantly between high and low EHT frequency treatments (PERMANOVA,  $F_{1,9} = 5.0$ ,  $P = 0.035$ ) but not plots ( $F_{4,9} = 2.9$ ,  $P = 0.138$ ) (Fig. 4a). This change was driven by a species-specific response to change in EHT frequency (species  $\times$  frequency:  $F_{2,6.87} = 7.97$ ,  $P = 0.0162$ ). The

**Table 1** The relative dominance of the three aphid (SA = *S. avenae*, SG = *S. graminum*, RP = *R. padi*) species in different areas with various average temperatures and hot-day frequencies during infestation periods.  $T_{\text{mean}}$  and F\_HIDs represent average temperature and frequency of EHTs during the main time period for aphid infestation, respectively

Country/region	Location	Relative dominance			Year	Reference	$T_{\text{mean}}$	F_HIDs
		SA	SG	RP				
Western Canada	Saskatoon, SK (52°08' N, 106°41' W)	3	1	2	1974	Gill, 1975	17.7	0.103
	Winnipeg, MB (49°53' N, 97°08' W)	3	1	2	1984–1987 –2011	Haber, 1987 Gavloski & Meers, 2011	19.1	0.094
Northwestern US	Spokane, WA (47°39' N, 117°25' W)	3	2	1	1988	Clement <i>et al.</i> , 1990	15.0	0.079
	Fresno, CA (36°45' N, 119°46' W)	1	2	3	1996–2000 –2013 –2006	Clement <i>et al.</i> , 2004 Washington State University, 2013 Godfrey <i>et al.</i> , 2006	18.5	0.261
Central US	Lincoln, NE (40°48' N, 96°40' W)	1	3	2	–2005	Hein <i>et al.</i> , 2005	16.4	0.123
	Denver, CO (39°44' N, 39°44' N)	1	3	2	2002–2006 2002–2006	Giles <i>et al.</i> , 2008 Giles <i>et al.</i> , 2008	15.8	0.144
Southern US	Great Bend, KS (38°21' N, 98°45' W)	1	3	2	2002–2006	Giles <i>et al.</i> , 2008	14.7	0.093
	Oklahoma City, OK (35°28' N, 97°32' W)	1	3	2	2002–2006	Giles <i>et al.</i> , 2008	17.9	0.095
Eastren US	Amarillo, TX (35°11' N, 101°50' W)	1	3	2	–1997	Hoelscher <i>et al.</i> , 1997	15.8	0.148
	Blackville, SC (33°21' N, 81°16' W)	3	1	2	2002–2006 1990–1999	Giles <i>et al.</i> , 2008 Chapin <i>et al.</i> , 2001	19.4	0.105
Southern Brazil	Richmond, VA (37°32' N, 77°25' W)	3	1	2	–2006 –2009	Flanders <i>et al.</i> , 2006 Herbert <i>et al.</i> , 2009	16.9	0.110
	Santa Maria, RS (29°41' S, 53°48' W)	1	2	3	1997–1998 2000 2009–2010 –2013 –1983	Ronquim <i>et al.</i> , 2004 Silva <i>et al.</i> , 2004 Parizoto <i>et al.</i> , 2013 Savaris <i>et al.</i> , 2013 Arriaga, 1983	21.5	0.175
Central Chile	Santiago (33°27' S, 70°40' W)	3	2	1	–1983	Arriaga, 1983	15.6	0.089
Central Argentina	Neuquén (38°57' S, 68°03' W)	2	3	1	–1983	Arriaga, 1983	17.3	0.111
	Harpenden (51°49' N, 0°21' E)	3	1	2	1942–1980 1996 –2007 –1990	Carter <i>et al.</i> , 1982; Collins <i>et al.</i> , 2002 Rothamsted Insect Survey, 2007 Poehling <i>et al.</i> , 1991	15.7	0.008
North Germany	Göttingen (51°32' N, 9°56' E)	3	1	2	1993–2002	Berhan-Mamo, 2003	17.3	0.030

Table 1 (continued)

