














RESEARCH ARTICLE

Microhabitat conditions remedy heat stress effects on insect activity

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Abstract

Anthropogenic global warming has major implications for mobile terrestrial insects, including long-term effects from constant warming, for example, on species distribution patterns, and short-term effects from heat extremes that induce immediate physiological responses. To cope with heat extremes, they either have to reduce their activity or move to preferable microhabitats. The availability of favorable microhabitat conditions is strongly promoted by the spatial heterogeneity of habitats, which is often reduced by anthropogenic land transformation. Thus, it is decisive to understand the combined effects of these global change drivers on insect activity. Here, we assessed the movement activity of six insect species (from three orders) in response to heat stress using a unique tracking approach via radio frequency identification. We tracked 465 individuals at the iDiv Ecotron across a temperature gradient up to 38.7°C. In addition, we varied microhabitat conditions by adding leaf litter from four different tree species to the experimental units, either spatially separated or well mixed. Our results show opposing effects of heat extremes on insect activity depending on the microhabitat conditions. The insect community significantly decreased its activity in the mixed litter scenario, while we found a strong positive effect on activity in the separated litter scenario. We hypothesize that the simultaneous availability of thermal refugia as well as resources provided by the mixed litter scenario allows animals to reduce their activity and save energy in response to heat stress. Contrary, the spatial separation of beneficial microclimatic conditions and resources forces animals to increase their activity to fulfill their energetic needs. Thus, our study highlights the importance of habitat heterogeneity on smaller scales, because it may buffer the consequences of extreme temperatures of insect performance and survival under global change.

KEYWORDS

animal movement, habitat composition, heat extremes, homogenization, microclimate, microhabitat variability, radio frequency identification, temperature increase, warming

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1 | INTRODUCTION

Anthropogenic global warming does not only imply generally higher average temperatures, but also imposes more frequent extreme heat events (Fischer & Knutti, 2015; IPCC, 2021; Luber & McGeehin, 2008; Rahmstorf & Coumou, 2011). Simultaneously, habitat modification by humans diminishes microhabitat variability and the accessibility of potential thermal refugia in preferred habitats through fragmentation (Travis, 2003). Increases in extreme heat events along with declines in thermal refugia, therefore, can have severe consequences for population dynamics, animal survival, and biodiversity patterns under progressing climate change (Harvey et al., 2020, 2022; Nakano et al., 1996; Suggitt et al., 2018).

Ectotherms commonly show unimodal responses to temperature in their physiology and performance (Ehnes et al., 2011), implying reductions in, for example, basal energy expenditure or movement activity at very high temperatures. Mobility is critical for individual performance (Cecchetto et al., 2020; Rezende & Bozinovic, 2019), because it allows organisms to access resources, reproductive sites, or refugia, thus enabling or preventing interactions (Bonte & Dahirel, 2017; Goossens et al., 2020). However, activity is also coupled with additional energetic costs (Alexander, 2005; Halsey, 2016). Thus, animals might risk a disproportionately high energy expenditure by being active during heat extremes if there are not enough resources available to compensate for elevated energy loss (Huey & Kingsolver, 2019). Consequently, reduced movement in response to heat extremes increases the thermal tolerance by reducing the metabolic demands but also decreases the energy gain by limiting the access to resources.

Microhabitat conditions can have important implications for this general response to heat stress (Kearney et al., 2021; C.-S. Ma et al., 2021; G. Ma et al., 2018; Scheffers et al., 2014; Thakur et al., 2020) and can thus be beneficial for species persistence under climate change (Hof et al., 2011; Suggitt et al., 2018). Generally, microhabitats can be interpreted as landscapes at a very small scale, depending on the organism's body size, which comprises the composition and the spatial arrangement of biotic as well as abiotic material (Beck, 2000; Bell et al., 1991; Byrne, 2007). For instance, different leaf litter types provide distinct physical conditions like habitat structure (e.g., for protection against predators, see Kalinkat et al., 2013) and resources (Ott et al., 2012), but also microclimates, for instance in terms of temperature, humidity, or light intensity. These microclimates can help animals cope with extreme temperatures (Scheffers et al., 2014; Suggitt et al., 2018) by enabling them to maintain the optimal body temperature and lowering the metabolic costs (Bennett, 2004; Kearney et al., 2009). The microhabitat can provide any combination of low or high availability in refugia and resource availability (Figure 1). One important component, which essentially shapes the structure as well as resource availability of a habitat, is stoichiometry, which describes the C:N:P ratios of resources and therefore their respective quality (Sturner & Elser, 2002). Stoichiometry has diverse effects on community structure and ecosystem functioning (Hillebrand et al., 2014) by driving decomposer

feeding rates (Jochum, Barnes, Ott, et al., 2017; Ott et al., 2012) and thus population densities of decomposers and higher trophic levels (Jochum, Barnes, Ott, et al., 2017; Ott et al., 2014). In our study, we use invertebrate communities inhabiting forest litter as an example. Here, we find distinct decomposition conditions determining not only the resource availability, but also the openness of a habitat (i.e., less or no substrate). Litter with high nutrient content usually yields high decomposition rates and high resource availability. Moreover, the secondary metabolites that plants and their litter release into the soil can limit the growth and activity of decomposers, yet little is known about the direct impact of secondary metabolites on the abundance and diversity of soil microorganisms and fauna (Chomel et al., 2016). When litter is quickly decomposed, the habitat often lacks potential refugia against predation or heat. This general pattern implies that only habitats with mixed litter types can provide refugia and resources simultaneously. In contrast, structurally separated habitats like monocultures can only provide either resources or refugia. Such scenarios on a smaller scale would force animals to switch between areas of benign microclimate and high resource availability resulting in overall higher activity rates at heat extremes. The decision between movement and therefore energy loss with the chance of encountering resources (i.e., energy gain) or inactivity to keep energy expenditure to a minimum (Black et al., 2019) should therefore vary with habitat conditions. To predict responses to temperature extremes, it is therefore important to investigate both the drivers (warming and habitat conditions) and physiological traits (metabolism and movement) in an integrative framework (Hof, 2021).

