



Within-patch and edge microclimates vary over a growing season and are amplified during a heatwave: Consequences for ectothermic insects

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ABSTRACT

Embedded in longer term warming are extreme climatic events such as heatwaves and droughts that are increasing in frequency, duration and intensity. Changes in climate attributes such as temperature are often measured over larger spatial scales, whereas environmental conditions to which many small ectothermic arthropods are exposed are largely determined by small-scale local conditions. Exposed edges of plant patches often exhibit significant short-term (daily) variation to abiotic factors due to wind exposure and sun radiation. By contrast, within plant patches, abiotic conditions are generally much more stable and thus less variable. Over an eight-week period in the summer of 2020, including an actual heatwave, we measured small-scale (1 m²) temperature variation in patches of forbs in experimental mesocosms. We found that soil surface temperatures at the edge of the mesocosms were more variable than those within mesocosms. Drought treatment two years earlier, amplified this effect but only at the edges of the mesocosms. Within a plant patch both at the soil surface and within the canopy, the temperature was always lower than the ambient air temperature. The temperature of the soil surface at the edge of a patch may exceed the ambient air temperature when ambient air temperatures rise above 23 °C. This effect progressively increased with ambient temperature. We discuss how microscale-variation in temperature may affect small ectotherms such as insects that have limited ability to thermoregulate, in particular under conditions of extreme heat.

1. Introduction

An array of anthropogenic processes are deleteriously affecting organisms across much of the biosphere, e.g., through habitat loss and fragmentation, modified species (trophic) interactions, changes in species distributions, and disease dynamics (Evans et al., 2008; Parmesan, 2006; Tylianakis et al., 2008; Walther et al., 2002). These changes are threatening the health and functioning of ecosystems (Duffy, 2003; Hautier et al., 2015; Moreno-Mateos et al., 2017). Many of these effects are directly driven by anthropogenic climate change, or are exacerbated by it (Bellard et al., 2012; Thomas et al., 2004). Not only does longer-term warming pose a threat to biodiversity, but the frequency, duration and intensity of short-term extreme heat events (heat waves) is also increasing (Christidis et al., 2015; Fischer and Schär, 2010). The effects of climate warming are not evenly distributed geographically; at higher latitudes in the Northern hemisphere warming is occurring at a

faster rate than elsewhere (Dillon et al., 2010). Moreover, the pace at which climate warming affects species distributions and abundances is open to conjecture (Beever et al., 2011). However, severe weather events and increasing climatic variability can drive populations below critical threshold sizes, affecting metapopulation dynamics and possibly resulting in extinction (Johansson et al., 2020; Piessens et al., 2009). The importance of studying the effects of climate extreme events as well as the effects of longer-term incipient warming is being increasingly acknowledged (Harvey et al., 2020b; Harvey et al., in press; Jentsch et al., 2007; Lynch et al., 2014).

Extreme climatic events, such as heatwaves, are likely to affect organisms more strongly than more gradual warming, in particular, when conditions during extreme weather events exceed thresholds that species normally do not experience (Harvey et al., 2020b). For instance, during heatwaves, temperatures may exceed upper critical thermal thresholds of organisms, strongly affecting their physiology,

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metabolism, behaviour, dispersal and ultimately survival (Agosta et al., 2018; Colinet et al., 2015; González-Tokman et al., 2020). Alternatively, climate extremes may affect the availability and timing of critical resources and thus indirectly affect the organisms that depend on them (Butt et al., 2015). Extreme heat may impact small ectotherms, such as arthropods (insects and arachnids), which are highly sensitive to changes in ambient temperature compared to endotherms that can regulate body temperature more easily, or larger ectotherms that have a smaller surface-to-volume ratio (Roitberg and Mangel, 2016). Moreover, many small arthropods, such as wingless or sedentary species, are limited in their ability to seek shelter in favourable microhabitats during climatic extremes. Consequently, the abiotic environmental conditions to which many small arthropods are exposed are largely determined by small-scale local conditions.

