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Warming causes contrasting spider behavioural responses by changing their prey size spectra

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Predators may adapt to global warming via behavioural plasticity. However, empirical evidence showing such adaptations in terrestrial ecosystems is scarce. Here we report behavioural shifts that alter the web mesh size of two dominant predatory spider species in response to experimental warming in an alpine meadow field. Experimental large open-top chambers increased the mean annual air temperature by 0.6 °C, resulting in a decrease in the web mesh size of the large spider (−43.6%), and an increase in the web mesh size of the small spider (+79.8%). Structural equation models indicated that the changes in mesh size and web area were primarily the result of warming-induced changes in prey size spectra, which in turn were impacted by warming-induced changes in soil moisture and plant community. These results indicate that predators can adjust their behavioural responses to warming-induced changes in the physical setting and prey community.

Global warming presents a challenge to animals. Predators confront particularly complex changes: not only do they suffer from warming-associated abiotic stresses, including increased temperatures[1,2] and variation in water availability[3], but they also have to adapt to warming-induced changes in their biotic environment, such as changes in prey species abundance or community composition[4]. Because predators often play a pivotal role in modulating community structure and ecosystem functioning[4,5] and may buffer the negative effects of climate change on biological communities and ecosystems[6], understanding how predators respond to warming is critical to accurately predict future community and ecosystem responses to climate change[7,8].

In addition to evolutionary adaptation in response to different long-term selection regimes, predators can adjust to warming-induced environmental changes through two pathways operating on ecological time scales. First, they may shift their spatial distributions to avoid warming-associated abiotic stresses, as predicted by many climate envelope models[9,10]. Second, they may show physiological and behavioural plasticity, a phenomenon permitting species to mitigate abiotic and/or biotic stresses[2,11] without changing their biogeographic distributions. For example, long-term field investigations[9–11] have shown that terrestrial predators can alter their foraging behaviour (a phenomenon known as 'prey switch') in response to warming-induced changes in herbivore abundance.

However, terrestrial field experiments assessing the response of predators to novel abiotic and biotic environments induced by warming are remarkably rare, particularly at the level of entire communities over time frames sufficient to measure consequential behavioural and ecological responses[12–14]. This paucity of information can be attributed in large part to the use of active infrared heaters[15,16] in warming experiments, which usually allows for the free movement of animals, making it very difficult to accurately determine the response of animal abundance to warming. In addition, limited space in the small, passive,

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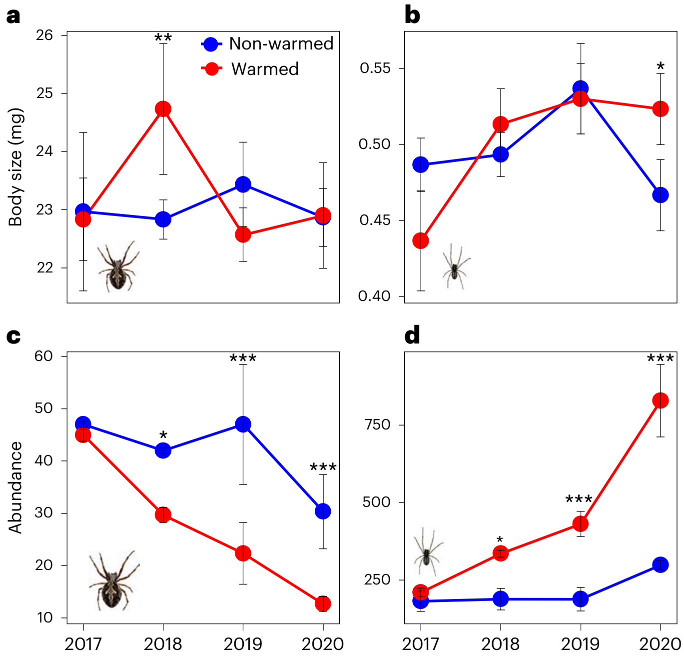