Although insects exist in enormous numbers on Earth and have tremendous functional importance for ecological patterns and processes (Wilson, 1987), we still lack systematic information on movement behavior and activity dynamics under natural conditions in the form of tracking data for invertebrates (Kissling et al., 2014), which is mostly caused by the difficulties of applying tracking technologies. Although automated image-based tracking technology has proven applicable in many ecological and behavioral experiments, it is difficult to apply in complex physical habitats (Dell et al., 2014). Tracking with heavier active tags is limited to vertebrates of larger body size (Wikelski et al., 2007). Passive tags are lighter and smaller because they do not require an additional power supply (Roberts, 2006). In this context, radio frequency identification (RFID), which is commonly used in the everyday life of humans to identify objects or persons, has found application in ecological research, mainly for tracking arrival and departure of social, flying insects (Barlow & O'Neill, 2020). Here, we developed a new RFID-based method to track the movement of invertebrates by an array of active sensors set up in the field or experimental units prior to the study. We provide a detailed description of this experimental approach and employ the method in a mesocosm experiment to assess the movement activity of an insect community in response to heat stress under different microhabitat scenarios (Figures 1 and 2). We hypothesize that animals can lower their activity in response to heat stress only under a mixed litter scenario as it provides a spatially homogeneous distribution of food and refugia. In contrast, animals would need to

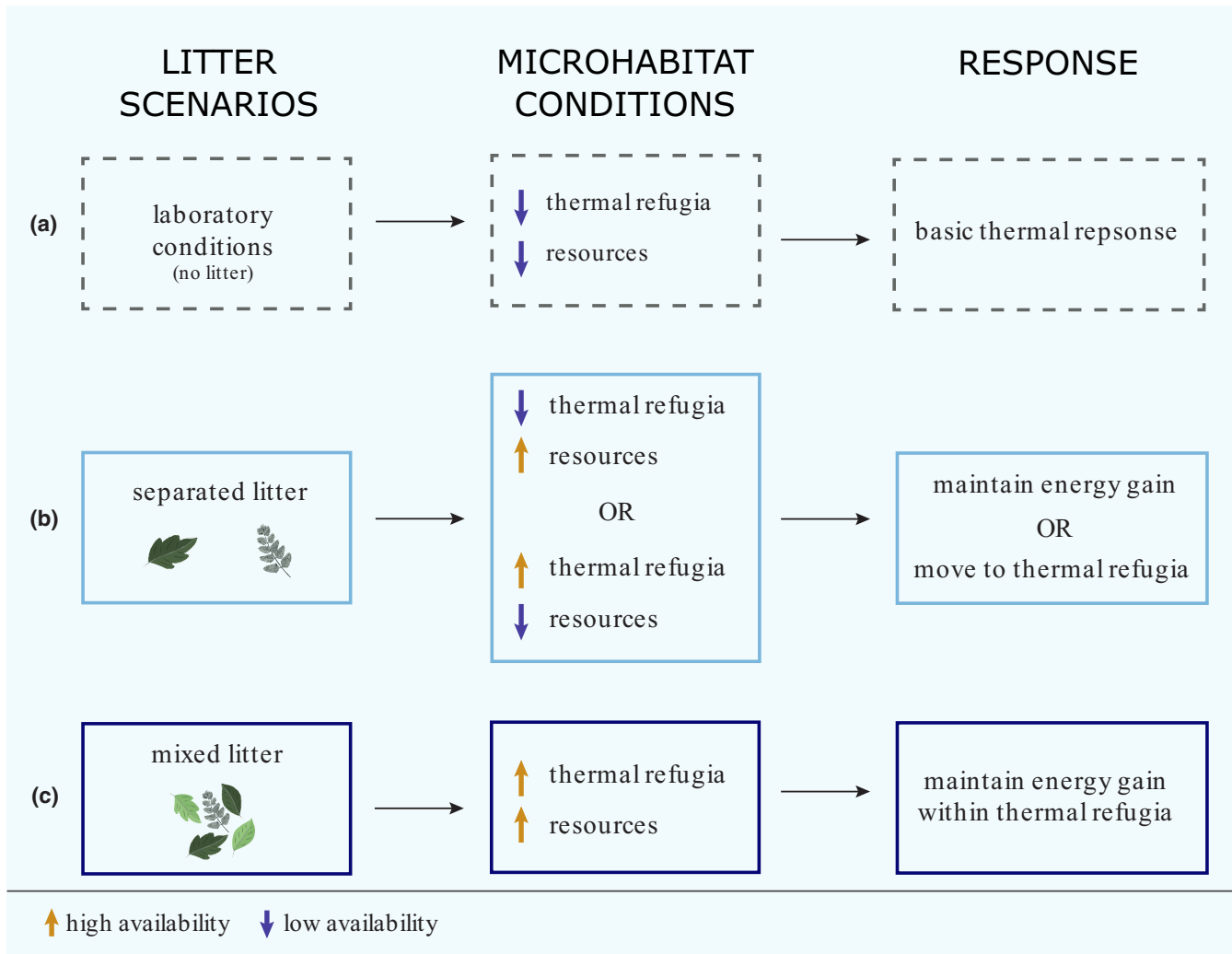


FIGURE 1 Conceptual illustration of the potential thermal consequences of different scenarios of microhabitat conditions. (a) Basic thermal response measured for instance under laboratory conditions without any habitat structure or resources. (b) Spatially separated or (c) simultaneous provision of refugia and resources under a mixed litter scenario.

maintain their activity in microhabitats that only provide either refugia or resources to meet their energetic demands.