In terrestrial habitats, diel temperature can fluctuate considerably depending on latitude, season and altitude (Angilletta, 2009; Taylor, 1981). Moreover, vegetation strongly influences microclimatic conditions through evapotranspiration and its effects on e.g., solar radiation and wind exposure, which often dampen the amplitude of diel temperature fluctuation (Rosenberg et al., 1983). Deforestation and other anthropogenic land use practices have increased the prevalence of edges, which are defined as transition zones between habitat types. These edges often exhibit gradients in abiotic conditions (Williams-Linera et al., 1998). However, the steepness of these gradients strongly depends on habitat type. Williams-Linera et al. (1998) reported a steep temperature gradient in the pasture, but not in the forest of a forest-pasture and riparian forest-pasture transition zone. How edges impacts on small ectotherms such as insect herbivores also depends also on habitat type (De Carvalho Guimarães et al., 2014). For instance, edges in grasslands were found to have lower levels of insect herbivory than contiguous grasslands, although insect herbivore abundance and species richness were not affected, whereas the opposite was found for forest edges (De Carvalho Guimarães et al., 2014). To what extent these patterns can be explained by differences in abiotic conditions, either by direct exposure or indirectly mediated by the plant, has been little studied. Even at micro-scales, heterogeneity in temperature, i.e. at the leaf surface, can affect the biology and ecology of small arthropods (Caillon et al., 2014). Caillon et al. (2014) showed that leaf surface temperature heterogeneity decreased with increasing temperature, reducing the ability of the spider mite *Tetranychus urticae* to effectively thermoregulate.

The aim of the present study is to examine and compare temperature differences during a summer season between the edge and the interior of forb assemblages at a spatial scale of 1 m². This is an ecologically realistic scale at which small arthropods are exposed to potentially fluctuating temperatures. More specifically, we monitored ambient air temperature, soil surface temperature at the edge and within a plant patch and temperature within the plant canopy. Temperatures were recorded two or three times a week from mid-June to mid-August in 2020 in a small experimental field in the Netherlands. The period included an official heatwave according to the World Meteorological Organization, which is a period of at least five consecutive days during which the daily maximum temperature is at least 5 °C higher than the average maximum temperature (Frich et al., 2002). We used an existing mesocosm experiment that was set-up to investigate effects of other aspects of global change, i.e. plant-range expansion and drought, on plant community functioning mediated through plant-soil feedbacks. Plant community composition and plant-associated interactions can be influenced by changes in biotic and abiotic soil characteristics induced by previous plant growth, a process that is often referred to as plant-soil feedback (Ehrendfeld et al., 2005; van der Putten et al., 2016). Climate warming has resulted in range shifts of many species pole-wards or to higher elevations (Bradley et al., 2009; Chen et al., 2011; Parmesan, 2006). Range-expansion of plant species and extreme climatic events can both affect soil communities and the assemblage of plant communities and their associated biota, potentially mediated through plant-soil

feedback processes (Le Roux et al., 2018; Pugnaire et al., 2019).

We chose this model system as it allowed us to record temperature under controlled conditions. The plots contained several native and range-expanding forb species, representing a patchy plant community with both exposed edges and areas covered by the vegetation. We hypothesise that surface temperatures of exposed soils will exhibit much greater temperature fluctuations over the duration of summer than surface temperatures of soils that are increasingly sheltered by the plant canopy. Similarly, temperatures within the plant canopies will also be buffered against direct incoming solar radiation. We also analysed the effects of the original factors of the experiment (soil origin, plant and drought legacy) on the temperature variables. Though, we did not collect data on insects here, we discuss our results from an insect perspective. The microscale variability in temperature recorded in this study is in particular relevant affecting the biology and ecology of small ectothermic organisms arthropods.