Fig. 1 | The effect of warming on spider abundance and body size. a–d, The body size (**a**,**b**) and abundance (**c**,**d**) difference for treatment of two dominant spider species (large spider *A. luosangensis* (**a**,**c**) and small spider *M. pusilla* (**b**,**d**)) in non-warmed and warmed OTCs during the experimental years 2017–2020. The data are shown as mean ± s.e.m. ($n = 3$). The treatment effects are determined by (G)LMMs with 'treatment' as a fixed factor and 'chamber identity' as a random factor. Significant differences: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. The statistical parameters (t and P values) are shown in Supplementary Table 4.

open-top chambers (OTCs) (typically <4 m^2) used to simulate warming may interfere with the successful completion of animal life histories requiring one or more years to unfold[14,17] and result in unnatural species loss in invertebrate communities. Consequently, the paucity of representative field experiments on biological communities precludes a general prediction regarding if and how predators will behaviourally respond to climate warming.

To address this gap in our knowledge, we conducted a field warming experiment in an alpine meadow using large OTCs (15 m × 15 m × 2.5 m (height)) (Methods) to elucidate the mechanisms underlying potential warming-induced population and behavioural changes in two locally dominant top arthropod predators, a large-bodied orb-weaver spider (*Aculepeira luosangensis*) and a small-bodied dwarf spider (*Microlinyphia pusilla*). We hypothesized that experimental warming would directly and/or indirectly alter spider behaviours (for example, behaviours related to resource acquisition) in this normally low-temperature site.

A number of behavioural responses are possible given this hypothesis. For example, increased temperature may increase per-capita respiration rates, and it may also increase spider foraging time and energy gain[18], particularly in low-temperature sites, such as the one studied here. If the energy gain overweighs the cost due to increased metabolism rate, spiders may have enough energy to increase web size and mesh size to increase their foraging efficiency. Moreover, increased temperature is often associated with decreased humidity[19], which could also alter spider behaviour, for example, decreased humidity may constrain the operation of silk-spinning organs, thereby decreasing web size and mesh size[20].

On the other hand, experimental warming may also indirectly affect spider behaviour by shifting the size spectrum of prey. For example, increased temperature may directly affect prey body size. Indeed, increased temperatures often reduce the body size of many arthropod species including those available to predatory spiders[21], and can shift the structure of arthropod communities by increasing the relative abundance of small-bodied species, while decreasing the abundance of large-bodied species[22]. In addition, increased temperatures can affect plant community composition to subsequently alter prey communities[23]. For example, experimental warming can shift an alpine meadow from a forb-dominated community to a graminoid-dominated community[24]. Arthropods feeding preferentially on graminoids are likely to be smaller than those feeding on forbs, as graminoids are less palatable (due to lower water content and specific leaf area), thereby limiting arthropod growth and reproduction[25]. Thus, warming-induced changes in plant community species composition may lead to decreased prey abundance and shift arthropod communities from a large-bodied-species-dominated community to a small-bodied-species-dominated community. Such a shift in the prey size spectrum may induce spiders to produce denser meshes (with smaller mesh sizes) as an adaptive behavioural response.

To test these possibilities, we investigated the plant community, prey abundance and body size, and spider abundance and behaviour (as reflected by the change in two important architectural components, namely, web diameter and mesh size[26]) in both non-warmed and warmed chambers for four consecutive years. In addition, we used structural equation models to assess the relative importance of direct and indirect effects on the behaviour of two dominant spiders differing in body size. Based on past empirical observations, we predicted that (1) the plant community would shift from a forb-dominated to a graminoid-dominated community, (2) the prey arthropod community would shift from a long-bodied to a short-bodied dominated community and finally (3) that spiders would decrease their web mesh size in response to a shifted prey size spectrum in the warmed chambers.