2 | METHODS

2.1 | General setup and experimental design

The iDiv Ecotron platform is an indoor mesocosm facility (Figure 2a) consisting of 24 independent, experimental chambers, the so-called “EcoUnits” (Schmidt et al., 2021). The Ecotron platform is located in Bad Lauchstädt, Saxony-Anhalt, Germany, at the Experimental Research Station of the Helmholtz Centre for Environmental Research (UFZ, 51.3917°N, 11.8762°E). Within each EcoUnit environmental conditions such as light, nutrient supply, and precipitation can be fully controlled and abiotic as well as biotic factors can be measured using non-invasive methods. Each EcoUnit consists of an aboveground and belowground part, with internal

dimensions of 1.46 m × 1.46 m × 1.50 m ($L \times W \times H$; aboveground) and 1.24 m × 1.24 m × 0.80 m ($L \times W \times H$; belowground). The soil surface area measured 1.5 m². We used in total 12 EcoUnits from the iDiv Ecotron platform.

We filled all EcoUnits with topsoil, which we bought from a local supplier. The duration of light was equal across all units. Dawn started at 5 a.m., increasing light intensity up to 25% until 6 a.m., then increasing light intensity up to 100% until 7 a.m. Dusk started at 7 p.m., decreasing light intensity to 25% until 8 p.m., and then decreasing light intensity to 0% until 9 p.m. (Figure S6). Irrigation treatments happened twice a day at 6 a.m. and 6 p.m. with 750 mL water per quadrant, yielding 6000 mL per day and unit (Figure S7). In addition, four oak clone phytometer (PhytOakmeters; Herrmann et al., 2016) per EcoUnit were planted and harvested at the end of the experiment to take samples of leaves, roots, rhizosphere and bulk soil. However, the data were not used for the analyses presented here. We kept up these treatments during the whole experimental phase.

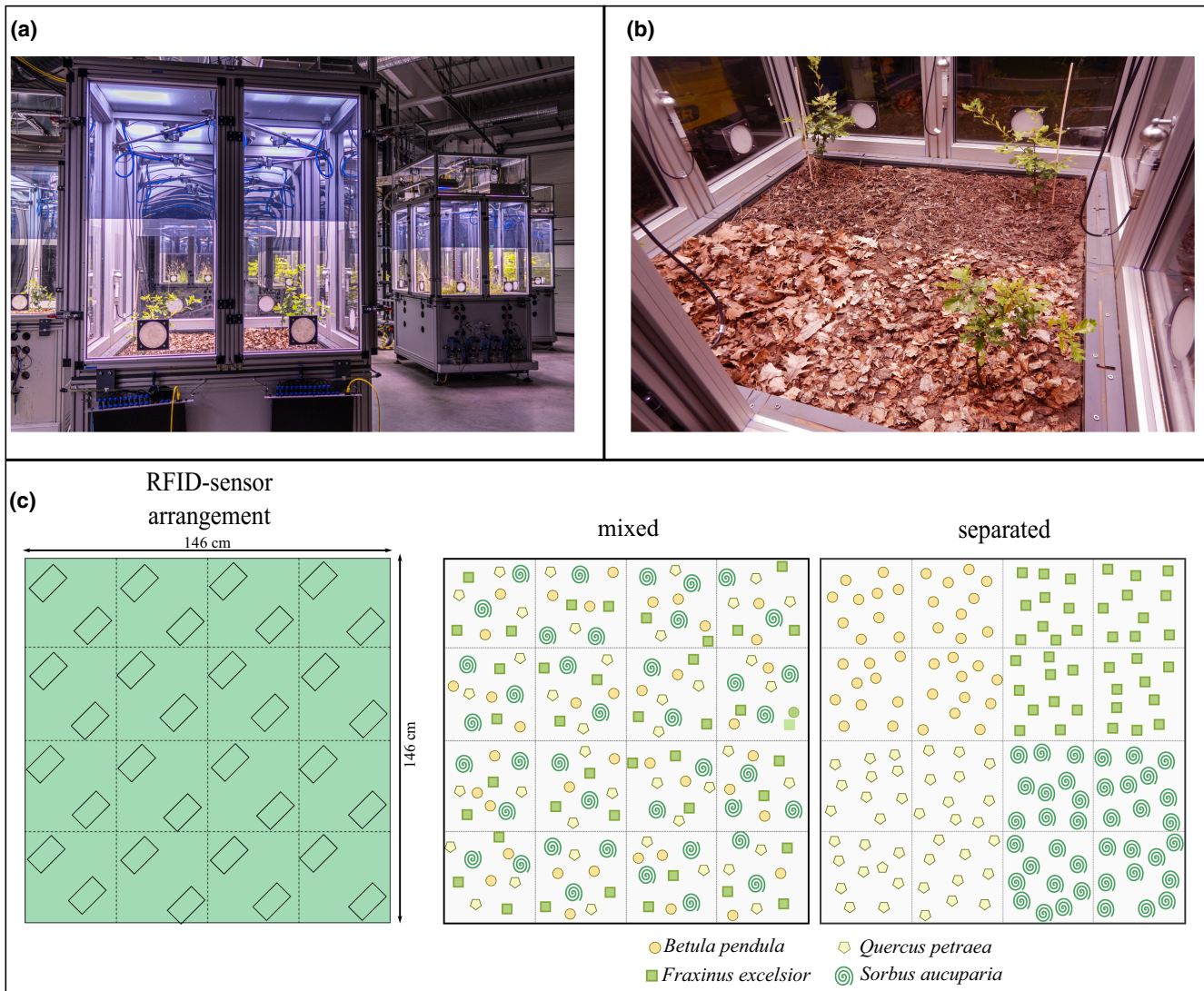


FIGURE 2 Experimental setup of the Ecotron experiment. (a) Ecotron facility in Bad Lauchstädt. (b) Experimental design in an EcoUnit. (c) On the left, the spatial arrangement of 32 RFID sensors (small rectangles) with a size of 75 mm × 50 mm (L × W) and a distance between each sensor of approximately 20 cm; in the middle, a scenario with mixed litter and on the right, a scenario with separated litter. The small symbols (circle, square, pentagon, and spiral) represent the four different litter types (*Betula pendula*, *Fraxinus excelsior*, *Quercus petraea*, and *Sorbus aucuparia*). Note that the figure is not true to scale. RFID, radio frequency identification.