Country/region	Location	Relative dominance			Year	Reference	$T_{\text{mean}}$	F_HDs
		SA	SG	RP				
Western France	Rennes (48°06' N, 1°40' W)	3	1	2	2001–2003 2008	Thies <i>et al.</i> , 2005 Gagic <i>et al.</i> , 2012	17.0	0.054
Northwestern Czech	Prague (50°05' N, 14°25' E)	3	1	2	1977–1982 1984–1985	Dedryver & Pietro, 1986 Henry, 1986	17.1	0.052
Western Bulgaria	Sofia (42°42' N, 23°20' E)	3	2	1	1956–1975 1987–2005	Stary, 1976 Leslie <i>et al.</i> , 2009;	17.4	0.069
Serbia	Belgrade (44°49' N, 20°28' E)	3	1	2	1996–1999 2006–2010	Krsteva & Bakrdzhieva, 2000 Maneva <i>et al.</i> , 2012	19.0	0.133
Northeastern Italy	Udine (46°04' N, 13°14' E)	3	1	2	2000–2004 2004–2006	Stamenkovic & Petrovic-Obradovic, 2005 Tomanovic <i>et al.</i> , 2008	20.4	0.097
Central Spain	Madrid (40°23' N, 3°43' E)	3	1	2	1983–2002	Coceano <i>et al.</i> , 2009	18.0	0.195
North China	Tianjin (39°08' N, 117°11' E)	3	2	1	1980–1982 1980–1985	Castanera, 1986; Castanera, 1986;	17.5	0.107
Northwestern China	Anyang, HN (36°06' N, 114°20' E)	3	1	2	1986–1988 1973–1991	Moriones <i>et al.</i> , 1993 Chen <i>et al.</i> , 1991	18.5	0.131
	Xining, QH (36°38' N, 101°46' E)	2	3	1	2008–2013	our unpublished data	16.2	0.044
	Tianshui, GS (34°35' N, 105°44' E)	2	3	1	–2004	Liu <i>et al.</i> , 2004;	18.9	0.102
	Luntai, XJ (41°46' N, 84°10' E)	2	3	1	–1995	Li <i>et al.</i> , 1995	17.2	0.139
Southwestern China	Yibin, SC (28°46' N, 104°37' E)	2	1	3	1962–1972	Tarim Experimental Station, 1973	20.7	0.162
Central China	Wuhan, HB (30°35' N, 114°17' E)	2	1	3	1976–1995	Huang <i>et al.</i> , 1996;	19.1	0.203
Hokkaido, Japan	Asahikawa (43°46' N, 142°22' E)	3	1	2	2008–2013	our unpublished data	18.4	0.066
North India	New Delhi (28°36' N, 77°12' E)	2	1	3	1978–1986	Kanehira <i>et al.</i> , 1988	19.6	0.171
Northwestern Iran	Kermanshah (34°18' N, 47°03' E)	3	2	1	1993–1996 1997–1999 1993–1994 1999–2001 2001–2003 2007 2009	Chander, 1996 Sekhar & Singh, 1999 Nouri & Rezwani, 1994 Shahrokhi-Khaneghah <i>et al.</i> , 2004 Kamangar & Malkeshi, 2011 Jialilian <i>et al.</i> , 2009 Alizadeh & Malkeshi, 2010	16.3	0.102



Table 1 (continued)