Response of spider body size, abundance and behaviour

Warming did not significantly affect the body size (dry mass) of *A. luosangensis* (linear mixed model (LMM): $F = 0.51$, $P = 0.48$, Fig. 1a) or

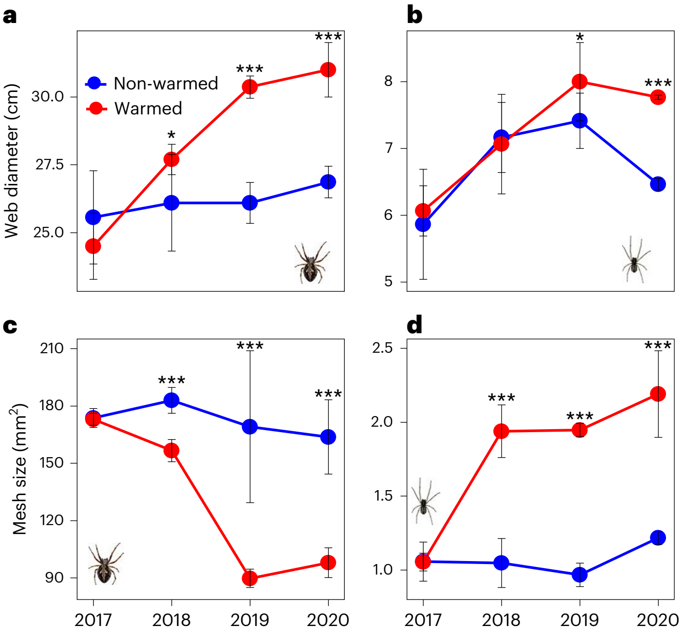

Fig. 2 | The response of web-building behaviours to warming in large and small spider species. a–d, The web diameter (**a**,**b**) and mesh size (**c**,**d**) of two dominant spider species (large spider *A. luosangensis* (**a**,**c**) and small spider *M. pusilla* (**b**,**d**)) in non-warmed and warmed OTCs during the experimental years 2017–2020. The data are shown as mean ± s.e.m ($n = 3$). The treatment effects are determined by (G)LMMs with 'treatment' as a fixed factor and 'chamber identity' as a random factor. Significant differences: $^{*}P < 0.05$; $^{***}P < 0.001$. The statistical parameters (t and P values) are shown in Supplementary Table 4.