2. Materials and methods

2.1. Experimental design of the mesocosms

Details of the experimental design are given in Manrubia et al. (2019). The experimental setup was established in 2013 in the experimental garden of the Netherlands Institute of Ecology (Wageningen, the Netherlands) and consisted of 40 mesocosms in elevated containers of approximately 1 m³ arranged in 5 rows of 8 mesocosms with a spacing of 0.5 m between them (Fig. 1). Each mesocosm was filled with approximately 80 cm bulk soil originating from a riparian area in Boven-Leeuwen in the Netherlands. Half of the mesocosms were inoculated with a 20-cm top soil layer originating from another riparian area in the Netherlands, the Millingerwaard. In an attempt to recreate the soil biota of the range-expanding species from their original range before they moved northwards, soil was collected from a floodplain near Solt in Hungary. The other half of the mesocosms was inoculated with this soil. Local Dutch soil was collected where native and range-expander are both present, whereas non-native soil was collected where the range-expanding species are still present. Soil origin in the present experiment refers to these two types of top soil.

In 2013 and 2014, all mesocosms were planted with riverine plant communities consisting of native grasses and native and range-expanding forbs. To create plant induced legacies, in 2015–2017, half of the mesocosms were planted with native forbs (eight species) whereas the other half was planted with eight congeneric or closely related range expanding species (Manrubia et al., 2019). Plant legacy refers to the two different plant communities, native or range-expanding, that were grown until 2018. In 2018 mesocosms were divided into four quadrants. Each year (2018–2020), all quadrants were planted with eight plants, four natives and four congeneric range expanders (Table 1). At the beginning of spring of each year, all remaining foliage and roots were removed. The plant species were a subset of the species used in the previous years. Seeds were collected from natural populations in the Netherlands or collected from a wild flower seed company (Cruydt Hoeck, Nijeberkoop, the Netherlands). Seedlings of each species, which had been germinated under greenhouse conditions, were randomly planted in each quadrant. Thus, all eight plant species were present four times in each mesocosm (Fig. 1). The soil was further conditioned in 2018 by a severe drought treatment. For this purpose all mesocosms were sheltered by rain-covers. Half of the mesocosms were exposed to extended drought by not watering the plants for a period of 6 weeks starting in late June and ending in early August, while the other half of the mesocosms were watered twice a week until they reached seasonal average precipitation levels of 34 L per week (source: Royal Dutch Meteorological Institute) or KNMI). After 6 weeks, the rain shelters were removed, and watering was supplemented when necessary to guarantee a minimum of 34 L/week. The latter watering regime was also applied in 2019 and 2020 to all mesocosms, while on extreme hot days mesocosms