2.2 | Temperature treatment

Generally, heat extremes describe a period of several consecutive days with hot temperatures during the day and also warm nights (Perkins et al., 2012). Since there are no unified definitions or indices in research of heat extremes or heat waves (Horton et al., 2016; Perkins, 2015), we simulated heat extremes based on data of the Deutscher Wetterdienst for the respective geographic region, where the experiments took place. Here the regional mean temperature during summer (July, August, September) for 2018 and 2019 was 20.1 and 20.2°C, respectively (Deutscher Wetterdienst, 2020a, 2020b). The highest temperature in August 2019, which was measured at the closest climate station (Leipzig/Halle), was 33.3°C (Deutscher Wetterdienst, 2019). To generate

heat extremes exceeding present and regional temperatures, we used construction dryers to blow hot air into each of the EcoUnits, thereby increasing the ambient air temperature. Thereby, we regulated the amount of hot air supplied according to the experimental target temperature in each of the EcoUnits. To allow for natural temperature fluctuations, we aligned the temperature regulation in each of the EcoUnits with the ambient temperature in the hall and then specified a temperature difference from this ambient temperature according to each treatment. Hence, we kept natural day–night cycles as well as daily temperature fluctuations. All EcoUnits were equipped with four sensors, each measuring the air temperature every minute. Across all experimental blocks and EcoUnits, we had temperatures ranging from a minimum of 18.5°C to a maximum of 38.7°C (Figure S8).

2.3 | Microhabitat scenarios

We established a mixed and a separated litter scenario and crossed those with the temperature treatments. For this, we used leaf litter mixtures of four different tree species: oak (*Quercus petraea*), ash (*Fraxinus excelsior*), mountain ash (*Sorbus aucuparia*), and birch (*Betula pendula*) that are part of the MyDiv Experiment (Ferlian et al., 2017). These litter species have distinct nutrient compositions, with ash and mountain ash having good stoichiometry (indicated by a high C/N ratio) compared to the rather poor stoichiometry of oak and birch (Ferlian et al., 2017). We filled six EcoUnits with mixed leaf litter and the other six EcoUnits with separated leaf litter in quadrants. The litter was collected in the MyDiv Experiment in Bad Lauchstädt (51.3917°N, 11.8855°E) and air-dried on a large tarpaulin over several weeks. We added the same biomass of litter per species and quadrant or of an equal mixture of all four species per quadrant to each of the EcoUnits (Figure 2b). We randomly assigned habitat scenarios to the EcoUnits. In addition, we randomized the respective leaf litter species to each quadrant for the EcoUnits with separated litter.

To test our hypotheses on microhabitat conditions, we measured for each EcoUnit with mixed litter as well as for each quadrant in EcoUnits with separated litter (1) the abiotic conditions as a proxy for the microclimate and (2) leaf litter biomass and (3) fungivore nematode densities as a proxy for resource availability. Higher decomposition of leaf litter leads to shifts from plant litter to animal biomasses. We used fungivore nematodes as an indicator for animal biomass at the decomposer level. It can be expected that these higher biomasses cascade to higher trophic levels in the food web providing an overall higher resource availability. Moreover, higher leaf litter biomass provides a thicker layer of foliage and thus better protection against predators (Figure 2b).

To assess microclimatic conditions, we used data loggers that measure soil moisture and soil temperature in a depth of 150–210mm below the soil surface every second. Measurements at soil surface below the leaf litter were not possible due to the applied RFID sensors. We then calculated the deviation of the specific soil temperature and moisture of the quadrant from the average conditions in the respective unit per experimental block (Table S3). At the end of the entire experimental period, we removed the litter from the EcoUnits and dried them in an oven at a temperature of 70°C. Afterwards, we weighed each litter sample per unit and quadrant to compare the final litter biomasses (Table S4). Nematodes were extracted from 25g of fresh soil using the Baermann funnel method (Barker, 1985) and counted using an inverted microscope (Nikon TS100) after fixation in 4% formaldehyde. The first 100 individuals encountered were identified to genus level. All nematode individuals were assigned to one of the five trophic groups: bacterivores, fungivores, omnivores, predators, and herbivores (Yeates et al., 1993) (Table S5).

We then conducted contrast analyses on our variables of interest (soil temperature and moisture, leaf litter biomass, nematode

density) between litter groups with good (*F. excelsior* and *S. aucuparia*) and poor stoichiometry (*B. pendula* and *Q. petraea*).

2.4 | Study animals

We used pitfall traps to collect most of the study organisms in Leipzig and its surrounding area, Saxony, Germany (51.3213°N, 12.3964°E and 51.2799°N, 12.4119°E). Our species selection depended on seasonal occurrences and densities, which yielded five species: *Carabus coriaceus* (Linnaeus), *Carabus nemoralis* (Müller), *Nebria brevicollis* (Fabricius), *Pterostichus melanarius* (Illiger) (Coleoptera), and *Pyrrochoris apterus* (Linnaeus, Heteroptera), which were complemented by *Acheta domesticus* (Linnaeus, Orthoptera) that was bought from a commercial supplier (Insektenfarm L. Seitz). Each of these six species was added to the EcoUnits at densities that reflect a natural abundance–mass relationship (Table S6). In total, we inserted 1020 insects across six species and three orders. Body masses ranged from 30 mg (*P. apterus*) to 2179 mg (*C. coriaceus*).