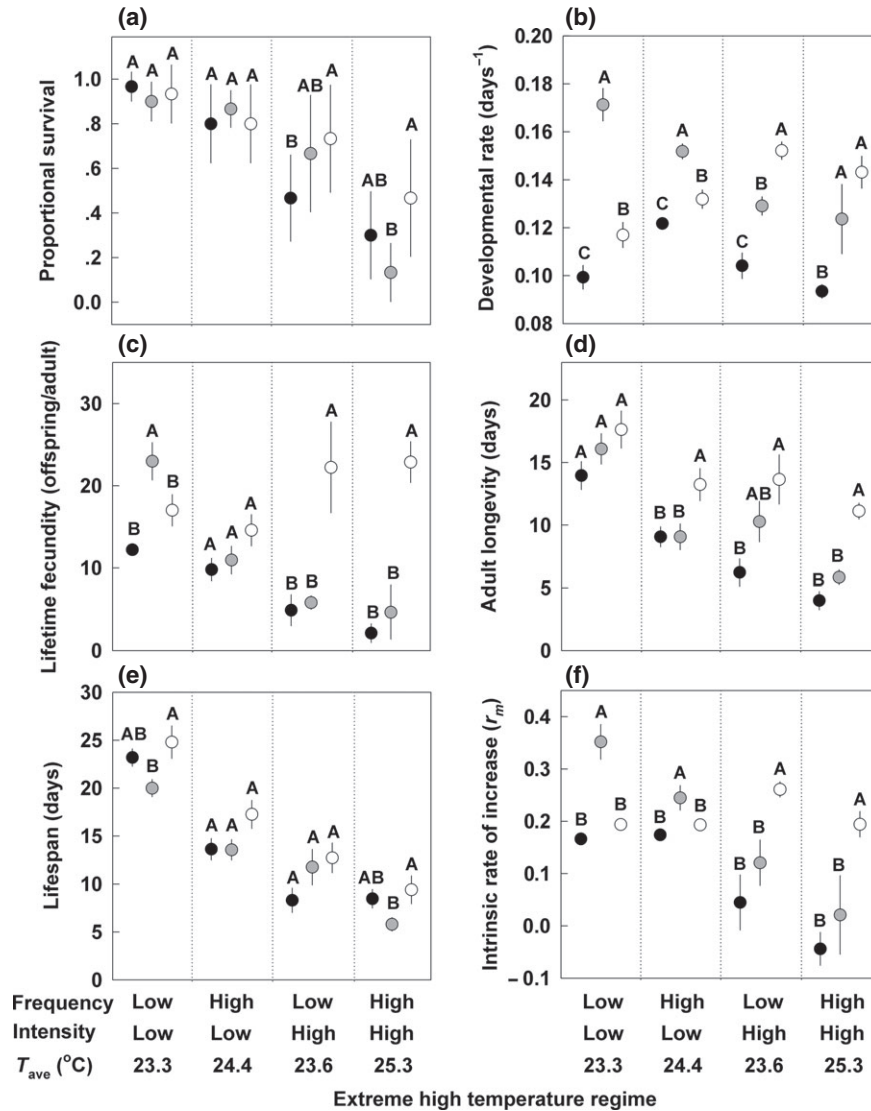
Country/region	Location	Relative dominance			Year	Reference	$T_{mean}$	F_HDs
		SA	SG	RP				
Lower Egypt	Cairo (30°03' N, 31°14' E)	2	1	3	-1992	Mossad <i>et al.</i> , 1992	20.2	0.192
Upper Egypt	Luxor (25°41' N, 32°39' E)	1	2	3	2011–2012 1987–1988 1995–1997 1998	Helmi & Rashwan, 2013 El-Heneidy & Attia, 1991 Abou-Elhagag & Abdel-Hafez, 1998 Mannaa, 2000	22.9	0.466
Southern Australia	Tarcoola, SA (30°42' S, 134°34' E)	2	1	3	2004–2005 –2009	Slman, 2006 Henry <i>et al.</i> , 2009	21.5	0.387
Western Australia	Perth, WA (31°57' S, 115°51' E)	2	1	3	–2012	Annetts & Welsh, 2012	18.8	0.170

See supporting information if the reference details were not included in the reference list.

Table 2 Effects of EHT intensity, frequency, and species identity on demographic rates of three aphid species