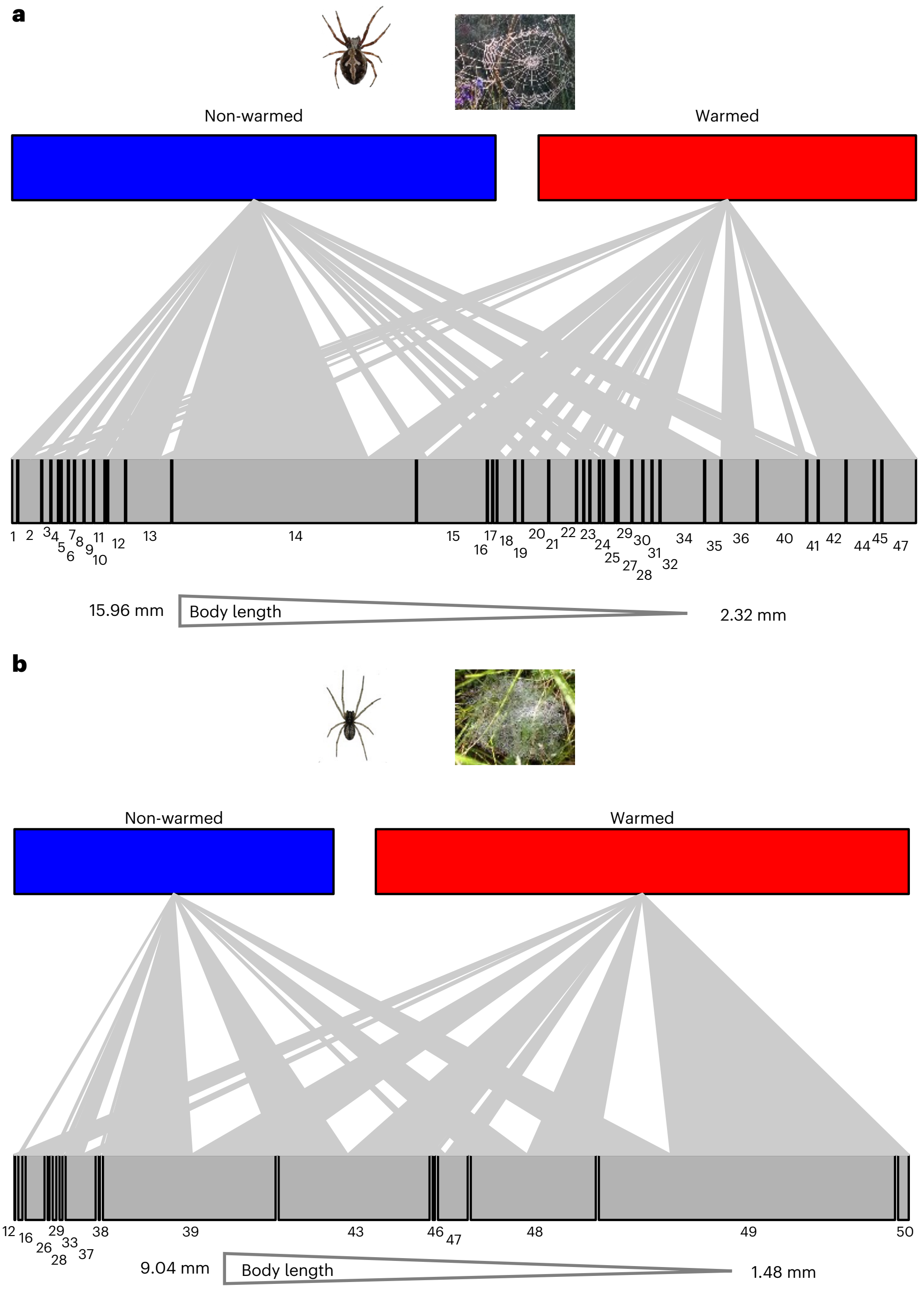

Fig. 3 | Prey species ordered by body size for both large and small spider species. a,**b**, The prey items of the two dominant spider species, that is, the large spider *A. luosangensis* (**a**) and the small spider *M. pusilla* (**b**), as shown in descending order of body length from left to right. The prey species denoted by the Arabic numerals are listed in Supplementary Table 2.

M. *pusilla* (LMM: $F = 0.15$, $P = 0.70$, Fig. 1b). However, it did differentially affect the abundance of both spiders, with a significant decline in *A. luosangensis* (−47.4%; generalized linear mixed model (GLMM): $\chi^2 = 57.66$, $P < 0.001$, Fig. 1c) and a significant increase in *M. pusilla* (+128.3%; GLMM: $\chi^2 = 47.18$, $P < 0.001$, Fig. 1d). Warming significantly increased the web diameter of *A. luosangensis* by 17.8% (LMM: $F = 63.51$, $P < 0.001$, Fig. 2a) and that of *M. pusilla* by 20.0% (LMM: $F = 22.40$, $P < 0.001$, Fig. 2b).

Warming had contrasting effects on mesh size, with a decrease in *A. luosangensis* webs by 43.6% (LMM: $F = 329.99$, $P < 0.001$, Fig. 2c) and an increase in *M. pusilla* webs by 79.8% (GLMM: $\chi^2 = 321.71$, $P < 0.001$, Fig. 2d and Supplementary Table 1).

Response of observed prey body length and foraging success

Warming significantly affected the community composition of prey species collected from the webs of both spider species (Fig. 3 and Supplementary Table 2). Warming significantly decreased the weighted body length of the observed prey of the large spider (Fisher–Pitman permutation test, $Z = 1.78$, $P < 0.05$, Fig. 4a), whereas the weighted body length of the observed prey items was indistinguishable between non-warmed and warmed chambers for *M. pusilla* (Fisher–Pitman permutation test, $Z = -1.10$, $P = 0.86$, Fig. 4b). The difference in prey body mass was indistinguishable at the species