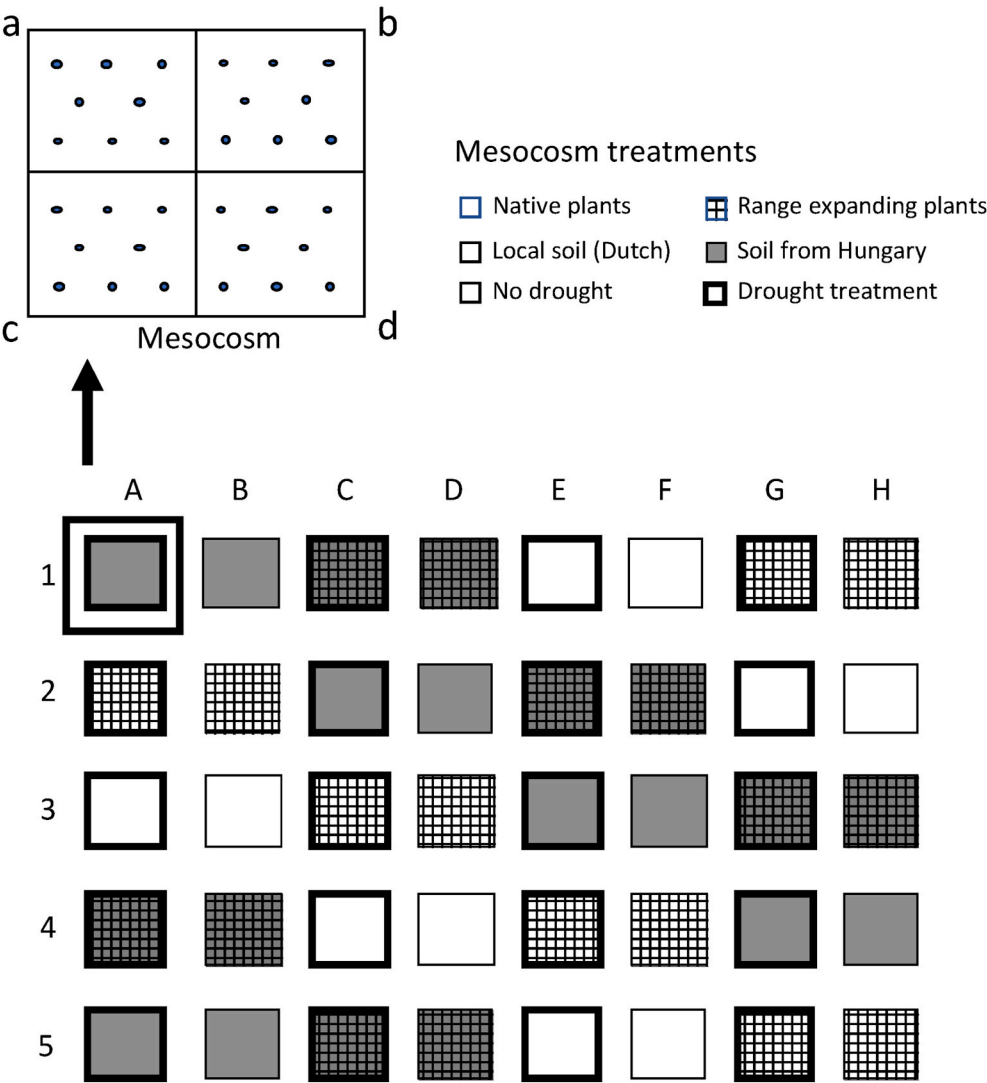


Fig. 1. Experimental design. Forty mesocosms of 1 m³ were created in a raster of 8 by 5 mesocosms with 0.5 m between them. Mesocosms were exposed to three treatments, each with two levels, according to a full factorial design, resulting in a total of 8 unique treatments (n = 5). The two conditioning treatments were plant origin (native or range expanding) and exposure to extreme drought (yes or no), whereas the soil was collected in the Netherlands (local) or from the geographical area where the range expanding plants originated (Hungary). Each mesocosm was divided in four quadrants (a, b, c, d) which all received the same treat. In each quadrant, one plant of each of the 8 species listed in Table 1 was planted.

Table 1
Plant species pairs, categorized as ‘native’ or ‘range expanding’ planted in the mesocosms.

Plant family	Native species	Range-expanding species
Asteraceae	<i>Centaurea jacea</i> (L.)	<i>Centaurea stoebe</i> (L.)
Asteraceae	<i>Geranium mole</i> (L.)	<i>Geranium pyrenacium</i> (Burm. F)
Geraniaceae	<i>Tragopogon pratensis</i> ssp <i>pratensis</i> (L.)	<i>Tragopogon dubius</i> (Scop.)
Brassicaceae	<i>Rorippa sylvestris</i> (L.) Besser	<i>Rorippa austriaca</i> (Crantz) Besser

were watered daily. The experiment had a full factorial design with three factors (soil origin, plant legacy and drought legacy), each with two levels, resulting in eight unique treatments (Fig. 1).

2.2. Microclimatic temperature measurements

Temperatures were measured two or three times per week in all mesocosms between June 17 and August 12, 2020, generating a total of 20 days on which temperatures were recorded. Temperatures were measured during the warmest part of the day, i.e. between 1400 and 1500 h. An infrared thermometer gun (BOSCH Thermodetector PTD1) was used to measure the temperature of the soil surface at the edge of the

mesocosm between two quadrants and within the mesocosm, as well as within the plant canopy. The thermo-detector of this apparatus generates a laser circle that indicates the measuring surface and a centre laser point that marks the centre of the measuring surface. The laser beam was aligned perpendicular to the surface at 0.05 m for 2 s. The apparatus generates a mean temperature reading, which we recorded. With the same device, we measured air temperature before and after all surface temperature were recorded. On each recording day, soil surface and canopy temperatures were measured twice or four times in each mesocosm.