Effect	Proportional survival	Development rate	Lifetime fecundity	Adult longevity	Lifespan	Intrinsic rate of increase ( $r_m$ )
Intensity	$\chi^2_{1,60} = 74.91^{***}$	$F_{1,68} = 7.27^{**}$	$F_{1,68} = 8.75^{**}$	$F_{1,68} = 40.12^{***}$	$F_{1,68} = 117.29^{***}$	$F_{1,64} = 52.23^{***}$
Frequency	$\chi^2_{1,60} = 20.17^{***}$	$F_{1,68} = 0.17ns$	$F_{1,68} = 5.74^*$	$F_{1,68} = 33.39^{***}$	$F_{1,68} = 31.98^{***}$	$F_{1,64} = 12.49^{***}$
Species	$\chi^2_{2,60} = 1.94ns$	$F_{2,68} = 67.83^{***}$	$F_{2,68} = 26.94^{***}$	$F_{2,68} = 21.41^{***}$	$F_{2,68} = 6.49^{**}$	$F_{2,64} = 22.44^{***}$
Intensity × Frequency	$\chi^2_{1,60} = 0.20ns$	$F_{1,68} = 5.96^*$	$F_{1,68} = 2.58ns$	$F_{1,68} = 2.60ns$	$F_{1,68} = 2.57ns$	$F_{1,64} = 2.39ns$
Intensity × Species	$\chi^2_{2,60} = 3.07ns$	$F_{2,68} = 32.89^{***}$	$F_{2,68} = 16.00^{***}$	$F_{2,68} = 1.88ns$	$F_{2,68} = 0.66ns$	$F_{2,64} = 23.99^{***}$
Frequency × Species	$\chi^2_{2,60} = 0.11ns$	$F_{2,68} = 3.50^*$	$F_{2,68} = 1.37ns$	$F_{2,68} = 0.95ns$	$F_{2,68} = 0.38ns$	$F_{2,64} = 1.60ns$
Intensity × Frequency × Species	$\chi^2_{2,60} = 5.41ns$	$F_{2,68} = 5.62^{**}$	$F_{2,68} = 1.32ns$	$F_{2,68} = 0.03ns$	$F_{2,68} = 3.15^*$	$F_{2,64} = 0.76ns$

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , ns $P > 0.05$



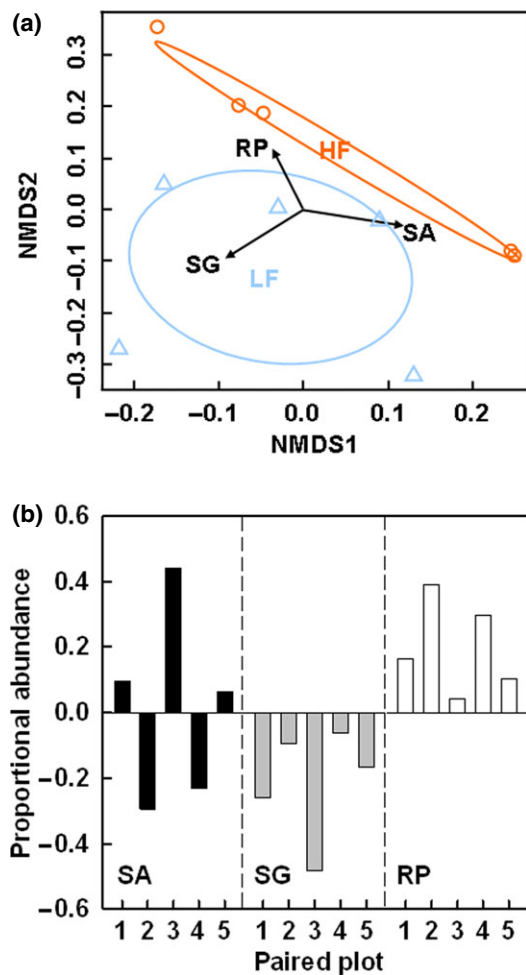
**Fig. 3** Means for (a) proportional survival, (b) developmental rate, (c) lifetime fecundity, (d) adult longevity, (e) lifespan, and (f) intrinsic rate of increase ( $r_m$ ) of the three aphid species, *S. avenae* (black), *S. graminum* (grey), and *R. padi* (white), under the four EHTs regimes (see Materials and methods for further details).  $T_{ave}$  = average temperature. Short vertical lines in the panels indicate (a) 95% CI or (b–f)  $\pm$  1SE. Different letters above the circles represent significant differences between species ( $P < 0.05$ ) under each regime.

proportional abundance of *S. graminum* significantly decreased by 21.4% ( $\pm 7.53$ , SE) ( $P = 0.047$ ), while *R. padi* significantly increased by 19.9% ( $\pm 6.4$ , SE) ( $P = 0.036$ ) with higher EHT frequency, while *S. avenae* did not differ significantly ( $P = 0.916$ ) between treatments (Fig. 4b).

#### Effect of EHTs on the structure of natural communities: field observation

During 2008–2013, aphid abundance of the three species varied substantially between years (Fig. 5a).