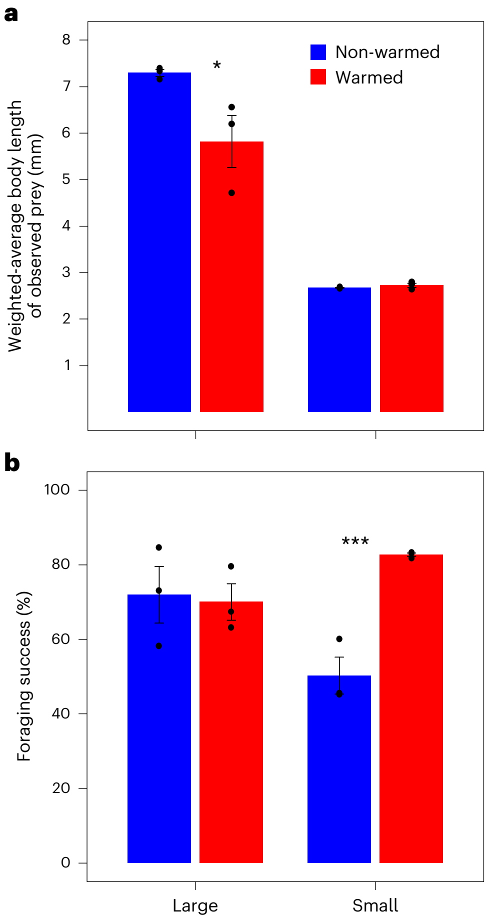

Fig. 4 | Experimental warming decreased the body length of observed prey for large spiders and increased foraging success for small spiders. a,**b**, Weighted-average body length of observed prey (**a**) and foraging success (**b**) for both large and small spider species (*A. luosangensis* and *M. pusilla*) in both non-warmed and warmed chambers. The data are shown as mean ± s.e.m. ($n = 3$). The treatment effect on body length was determined by one-sided Fisher–Pitman permutation tests; the treatment effect on foraging success was determined by a GLMM with 'treatment' as a fixed factor and 'chamber identity' as a random factor. Significant differences: $^{*}P < 0.05$; $^{***}P < 0.001$. The P value is 0.038 for the weighted-average body length of observed prey in the large spider species, and <0.0001 for foraging success in the small spider species.

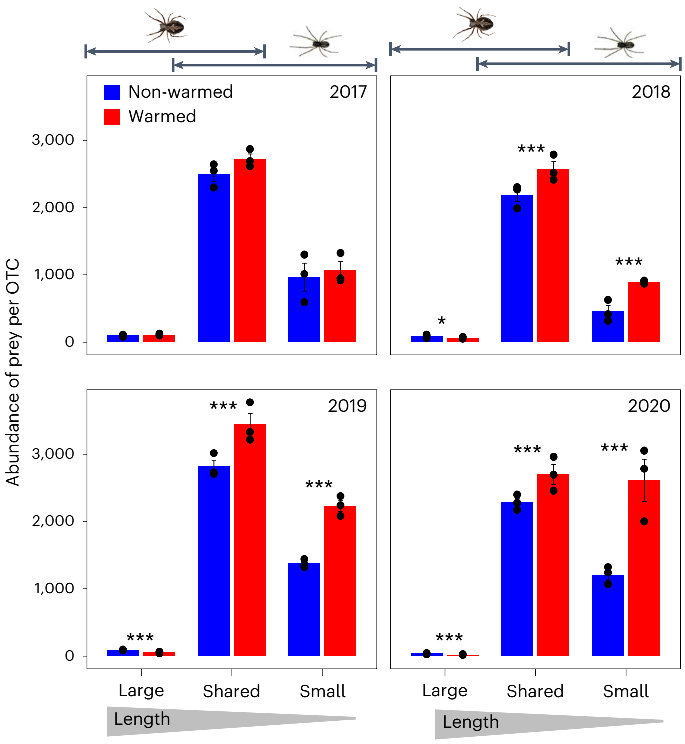

Fig. 5 | Experimental warming increases the abundance of prey shared by large and small spiders. The abundance distribution of prey body length in non-warmed and warmed OTCs from 2017 to 2020. The data are shown as mean ± s.e.m. ($n = 3$). The black bidirectional arrows above each column represent the diet range of each spider species (left: large spider *A. luosangensis*; right: small spider *M. pusilla*) depending on the observed data in 2020. The overlapped part between the two arrows in the middle represents shared prey of both spiders. The treatment effects are determined by a GLMM with 'treatment' as a fixed factor and 'chamber identity' as a random factor. Significant differences: $^{*}P < 0.05$; $^{***}P < 0.001$. The statistical parameters (t and P values) are shown in Supplementary Table 4.

level between non-warmed and warmed chambers (Supplementary Table 3).