2.3. Processing and statistical analysis of the temperature data

For each recording day, we calculated four mean microclimatic temperatures per mesocosm based on two or four measurements: 1) soil surface temperature at the edge of a quadrant, 2) soil surface temperature within a quadrant, 3) temperature in the canopy, and 4) air temperature. These mean values were used for further analysis using the statistical program SAS 9.4. Thus, we consider a mesocosm as the experimental unit in the statistical analysis. To investigate how the ambient air temperature may impact on the other three microclimatic temperature variables, we used a mixed model with location (soil edge of the quadrant, soil within the quadrant, and canopy) as a fixed factor, air temperature as a covariate and recording date as a random factor. We

were specifically interested whether the slopes differed for each of the three location-air temperature relationships. To compare differences between slopes we used t-tests.

To investigate whether the treatment of the mesocosm had an effect on the microclimatic temperature, we also used a mixed model approach. Soil origin (local or range-expander origin), plant legacy (native or range expander) and drought legacy (yes or no) were entered as fixed factors. As the temperature was measured in each mesocosm repeatedly, recording date was entered as a random factor. Air temperature correlated significantly with microclimatic temperature (see results), therefore we entered air temperature as a covariate. We started with a model with all 2 and 3-way interaction terms and progressively removed terms when they were not significant. Models were run for each of the three temperature variables, edge soil, within quadrant soil, and canopy, respectively.

3. Results

During the recording period, we experienced four days (July 23–26) of relatively warm summer weather compared with maximum temperatures historically registered for the Wageningen area, and a record-breaking national heat wave was recorded in early-to mid-August (August 6–14). The highest daily temperatures measured during these warm to hot periods ranged between 30 and 36 °C at the nearest official KNMI (Royal Netherlands Meteorological Institute) weather station in Deelen, which is located 19 km from Wageningen.

Mean soil surface temperatures within quadrants ranged between 8.1 and 40.9 °C and at the edge between 10.4 and 59.3 °C. Temperature of the soil surface both at the edge of and within quadrants, as well as the temperature within the canopy correlated with air temperature ($F_{1,18.2} = 68.9$, $P < 0.001$), but the slopes of these linear relationship depended on where it was measured ($F_{2, 35.2} = 12.3$, $P < 0.001$, Fig. 2). The slope of the line for the soil surface temperature at the edge was significantly steeper than the slope for the soil surface temperature within quadrants ($t_{36} = 3.04$, $P = 0.004$) and the one for the canopy ($t_{35} = 2.71$, $P = 0.01$). The slopes of the lines for canopy and within quadrants were not significantly different ($t_{35} = 0.32$, $P = 0.74$). Moreover, when we compared the slopes with the situation in which we assume that soil and air temperature are the same (black solid line in Fig. 2), we see that for the relationship between air and soil-edge temperature, the predicted line crosses the soil ~ air-line at 22.8 °C. This means that at temperatures of 22.8 and higher the soil temperature at the edge is higher than the air temperature and that this difference progressively increases with

air temperature. In contrast, the line for soil ~ within quadrant vs air temperature parallels the soil ~ air-line but with a lower intercept. This means that the vegetation within the quadrant has a cooling effect and that this cooling effect is similar irrespective of air temperature. The cooling effect is approximately 5.2 °C. Also, the line for the canopy parallels the soil ~ air-line. The cooling effect of the vegetation is greater in the plant canopies (by approximately 3.1 °C) than on the soil, within the plant patches but this was not statistically significant ($t_{35} = 0.49$, $P = 0.62$) (Fig. 2).