More importantly, relative abundances of each species were also significantly influenced by EHT frequency (PERMANOVA,  $F_{1,28} = 23.0$ ,  $P = 0.001$ ). This change in community structure was driven by a species-specific response to EHT frequency. Consistent with the laboratory study, the proportional abundance of *S. avenae* ( $y = 0.94 - 4.91x$ ,  $F_{1,29} = 18.08$ ,  $R^2 = 0.392$ ,  $P < 0.001$ , Fig. 5b) and *S. graminum* ( $y = 0.35 - 1.86x$ ,  $F_{1,29} = 9.61$ ,  $R^2 = 0.256$ ,  $P = 0.004$ , Fig. 5c) decreased whereas that of *R. padi* ( $y = -0.28 + 6.77x$ ,  $F_{1,29} = 31.81$ ,  $R^2 = 0.532$ ,  $P < 0.001$ , Fig. 5d) increased with EHT frequency.



**Fig. 4** (a) Change in aphid community structure with warming (60% increased EHTs frequency). Triangles represent ambient (low frequency, LF) plots and circles heated (high frequency, HF) plots. The 95% confidence ellipses are shown with letters indicating the centroids of the respective treatments. Vectors indicate the correlation of each species with the NMDs scores. Stress = 0.035. (b) Change in proportional abundance of the three coexisting species with increase in EHTs frequency between each of the five paired plots. SA = *S. avenae*, SG = *S. graminum*, RP = *R. padi*.

#### Linking EHT frequency and community structure on a global scale: a meta-analysis

The relative dominance of *S. avenae* did not change significantly with mean temperature, but significantly decreased with EHT frequency (regression coefficient  $\beta = -10.88$ , 95% CI:  $-18.1$ – $4.25$ ,  $P < 0.001$ ). In contrast, the relative dominance of *R. padi* strongly increased with EHT frequency ( $\beta = 12.1$ , 95% CI:  $2.95$ – $22.4$ ,  $P = 0.008$ ), even after accounting for the positive effect of mean temperature ( $\beta = 0.40$ , 95% CI:  $0.09$ – $0.74$ ,  $P = 0.01$ ). The relative dominance of *S. graminum* also

increased with EHT frequency ( $\beta = 11.86$ , 95% CI:  $1.43$ – $22.23$ ,  $P = 0.03$ ) but instead was negatively related to mean temperature ( $\beta = -0.83$ , 95% CI:  $1.46$ – $0.31$ ,  $P = 0.004$ ).

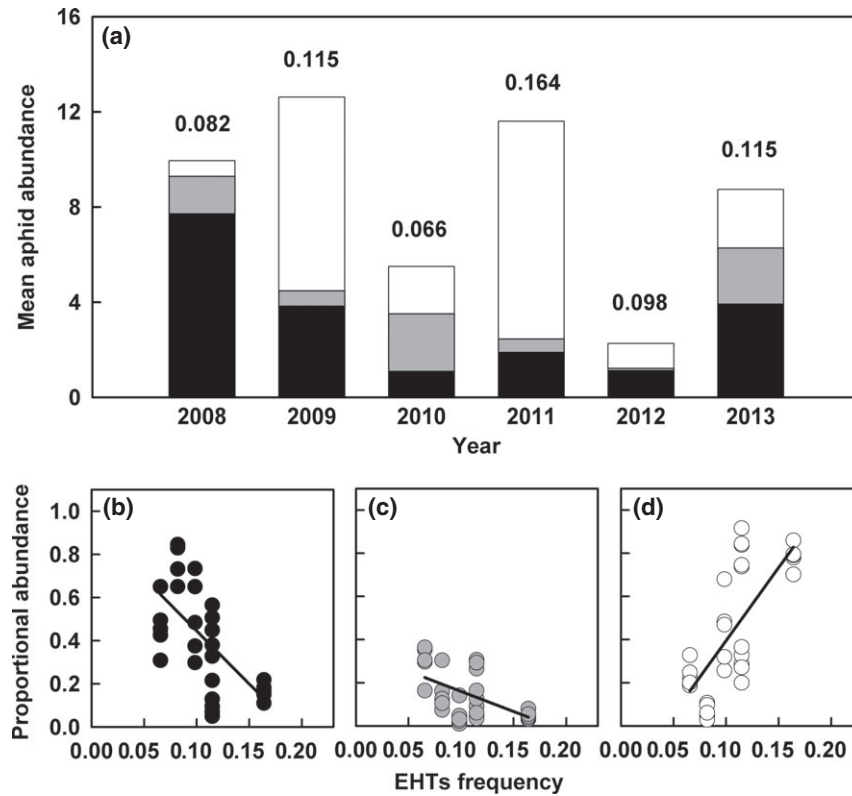
There were significant differences between dominant species in frequency of EHTs (ANCOVA,  $F_{2,35} = 5.94$ ,  $P = 0.006$ ;  $T_{\text{mean}}$ :  $F_{1,35} = 6.21$ ,  $P = 0.018$ ). On a global scale, *R. padi* was dominant in areas with the highest EHT frequencies ( $0.243 \pm 0.110$ ). Frequency of EHTs did not differ between *S. avenae* and *S. graminum* ( $0.090 \pm 0.042$  and  $0.111 \pm 0.033$ , respectively) (Fig. 6).