2.5 | RFID tracking system

The RFID tracking system we designed for our study consists of three standard components: passive RFID tags, RFID sensors (transceivers), and a host system (controller). Each of the sensors is equipped with an antenna that emits radio waves at a certain frequency, thereby activating the passive tag when it is in the vicinity. In this way, the tag transmits its tag information (a unique tag ID), which is detected by the sensor's antenna (Roberts, 2006). So far, several studies have used this technology to investigate the activity (e.g., coming and going) and behavior of pollinators (e.g., social insects and hummingbirds) at a central location, such as a hive or feeding station (Barlow & O'Neill, 2020; de Souza et al., 2018). However, the tags used in these studies often had an exterior, long-range antenna, which is not suitable for tracking movements in a complex habitat. Therefore, we used modified tags (see below) without antennas for our approach.

We equipped all EcoUnits with 32 RFID sensors (see Supplementary Information for a detailed description on manufacturing and technical information, Tables S1 and S2; Figures S1–S5) evenly distributed on the ground, loosely covered by soil (Figure 2c). These RFID sensors were cable-connected to a controller (fabricated by UP GmbH) that stored the data of the sensors on a database.

One day before the start of each experimental block, we weighed the animals and tagged each individual with an RFID tag. For this, we chilled the insects at 5°C for 15 min. We then applied a small amount of multi-purpose instant contact adhesive (Evo-Stik) to the elytra of the beetles or the center of the thorax of the other orders. We recorded the ID of the tag together with the identity and weight of the individual. The size and weight of the RFID tag was chosen according to the individual body mass. We used medium-sized and small RFID tags from Murata Manufacturing Co. Medium-sized tags measured

8.3×8.3×10.7 mm (product number LXMSAPHA17-176) and the small tags 3.2×3.2×0.75 mm (product number LXMS33HCNK-171). Pre-experiments showed that the reading range (maximum distance to the sensor yielding a successful read of the tag ID) of the medium-sized and small tags is 25 and 12 mm, respectively, which corresponds to the differences in leg length of the insects and thereby differences in the distance to the ground while moving.

Each tag had a unique identification number. When crossing the sensors in the EcoUnit, each individual was identified with a unique timestamp (i.e. time of detection) as well as the x- and y-coordinates corresponding to the exact position of the sensor within the respective EcoUnit. Each detection was used as an indicator of activity. To exclude cases where an individual stopped on or near a sensor and was thus sequentially detected, we defined detections as distinct when at least 10 s elapsed between them.

The entire experiment ran from June to October 2019 and was conducted in collaboration with other research groups. During this time, we introduced new insects three times followed by 10–14 days of no disturbance (e.g., opening chambers). For our main analysis, we only used these three experimental blocks. Nonetheless, detections between the experimental blocks were continuously recorded.

To analyze movement activity in response to temperature and microhabitat conditions, we tested how the sum of detections per species in an EcoUnit per day/night depended on the average day and night temperature (°C) and the microhabitat scenario (separated vs. mixed) (Terlau et al., 2023, data set available in “Zenodo”). We defined day and night times based on the monthly times for sunrise to sunset (day) and sunset to sunrise (night) from 2022 [Laenderdaten.info](https://laenderdaten.info) (2022). This way, we ensured that a broader temperature range of the daytime during which detections occurred was related to movement activity. We fitted a generalized linear mixed model using template model builder by applying the `glmmTMB` package (Brooks et al., 2017). Due to overdispersion, we used a negative binomial distribution. We used the sum of detections as the response variable, temperature and the microhabitat scenario as fixed factors with interaction term and the experimental block as a random factor. We also accounted for temporal autocorrelation of the detections within each block. We performed an analysis of deviance (ANOVA) on our model using the `car` package (Fox & Sandford, 2019). To examine the sensitivity of our analysis to the shorter time scale of our three experimental blocks, we also performed the statistical tests on the full data set.

In a second analysis, we analyzed the temperature effect on activity for the different litter species separately using the sum of detections as the response variable, temperature and the litter species as fixed factors with interaction term, and the experimental block as a random factor for the subset of the separated litter scenario.

All statistics were performed using R 4.2.1 (R Core Team, 2022).

3 | RESULTS

We found significantly different microhabitat conditions in the four quadrants of the separated litter scenario. Regarding microclimatic

conditions, quadrants with litter of poor stoichiometry (*B. pendula* and *Q. petraea*) had significantly lower soil temperature ($p=.001$, Figure 3a) and higher soil moisture ($p=.005$, Figure 3b) compared to quadrants with litter of good stoichiometry (*F. excelsior* and *S. aucuparia*). Regarding resource availability, we found significantly higher litter biomass densities at the end of the experiment under poor than good stoichiometric conditions ($p<.001$, Figure 3c), indicating higher decomposition rates in quadrants with good litter stoichiometry. The lower litter biomass densities in quadrants with *F. excelsior* and *S. aucuparia* results in a thinner foliage layer and thus a poorer temperature buffer and higher evapotranspiration, contributing to the higher soil temperatures and lower soil moisture in these quadrants (Figure 3a,b). Consistently, we found significantly higher densities of fungivore nematodes for these litter types ($p=.002$, Figure 3d). We chose fungivore nematodes as an indicator group for the conversion of plant to animal biomass and thus resource availability at the base of the food chains, but similar results were found when considering the full nematode community ($p=.009$, Figure S9). As expected, the EcoUnit-level microhabitat conditions in the mixed litter scenario are intermediate between conditions of the individual litter types (Figure 3, mixed). Overall, these results suggest poorer microclimatic conditions (i.e. higher temperature and lower soil moisture) but higher litter decomposition rates and higher animal densities in quadrants with litter of high stoichiometric quality (*F. excelsior* and *S. aucuparia*). Moreover, we find intermediate but spatially homogeneously distributed microhabitat conditions in the mixed litter scenario.

To investigate how activity of insects responds to temperature extremes and how this is affected by different types of habitat heterogeneity, we analyzed RFID tracking data of 465 detected insects (n). In the mixed litter scenario, we found a significant negative effect ($p\leq.0001$, $n=235$) of temperature on the overall number of detections across the community (Table 1, slope = -0.06 , implying decreases in the sum of detections from ~ 11 at 20°C to ~ 2 at 38°C). Contrary, we found a significant positive temperature effect in the separated litter scenario ($p=.04$, $n=230$, Table 1; Figure 4). This indicates significantly different (ANOVA, $p\leq.0001$, Table S7) and opposing temperature effects on insect activity depending on the microhabitat conditions.