In addition, the foraging success of *A. luosangensis* was indistinguishable between non-warmed and warmed chambers (Fisher–Pitman permutation test, $Z = 0.24$, $P = 0.60$, Fig. 4a), whereas the foraging success of *M. pusilla* increased in the warmed chambers (Fisher–Pitman permutation test, $Z = -2.15$, $P < 0.05$, Fig. 4b).

Responses of plant and prey communities

Warming substantially increased aboveground plant biomass at the community level (+30.4%; LMM: $F = 159.45$, $P < 0.001$, Extended Data Fig. 1a), increased the relative biomass of graminoids (+82.85%; LMM: $F = 590.35$, $P < 0.001$, Extended Data Fig. 1b) and decreased the relative biomass of forbs (LMM: $F = 587.39$, $P < 0.001$, Extended Data Fig. 1b).

Warming significantly decreased the abundance of potential prey (−25.4%, GLMM: $\chi^2 = 15.35$, $P < 0.001$, Fig. 5) available specifically to the large spider species *A. luosangensis*, and increased the abundance of the potential prey (GLMM: $\chi^2 = 49.56$, $P < 0.001$, Fig. 5) available specifically to the small spiders *M. pusilla*. Warming significantly increased the abundance of the shared prey (+125.6%, GLMM: $\chi^2 = 41.65$, $P < 0.001$, Fig. 5).

Direct and indirect effects on abundance and behaviour

Structural equation modelling (SEM) indicated that warming has important direct and indirect effects in driving changes in spider web-building behaviours and abundance (Fig. 6). Specifically, the most significant pathways were the warming-induced and soil-moisture-induced bottom-up effects on the plant community to the abundance and behaviour of both spider species (reflected by both their mesh size and web diameter) as a result of altered prey abundance. The abundance of specialized prey positively and the abundance of shared prey directly and negatively affected the web mesh size of the large spider species. The abundance of specialized prey directly and positively affected the web mesh size of the small spider species. The direct effects of warming on the abundance and behaviour of the large spider species were not statistically significant. However, the warming effect was statistically significant on the mesh size of the small spider species. In addition, the correlation between spider abundance and behaviour was significant for the small spider species but not for the large spider species.

Discussion

The results of our study indicate that a large- and a small-bodied spider species (*A. luosangensis* and *M. pusilla*, respectively) show contrasting responses to warming, both in terms of their abundance and their web-building behaviour. Moreover, our provisional SEM shows that the responses of the two spider species are largely a consequence of a warming-induced, bottom-up effect from changes in plant community