#### Discussion

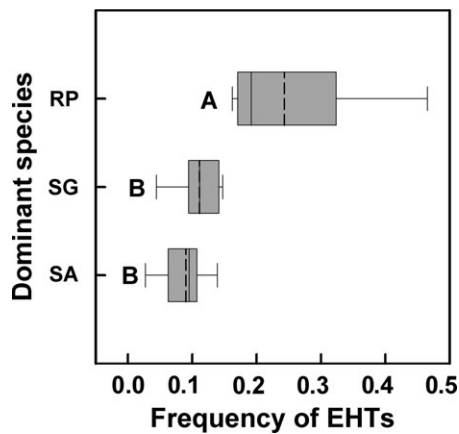
Extreme climatic events are predicted to increase in both frequency and severity under future climate change scenarios. Despite recent progress, predicting how extreme climate events influence the structure and dynamics of natural communities and identifying the underlying mechanisms have been difficult (Kreyling & Beier, 2013; Reyer *et al.*, 2013). Here, we found that changes in the frequency and severity of EHTs altered a range of demographic rates of coexisting species, but these effects were species-specific. As a consequence, changes in EHTs altered the relative fitness of species. Importantly, these changes in relative fitness were predictive of how changes in EHT frequency across time or space altered the relative dominance of species in natural communities. Together, these results emphasize the importance of accounting for EHTs and the biology of species for predicting how climate change will affect natural ecosystems.

#### Changes in heat frequency and amplitude alter relative fitness of species

Episodic extreme high temperatures can cause multiple physiological and developmental problems in organisms (Denlinger & Yocum, 1998; Zhang *et al.*, 2013). Thus, even small shifts in temperature extremes may significantly influence fitness and population dynamics of organisms (Karl *et al.*, 2011). Consistent with these predictions, we found that increasing EHT amplitude had strong negative consequences on most demographic rates of species. However, we also found that increasing the frequency of EHTs significantly reduced the fitness of two (*S. avenae* and *S. graminum*) of the three species. Frequent EHTs mean that organisms may not have sufficient time and/or resources to recover themselves from potential heat injury (Sentis *et al.*, 2013). Consequently, frequent EHTs can cause much more severe damages, which could explain the observed negative effects. These results emphasize the importance of accounting for change in both amplitude



**Fig. 5** (a) Temporal variation in abundance (cumulative number per tiller) of three co-infesting aphid species, *S. avenae* (black bars), *S. graminum* (grey bars) and *R. padi* (white bars) in Wuhan during 2008–2013. The number above each bar indicates the annual EHTs frequency. (b–d) Relationships between annual EHTs frequency and proportional abundance of the three aphid species, (b) *S. avenae* ( $R^2 = 0.392$ ,  $P < 0.001$ ), (c) *S. graminum* ( $R^2 = 0.256$ ,  $P = 0.004$ ), and (d) *R. padi* ( $R^2 = 0.532$ ,  $P < 0.001$ ).



**Fig. 6** Differences in frequency of extreme high temperatures between dominant species. SA = *S. avenae*, SG = *S. graminum*, RP = *R. padi*. Different letters represent significant differences between dominant species. Dashed lines indicate mean values.

and frequency of EHTs to predict how EHTs affect the natural populations.