When the treatments/conditioning of the mesocosms are considered while controlling for the influence of air temperature, the drought treatment had a significant effect on soil surface temperature but only at the edge of a quadrant (Table 2). When mesocosms had experienced a drought treatment, the soil temperature at the edge was approximately 1 °C warmer than soils that were not exposed to drought. Soils originating from the native range of the range-expanding plants tended to be cooler by almost 1 °C at the edge, and although this was not significant ($P = 0.06$), a trend was apparent.

4. Discussion

The results of this study show that even in vegetation patches at micro-scales (here, 1 m), contrasts in temperature can increase dramatically from the heart of the patch to its edge with rising ambient temperatures, and these effects can be exacerbated by drought. We found that soil surface temperatures at the edge of plant patches consisting of forbs were significantly more variable than soil surface temperatures within plant patches. Within a plant patch, both at the soil surface and within the canopy, the temperature was always lower than the ambient air temperature. More importantly, the temperature of the soil surface at the edge of a patch may exceed the ambient air temperature when it rises above 23 °C. This effect progressively increases with ambient temperature. Such increases in spatial temperature variation experienced during heat waves may have significant impacts on the physiology and survival of small ectothermic arthropods that are limited in their ability to move over larger distances unless cooler microclimates are easily available.

Ectotherms such as insects have a limited ability to thermoregulate. As a consequence of this, their body temperature is largely determined by the ambient temperature. The relationships between insect performance traits and their body temperature can be described by thermal performance curves, which typically have a rising part before they reach an optimum, followed by a steep drop when temperature further

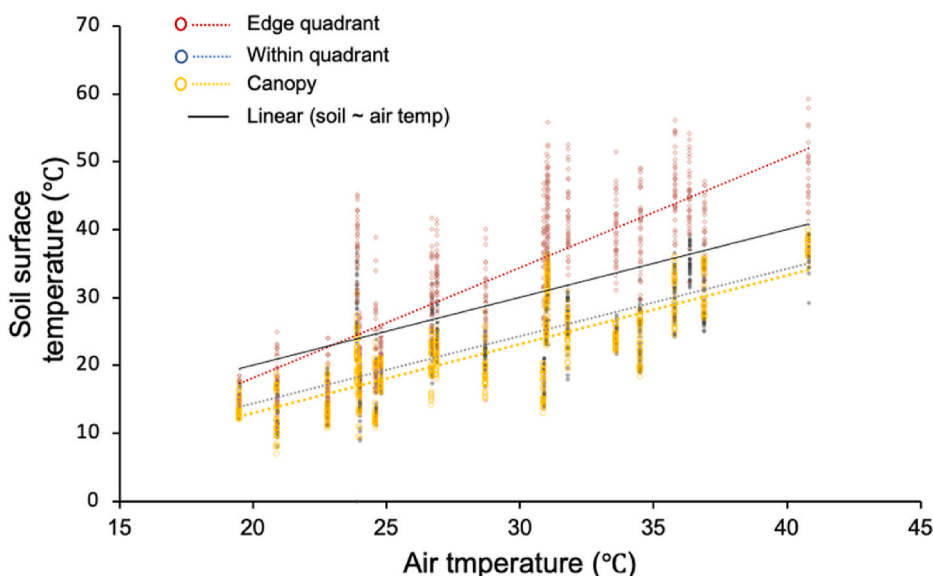


Fig. 2. Linear relationships between air temperature and temperature measured at the soil surface at the edge of a quadrant (red), at the soil surface within a quadrant (blue) or in the canopy (yellow), respectively. The circles represent the mean values for a mesocosm on a given day. The dotted lines depict the predicted linear relationships using the same colour codes. The solid black line represents the situation in which the soil surface temperature is assumed to be equal to the air temperature.

Table 2

Statistical results of the effect of soil origin, plant legacy and drought on temperature measured at different locations of the mesocosms, at the surface of the soil at the edge (Soil_edge) or within quadrants (Soil_within), or within the canopy (Canopy). Air temperature was entered as a covariate as it strongly influences microscale temperature measurements (F-statistic for air temperature is given with the degrees of freedom (df) between brackets). All 2 and 3-way interaction terms were progressively removed when they were not significant, resulting in a model with only main effects.