To test if this short-term response observed within our undisturbed experimental blocks (10–14 days) mirrors the long-term effect across the full experimental period (111 days), we conducted a sensitivity analysis on the full data set ($n=602$). In line with our main results, we found a significant negative effect of temperature in the mixed litter scenario ($p\leq.0001$, slope = -0.09) and a significant positive temperature effect in the separated litter scenario ($p=.004$, slope = 0.04 , Figure S10; Table S8).

This implies that animals generally reduce their movement activity in response to heat extremes when the litter is well mixed. In contrast, they increase their activity under spatially distinct microhabitat conditions (Figure 4).

To investigate in detail how activity of insects responds to temperature extremes depending on the different litter species, we analyzed a subset of the tracking data for the separated litter scenario

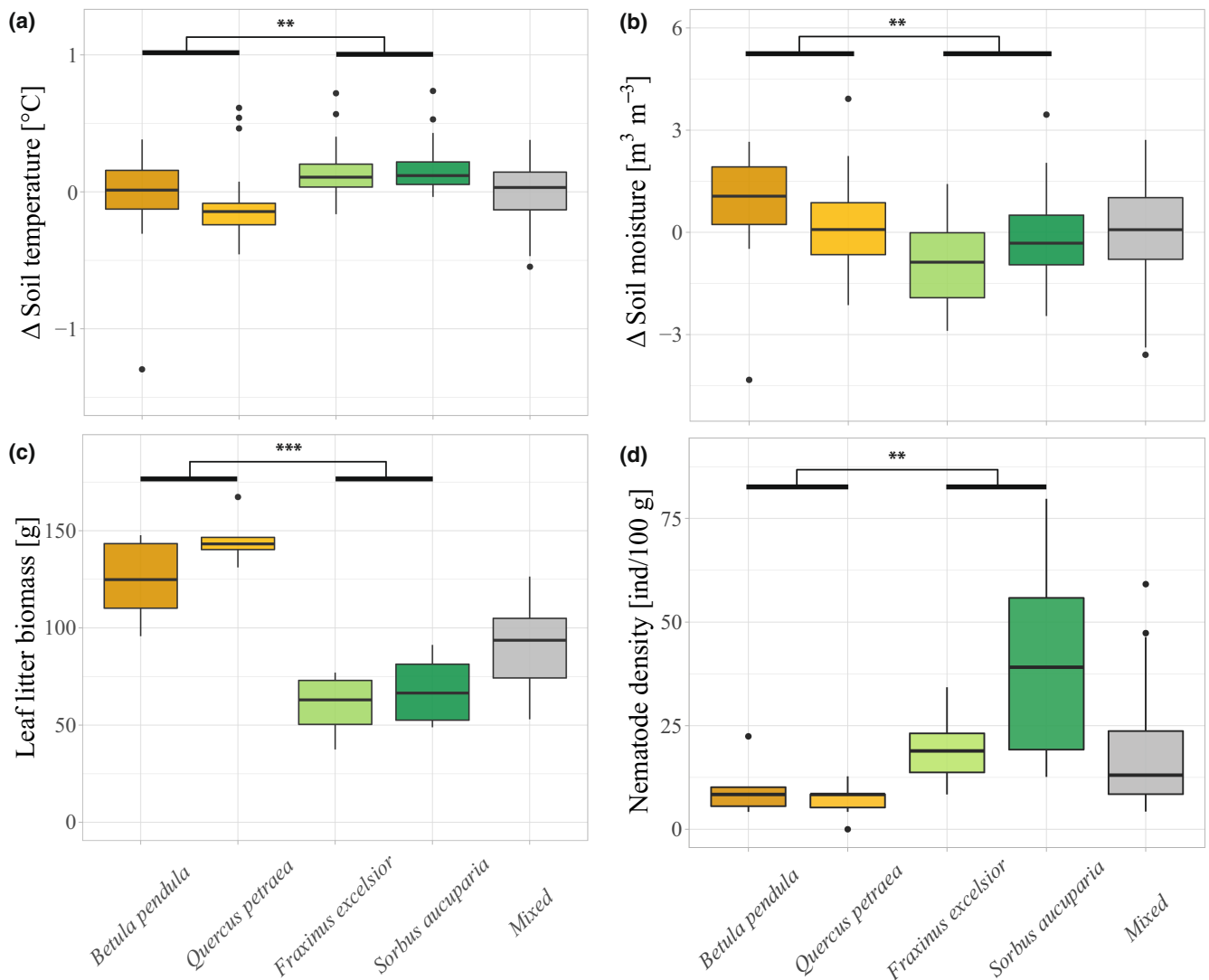


FIGURE 3 Microhabitat conditions in the different quadrants of the separated litter scenario and average conditions in EcoUnits with mixed litter. (a) Deviation of soil temperature and (b) soil moisture from the average conditions in the EcoUnit. (c) Leaf litter biomass and (d) fungivore nematode density at the end of the experiment. Yellow color code represents quadrants with poor and green color code quadrants with good stoichiometry. The significance levels are $**p < .01$ and $***p < .001$.

TABLE 1 Statistical results of the generalized linear mixed effects model using model template builder (glmmTMB) for sum of detections ~ temperature * microhabitat variability as fixed factors and the experimental block as a random factor using a negative binomial distribution.