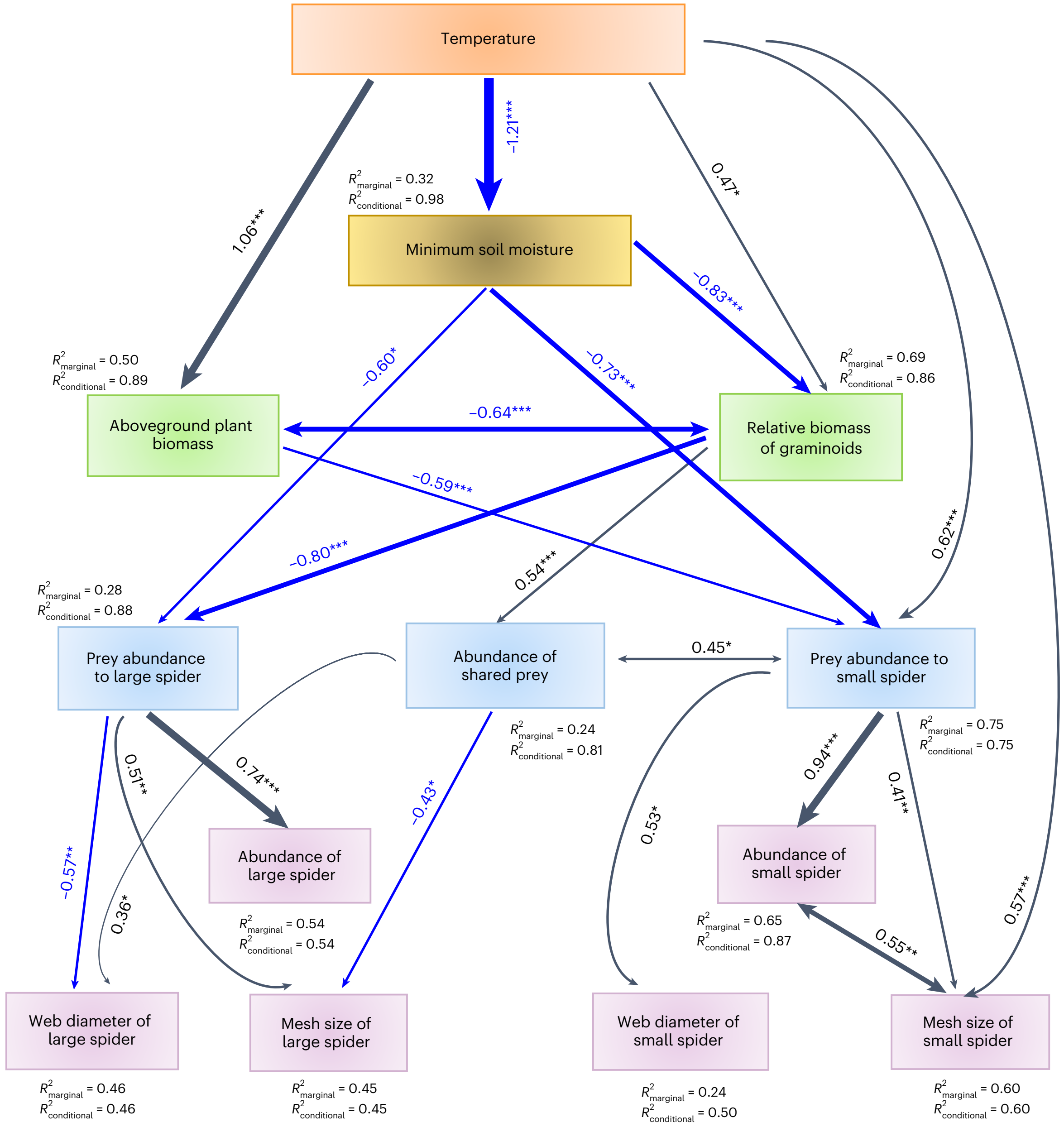

Fig. 6 | Warming-induced bottom-up effects on the plant community cascade affect the abundance and behaviour of spiders. The structural equation models for direct and indirect effects of warming on the web properties and abundance of two dominant spider species (large spider *A. luosangensis* and small spider *M. pusilla*). Solid black and blue arrows represent positive/negative paths ($P <= 0.05$ piecewise s.e.m.). The line thickness represents the effect size. Parameters next to arrows indicate standardized partial regression coefficients. R^2 values (R^2_{marginal} and $R^2_{\text{conditional}}$) are shown for all response variables. The model fitted the data well, as indicated by Fisher's $C = 109.21$, $P = 0.557$, d.f. = 112, AIC = 685.03.

species composition to changes in the size spectrum of their prey (mostly reflected by the increased abundance of the shared prey, and a warming-induced increase in the abundance of the prey of the small spider *M. pusilla*). This study appears to be the first experimental attempt to explicitly demonstrate the behavioural responses of terrestrial predators to the novel conditions induced by warming over a long time span (that is, four years). It also further stresses the importance of field experiments at the community level to accurately predict organismic responses to a future global climate change.

The warming-induced increase of insect abundance observed under laboratory conditions and mesocosm field studies in terrestrial systems has been attributed to direct temperature effects on survival and reproduction[27–29]. Similarly, the increased abundance of small-bodied species in both aquatic systems[30,31] and soil invertebrate communities[32] has been hypothesized to indicate that small-bodied species profit more from climate warming[33,34], possibly because small-bodied species can dissipate heat more efficiently with their larger surface area per volume[35,36]. The data presented in our study are consistent with these observations, because warming significantly increased the abundance of short-bodied prey specialized by the small species *M. pusilla*, which were available prey only for the small of the two spider species examined in our study.