While increasing severity and frequency of EHTs clearly affected individuals, we also found that the

effects varied among species and demographic rates. Increasing the severity and frequency of EHTs had generally a negative consequence on lifespan, adult longevity, and proportional survival of all species. However, *R. padi* was able to compensate for these negative effects with an increase in lifetime fecundity and developmental rate. This was not the case for the other two species where both rates either did not change or declined dramatically. As a consequence, the fitness (intrinsic rate of increase) of *R. padi* was not negatively affected by increasing the frequency or amplitude of EHTs, while the other species experienced a clear decline (Fig. 3). These results indicate that, depending on the specific species, changes in EHTs can have both negative and positive effects on demographic rates. These findings are consistent with previous studies which found that in the absence of predators, increasing amplitude or frequency of EHTs had either no effect on the abundance of aphid species (Gillespie *et al.*, 2012), or decreased aphid abundance (Sentis *et al.*, 2013). Together, these results emphasize the importance studying all major demographic rates to predict the net effects of EHTs on the fitness of species.

*Frequent extreme temperature events alter the spatial and temporal structure of natural communities*

Our study found several independent lines of evidence indicating a clear connection between the spatial and temporal dynamics of natural communities and frequency of extreme temperatures. It also suggests that this variation is driven by asymmetric effects of extreme temperatures on demographic rates of species. In our field experiment, we found a strong change in relative abundance of species in warming treatments with had 60% more EHT events than the controls (Figure S2 and Fig. 4). In addition, our field observations revealed that inter-annual variation in species abundance and community structure was strongly correlated with changes in EHT frequency (Fig. 5). Importantly, these changes in community structure in the field were similar in both field studies and could not be predicted based on changes in mean temperature (see Table S3 and discussion below). However, the changes were consistent with shifts in relative fitness observed in our laboratory experiments. This consistency is especially impressive given that species were raised in isolation under controlled conditions in the laboratory, while they were embedded in a complex natural community in the field, with interspecific competitors, predators, and parasitoids, and other abiotic variation (which likely explained much of the remaining variation). Finally, we found the same general pattern again in our meta-analysis, where variation in EHT frequency across large spatial scales was correlated with shifts in the relative abundance and distribution of the three species (Fig. 6). In the meta-analysis and our field observations, these effects were observed even after accounting for potential effects associated with changes in mean temperature. Taken together, results of these four studies clearly indicate that the observed spatial and temporal variation in the structure of natural communities was driven by asymmetric effects of EHT frequency on the relative fitness of species. These predictions from our study are consistent with long-term observations in southwest China which found that *S. avenae* was the dominant species before the mid-1970s when the frequency of EHTs was at a lower level. However, *R. padi* became dominant starting 1975 when the frequency of EHTs was much higher (Huang *et al.*, 1996; Hu *et al.*, 2008). Given that small changes in mean temperatures can lead to disproportionately large changes in EHT frequency (Schär *et al.*, 2004; IPCC, 2013), our results suggest that some of the main effects of climate change on the structure of natural communities are likely mediated through changes in EHT frequency.

*Effects of changes in mean vs. frequency of extreme temperatures*

Separating the effects of changes in mean vs. extreme temperatures is a challenge because both factors are inherently correlated. Any attempt to prevent that correlation (i.e. keeping the mean constant) requires changes in other aspects of the temperature regime. These changes could, however, confound the effects of changes in EHT regimes and there is no a priori reason to believe that keeping the mean constant is more important than keeping any other aspect of the temperature pattern constant. For instance, previous studies in our system have demonstrated that altering minimum temperatures can significantly alter the effect of temperature extremes (Zhao *et al.*, 2014). Thus, we intentionally avoided changing any other aspects of the temperature regime (e.g., changes in minimum temperature) with changes in EHT severity or frequency. While this also inevitably slightly changed the mean temperature among treatments in both the laboratory and field experiment, several lines of evidence suggest that results in both cases were driven by changes in EHT patterns and not by changes in mean temperature. First, differences in mean temperatures were small in the life-table ( $\leq 2$  °C) and field experiment ( $\sim 1.5$  °C). Second, although we did not test how constant temperatures (i.e. without EHT) affect species, all previous studies indicate that demographic rates and fitness ( $r_m$ ) of these species changes little under the mean temperatures we used in life-table and field experiment (see Tables S3 and S4). If anything, the increase in mean temperature should have slightly increased growth rates of all species without changing their relative fitness ranking. Yet at least some demographic rates of all species and the fitness of two species were negatively affected by higher frequency and strength of EHTs, and the relative fitness and relative abundances changed dramatically with shifts in EHT patterns in our life-table and field experiments respectively. In addition, the difference in mean temperature between both low intensity treatments in the life-table experiment (1.1 °C) was higher than differences between either one of the low intensity (0.8 °C) or high intensity treatment (0.9 °C). Yet, relative fitness of species was largely the same in low intensity treatments while their relative fitness was reversed in the high intensity treatments (Fig. 3f). Finally, we found the same pattern (i.e. changes in relative fitness and abundance of species) also in our long-term field observations and meta-analysis after accounting for potential effects due to changes in mean temperatures. Together, all four studies clearly suggest that changes in EHTs were the dominant driver changing the demographic rates, relative