Location	Factors								Covariate	
	Soil origin			Plant legacy		Drought		Air	F-stat	P-value
	df	F-stat	P-value	F-stat	P-value	F-stat	P-value			
Soil_edge	1,36	3.87	0.056	<0.001	0.97	5.72	0.02	1542 _(1,743)		<0.001
Soil_within	1,36	0.08	0.77	0.40	0.53	2.91	0.096	951 _(1,743)		<0.001
Canopy	1,36	<0.001	0.98	0.01	0.91	2.56	0.11	1222 _(1,703)		<0.001

increases (Sinclair et al., 2016; Stoks et al., 2017). Moreover, insects are known to exhibit plasticity in thermal tolerance maxima through acclimation and hardening (Colinet et al., 2015), but their effects on increasing thermal tolerance are only small (Gunderson and Stillman, 2015). As long as insect body temperature is lower than or near the temperature at which performance is optimal, elevated ambient temperatures can be beneficial in terms of e.g. growth rate, and development time. Insects may even actively choose warmer sites to increase their body temperature. For example, basking behaviour by the larvae of the butterfly *Euphydryas aurinia* increased their body temperature and as a result increased their feeding efficiency (Porter, 1982). However, when body temperature reaches or exceeds the relatively narrow range in which performance deteriorates quickly, insects risk to overheat and this may critically impact on insect physiology and ultimately their survival. (González-Tokman et al., 2020). When exposed to temperatures over 40 °C, even for a short period (min), many insects are physiologically or behaviourally impaired (Denlinger and Yocum, 1998; Gunderson and Stillman, 2015). Moreover, in some insects the upper thermal limits for reproduction are often several degrees lower than for survival. Exposure to high temperatures at which insects can survive nevertheless can destroy their eggs and/or sperm, rendering the insects sterile (Janowitz and Fischer, 2011; Sales et al., 2018; Walsh et al., 2019). The soil surface temperatures that we measured on hot summer days with ambient temperatures higher than 35 °C potentially fall into the range of upper limits for both reproduction and survival (Gunderson and Stillman, 2015). Under these conditions, small ectotherms critically depend on availability of cooler sites.

Temperature heterogeneity generated by landscape topography can buffer plant and insect populations against extinction under climate warming conditions (Suggitt et al., 2018). At a finer spatial scale, plant vegetation can provide animals with refuges during periods of unfavourable conditions such as those perceived during drought, heavy rainfall, extreme heat or cold (Mackey et al., 2012; Pavey et al., 2017). As the present study and others have demonstrated, the temperature within vegetation is lower at the soil surface and within the canopy than the ambient air temperature. Thus the vegetation can buffer insects from being exposed to temperatures near or above their upper critical reproductive or thermal limits (Addo-Bediako et al., 2000; Bowler and Terblanche, 2008; Walsh et al., 2019). Hot summer days increase temperature heterogeneity in small plant patches, due to the stronger radiation and concomitant rise in temperature at the edge than within the patch. How this affects insects depends on their physiology, motility and on the location in the patch where they reside normally. For example, soil dwelling arthropods may be more negatively impacted than those that live primarily within plant canopies or plant tissues and motile species may be less impacted than those that have limited ability to move to cooler sites. However, moving to sites with more favourable environmental conditions can also have energetic and ecological costs (e.g. exposure to predators, being restrained from feeding).