Predictors	Estimates	SE	p-value
Intercept [mixed habitat]	4.38	0.47	<.0001
Intercept [separated habitat]	1.48	0.52	.004
Slope [temperature: mixed habitat]	-0.06	0.02	<.0001
Slope [temperature: separated habitat]	0.04	0.02	.014

including 230 detected individuals. We only found a significant positive effect of temperature in the quadrants with the low-quality litter of *B. pendula* ($p = .0008$, Figure 5a) and *Q. petraea* ($p = .002$, Figure 5c), whereas the quadrants with the high-quality litter of *F. excelsior* and *S. aucuparia* did not show any significant temperature effect on activity (Figure 5b,d; Table S9). This implies that beetles only showed an increased activity in response to heat in areas with favorable microclimatic conditions.

4 | DISCUSSION

Here, using a novel RFID tracking approach, we showed that the movement activity of a ground-dwelling insect community to heat stress strongly depends on the microhabitat conditions.

Within the tracking experiment, we overall detected 465 of the 1020 tagged individuals, or approximately 46% of all individuals that have been inserted into the EcoUnits. Some individuals might

not have been detected because they lost their tags during the first hours of the experiment. In addition, due to the shorter detection range of passive tags (Roberts, 2006), sensors cannot detect animals that are not close enough to the RFID sensor or pass it too quickly. For the individuals detected, however, we found an opposing response of activity to heat depending on the respective microhabitat conditions.

Consistent with other studies (Cecchetto et al., 2020; Rezende & Bozinovic, 2019; Terlau et al., 2022), we found that animals become less active in response to heat extremes, but only in the mixed litter scenario. In contrast, we found a general increase of movement activity in the separated litter scenario. This is likely driven by the

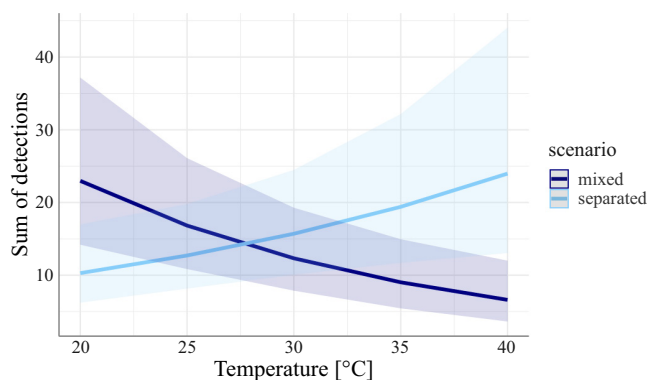


FIGURE 4 Insect activity in response to temperature across all six insect species and experimental blocks for the different types of microhabitat condition scenarios.

difference in microhabitat conditions provided by these scenarios, which are in litter habitats highly dependent on stoichiometry. Thus, the litter species, providing each a distinct stoichiometric composition, plays a crucial role regarding resource quality, quantity, and decomposition conditions. Qualitatively poor resources imply a low decomposition activity (Güsewell & Gessner, 2009; Ott et al., 2012). In this vein, poor litter stoichiometry leads to low decomposer densities and growth rates implying less resources for predators (Rosenblatt & Schmitz, 2016), which causes lower predator biomass densities in habitats with stoichiometrically poor litter (Jochum, Barnes, Weigelt, et al., 2017). This is consistent with our results showing distinct structural, microclimatic, and resource conditions in the separated litter scenario. While the litter types with poor stoichiometry (*B. pendula* and *Q. petraea*) provided a thicker layer of foliage at the end of the experiment and thereby better microclimatic conditions and protection against, for example, predators (Kalinkat et al., 2013), their lower decomposition rates also lead to lower animal densities (indicated by low nematode densities with likely cascading effects to higher trophic levels, see also Kalinkat et al., 2013). This supports our initial hypothesis on the spatial separation of areas providing shelter vs. resources in the separated litter scenario. Contrary, the mixed litter scenario offered a homogeneous distribution of intermediate microhabitat conditions across the EcoUnits. This had profound consequences for the movement activity of the larger invertebrate community.

The mixed litter scenario with its homogeneous distribution of resources and refugia, thus, allows animals to lower their activity

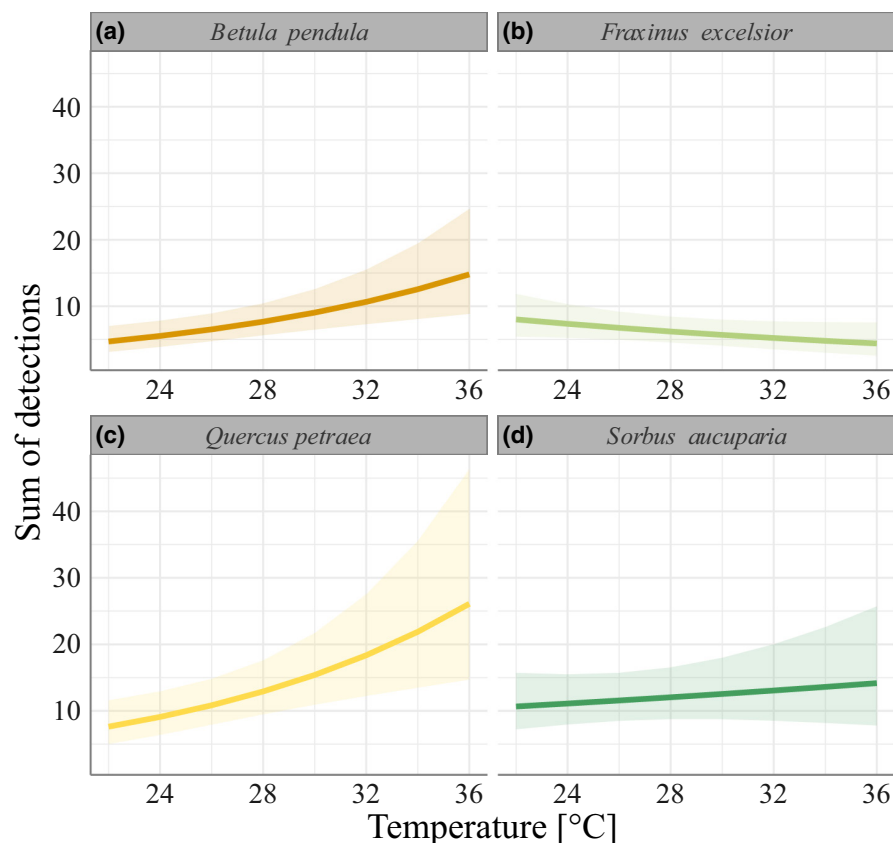


FIGURE 5 Insect activity in response to temperature in the separated litter scenario for (a) *Betula pendula*, (b) *Fraxinus excelsior*, (c) *Quercus petraea*, and (d) *Sorbus aucuparia*. Yellow color code represents quadrants with poor and green color code quadrants with good stoichiometry.