fitness, and relative abundance of coexisting species in a manner that cannot be predicted by changes in mean temperatures. Similar discrepancies between predictions based on mean vs. fluctuating temperatures have been observed in other studies (Sentis *et al.*, 2013). This suggests that the effects of climate change on natural communities could potentially be driven more by changes in extreme climatic events (e.g., EHTs) than by changes in average conditions, emphasizing the need to examine both climatic factors in future studies to make reliable predictions.

#### *Ecological consequences and potential applications*

Our results indicate that changes in EHTs can alter the temporal and spatial distribution of species and structure of communities. Such changes can have important consequences of the functioning of natural and agricultural communities. For instance, our focal species differ in their transmission efficiency of different virus species (Miller & Rasochova, 1997) which may cause serious yield losses on cereals (Dixon, 1977). Shifts in community structure of these species may therefore strongly affect virus co-infection rates in hosts and consequently overall disease prevalence (Seabloom *et al.*, 2009, 2013). In addition, the three species differ in preferred feeding sites and spatial distribution within cereal canopy. *S. avenae* is predominantly feeding on ears and thus affecting yield or crop quality directly (Dixon, 1977). By contrast, *S. graminum* and *R. padi* mainly prefer primary leaves and stems, respectively (Qureshi & Michaud, 2005b) and impact yield or crop quality indirectly. Shift in relative abundance of these aphid species is likely to cause changes in the methods for pest management (Dixon, 1977). Moreover, these species usually share multiple predators but differ in their specific interactions. Changes in relative abundance may therefore alter the spatial distribution of prey species which can influence the predation efficiency and population growth of predators (Barton & Schmitz, 2009). Given that most coexisting species differ in their ecological niche (and thus functional roles), EHT-mediated changes in community structure are likely to have important consequences for the functioning of a large range of ecosystems.

Changes in temperature extremes are thought to be more important to organisms, communities and ecosystems than changes in mean under climate warming (Easterling *et al.*, 2000; Parmesan *et al.*, 2000; Kreyling & Beier, 2013; Reyer *et al.*, 2013). However, linking climate extremes to the spatio-temporal dynamics of natural communities is a major challenge in the 21st century. We have used a combination of approaches which allowed us to overcome limitations of previous

studies and to identify a clear mechanistic link between the demographic rates and relative fitness of species, changes in the frequency and amplitude of EHTs, and the spatial and temporal structure of natural communities. These results also confirmed that small increases in average temperature can lead to a substantially increase in EHT frequency and concurrent changes in community structure, indicating that species and community are more sensitive in response to climate warming than we expected.

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## Supporting Information

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

**Figure S1.** Four temperature regimes used in laboratory experiment.

**Figure S2.** Daily maximum temperatures and EHT frequency for ambient and heated treatments for the field experiment.

**Figure S3.** Daily maximum temperatures in Wuhan during April–May (1954–2013) and the differences between weather station records and field observations in 2013.

**Table S1.** Average temperatures and EHT frequency for the field observations.

**Table S2.** Upper critical mean temperatures for population growth of the three species.

**Table S3.** Fitness of the three species at different mean temperatures.

**Table S4.** Demographic parameters for the three species at constant temperatures.