Microclimatic heterogeneity at scales smaller than 1 m has been little studied. However, it is important to study microclimatic variation at relevant ecological scales (Pincebourde and Woods, 2020; Potter et al., 2013; Suggitt et al., 2018). Behavioural and physiological responses of

insects and other arthropods clearly depends on their biology and ecology. For small herbivorous arthropods this could be the plant or plant organ on which they prefer to feed or even spend most of their lives. Heterogeneity in temperature can occur even on the surface of a single leaf and further depends on whether the leaf is exposed to direct sunlight, whether it is damaged by herbivores, and on ambient air temperature (Caillon et al., 2014; Pincebourde, Woods and Fox, 2012). Furthermore, Caillon et al. (2014) reported that at higher ambient temperature, heterogeneity in leaf surface temperature decreased, limiting the possibility of the leaf-surface dwelling spider mite *T. urticae* to thermoregulate behaviourally. Non-motile species, such as web-building spiders, may adapt to climatic extremes by selecting sites to build their webs based on their microclimates or else seek shelter under leaves when conditions become too hot (Johnson et al., 2020). Although we measured temperature only within the canopy of plants, it is likely that variation in temperature also exists depending on where in the canopy the temperature is measured, i.e. at sites where it is exposed to direct sun radiation or in shaded areas.

Soil dwelling arthropods are exposed to variation in temperature at the soil surface and in the soil itself. Soil conditions strongly affect plant growth and *vice versa* plants impact on the soil for instance by changing hydrological properties as well as reducing direct energy input through shading (Ehrenfeld et al., 2005). In addition, water content of the soil impacts soil surface temperature and this is, in particular, evident in bare soils (Qiu et al., 1998). In this study the drought treatment two years earlier still increased the soil surface temperature by approximately 1 °C, but only at the edges of the quadrants where the soil was more exposed to direct sunlight. Meisner et al. (2018) found that extreme drought had a lasting effect on soil microbial community composition that was detectable three weeks after abiotic condition had been restored. Which microbial or physical properties of the soil still have a signature two years after a severe drought treatment needs to be investigated in more detail.

Habitat fragmentation has resulted in a more patchy distribution of plant assemblages and this has increased the presence and extent of habitat edges (Ries et al., 2004). These edges are often characterised by patches of less dense vegetation that in turn affect microclimatic conditions, such as increased temperature variability and reduced humidity (Saunders et al., 1991). Furthermore, in agricultural landscapes, the harvesting of crops during the growth season has resulted in expansive areas of bare soil, especially in temperate regions where crops are grown only once a year. The surface temperature of bare soil increases rapidly when exposed to direct sunlight, compared to soils that are heavily shaded by the plant canopy. Thus, in landscapes existing of natural and agricultural fields, heterogeneity in thermal conditions in transition zones is highly variable and this may be enhanced under the conditions of climate warming where the incidence and intensity of heatwaves is predicted to increase.

Recently, several papers have reported on dramatic declines of insect abundance, with profound implications for the functioning of ecosystems and the potential loss of important ecosystem services that insects provide, e.g. pollination, pest control and nutrient cycling (e.g. Goulson, 2019; Leather, 2017; Sánchez-Bayo and Wyckhuys, 2019; Wagner,

2020). Although climate warming is not believed to be the most important driver of insect declines (Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019), extreme climatic events, such as drought and heat waves, which often overlap or occur in sequence, may expose insect populations to unprecedented conditions and may amplify the deleterious effects of other anthropogenic stresses (Harvey et al., 2020b; Ma et al., 2021). The data reported here show that on hot summer days, microclimatic temperatures can reach critical levels for insect performance and survival. Under conditions of climate warming, extreme climatic events are predicted to increase in intensity and duration. During these periods, less favourable conditions may prevail and reduce the availability of sheltered cooler areas, which are critically important for insects and other small arthropods with limited motility, especially in open fragmented habitats, characteristic for highly managed landscapes. As mentioned above, it is important to consider relevant spatial scales when studying the effects of climatic conditions on biotic interactions. In microhabitats smaller than 1 m, the microclimatic conditions can be highly variable strongly impacting on their ectothermic inhabitants. Microclimatic refuge availability is of crucial importance for insect conservation as a strategy to cope with climate change (Thakur et al., 2020). Programs aimed at insect conservation and recovery thus need to acknowledge the importance of microclimates along with other habitat management options (Harvey et al., 2020a).

Declaration of interest

The authors declare no competing interests.

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