rates. Although this lower activity can cause lowered feedings rates and therefore lowered energy gain, inactivity also reduces the energetic costs that would have been generated by movement (Terlau et al., 2022). In the short term, reduced activity is thus a good strategy to buffer against heat stress and avoid overheating (Kearney et al., 2009). If these extreme heat periods occur numerous times or over longer periods, however, this can cause energetic struggles leading to shifts in activity periods (seasonal and diurnal). This can potentially create activity mismatches between trophic levels, hence imposing cascading effects across food webs (Seebacher & Post, 2015).

In the separated litter scenario, animals increase their overall activity in response to heat stress, which is likely due to the spatial segregation of thermal refugia, which may force animals to move more to find good microclimatic conditions and simultaneously fulfill their energetic needs through feeding. This simultaneously increases the energetic costs due to higher metabolism and higher movement, indicating that animals are at a greater risk of overheating. At the same time, if feeding rates increase less than the energetic costs, this can yield severe energetic mismatches (Huey & Kingsolver, 2019). Overall, poorer microhabitat conditions, for example, due to low habitat heterogeneity, can thus enforce the negative impacts of heat stress on performance and survival of invertebrates. In consequence, animals would either need to adapt genetically to adjust their thermal range (Somero, 2010) or move to thermally preferable areas (Kearney et al., 2009) in response to climate change.

4.1 | Future perspectives

Here, we conducted a closed mesocosm experiment to take advantage of the fully controlled but close to natural environmental conditions of the iDiv Ecotron (Schmidt et al., 2021), which allowed us to analyze the implications of heat stress on insect moving activity without any major confounding factors. Moreover, the setting allowed us to apply an RFID tracking system and track the movement of invertebrates for the first time in a near-natural environment. This experiment provided empirical evidence that microhabitat conditions play a crucial role for the thermal response of some terrestrial invertebrates to heat stress. If this pattern also holds for other taxa, this might represent a general response to temperature extremes with implications for a range of terrestrial ecosystems that experience severe modifications of their spatial structure and heterogeneity (Dainese et al., 2019; Gols et al., 2021). The next step would be to verify if this pattern also holds in the field where other factors and mechanisms come into play, such as species interactions.

While we used the sum of detections as a proxy for activity, future work could also focus on disentangling the underlying movement paths, which include duration of activity or movement speed of single individuals. This could also help to reveal spatial patterns of habitat use in response to temperature. This, however, would require a higher density of RFID sensors. Recent developments in

RFID technology (Barlow & O'Neill, 2020) are a great opportunity to expand this experimental approach to larger scales and a higher range of taxonomic groups.

Our experimental setup allowed us to study the effect of heat stress on local movements. However, temperature extremes will also have consequences for other movement processes, such as dispersal. Chances of survival are higher for active species, while temperature extremes have severe consequences for species with low dispersal capabilities (e.g., sessile species) (Peck et al., 2009). Moreover, the effects of thermal stress are often interactive and can be mitigated or intensified. For instance, desiccation and starvation enormously alter the thermal tolerance (Terblanche et al., 2011). Here, we kept irrigation constant over the duration of the experiment and thus tested only the pure temperature effect. However, global change drivers do not occur in isolation, but in combination causing and pushing on the collapse of diverse biomes and ecosystems (Rillig et al., 2019; Sage, 2020; Thakur et al., 2018). Thus, to gain a more realistic picture of the consequences of heat extremes for invertebrate activity, additional factors like drought (desiccation effects) or fragmented landscapes (dispersal success) should be included.

5 | CONCLUSION

By giving RFID tags a piggyback ride on insects, we showed that extreme temperatures may have opposing consequences for insect activity and therefore performance depending on the habitat conditions. Spatial separation of resources and suitable microclimates in different microhabitats imposes greater heat stress as animals must choose between lowered activity to achieve metabolic downregulation and access to resources. Generally, due to their body size, invertebrates experience their environment on a smaller spatial scale. Thus, we need further small-scale data on microhabitat conditions to get an idea of real-world microhabitat heterogeneity and the consequences of anthropogenic land transformation across the respective spatial scales. Our study underpins the importance of considering the habitat composition and configuration to understand the combined effects of heat extremes and land-use change on invertebrate performance and survival.

AUTHOR CONTRIBUTIONS

Jördis F. Terlau, Ulrich Brose, and Myriam R. Hirt conceptualized the study. Ulrich Brose, Myriam R. Hirt, Nico Eisenhauer, and Anja Schmidt designed the litter arrangement. Alban Gebler and Thomas Boy designed the technical setup. Jördis F. Terlau, Myriam R. Hirt, Ulrich Brose, Angelos Amyntas, Tao Liu, Anja Schmidt, and Alexander Dyer conducted experiments. Jördis F. Terlau, Myriam R. Hirt, Ulrich Brose, Christoph Scherber, and Ulrike E. Schlägel analyzed output data. Jördis F. Terlau wrote the first draft of the manuscript. Jördis F. Terlau, Myriam R. Hirt, Ulrich Brose, Nico Eisenhauer, Christian Hof, and Alexander Dyer contributed to data interpretation. All authors contributed substantially to revision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in "Zenodo" at [10.5281/zenodo.7784702](https://doi.org/10.5281/zenodo.7784702).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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