However, in contrast to the inferences drawn by the majority of previous studies, our data indicate that warming had no direct effect on the abundance of the other prey of either spider species, but rather had an indirect effect on spider abundance and behaviour. Warming induced changes in the plant community that, in turn, affected prey community composition that then affected two critical features of spider behaviour. Specifically, experimental warming increased the aboveground plant biomass and relative biomass of graminoids, and decreased the aboveground biomass of forbs, resulting in a shift from a forb-dominated to a graminoid-dominated plant community, which is similar to the results reported by other researchers working in alpine meadows[37,38]. The shift in plant community species composition is often explained by warming-induced drying[37,38], which can differentially affect the vegetative growth, seed production and germination of different species. In our study, the reduction in soil moisture is especially conspicuous (for example, 12% v/v in August 2017) during the dry season (Extended Data Fig. 2), and probably favoured the growth of graminoids, which tend to be more tolerant to dry conditions compared to forbs[39].

In addition, the data show that the plant community shift further affected the prey size spectrum by decreasing the abundance of long-bodied prey and increasing the abundance of the prey shared by both spider species. This phenomenology can be attributed to the fact that graminoids are typically less palatable than forbs species because of their reduced water content and specific leaf area[25]. It has been reported that insects feeding preferentially on graminoids tend to grow slower than insects feeding on forbs[40]. Indeed, graminoids tend to support short-bodied herbivorous prey species such as Cercopidae and *Notostira* spp.[41], whereas some long-bodied herbivorous prey, including Tenthredinidae and Gelechiidae species, are almost exclusively supported by forbs. Therefore, it is expected that the abundance of the shared prey species including Cercopidae and *Notostira* spp. should increase in the warmed chambers.

The shift of the prey size spectrum induced changes in the abundance and behaviour of the two spider species. The overwhelming effect of the reduction of the abundance of the specialized prey of the large spider species resulted in a decrease in this spider's abundance. In addition, warming resulted in the large spider species decreasing its mesh size and increasing its web diameter, because the abundance of the short-bodied prey increased but that of large-bodied prey decreased. These observations are consistent with previous studies showing that orb-web-weaving spiders increase the surface area of their webs when the abundance of their prey is reduced[42,43], and that food-deprived spiders increase their web area and/or decrease their mesh size[44,45]. Although both behavioural responses are probably costly (thread length increased on average by 41.6%), an increase in the frequency of prey capture can counterbalance and potentially outweigh the cost, as indicated by the unchanged foraging success in the warmed chambers.

Clearly, the small spider species *M. pusilla* confronts different conditions than the large spider species *A. luosangensis*. Among the prey items, the abundance of long-bodied species increased much more than that of the short-bodied species in the warmed chambers. Consistent with this change, the small spider species manifest a different behavioural response to the warming-induced change in the prey community by tending to produce larger webs with larger mesh size capable of capturing longer prey. The small spider species increased its web area by 25.2% and its mesh size by 79.8%, thereby decreasing its thread length and cost on average by 19.9%. Moreover, the change in mesh and web size probably increased the possibility of capturing larger, more nutritionally profitable prey without losing the capacity to capture smaller prey, as indicated by a higher foraging success and increased *M. pusilla* abundance in the warmed chambers. In addition, SEM analyses indicate that warming directly and positively affected the mesh size of *M. pusilla*, which is consistent with the results reported by Blamires et al.[46]. The positive warming effect on the spider mesh size can be attributed to the increase in temperature, which increases body metabolism, thereby aggravating the expenditure of energy[47].

We attribute these observed behavioural responses to the fact that spiders physiologically detect slight changes in the kinetic energy of their prey[48], and alter their web design in response to shifted prey size spectra. In addition, phenotypic plasticity, particularly transgenerational phenotypic plasticity[49], might have been involved in the behavioural response of spiders, as suggested by the progressive changes of web properties across the study years. Additional studies are required to determine the evolutionary significance of these trends given the limited experimental duration of our study and the limited number of four generations relative to evolutionary time scales[50]. Moreover, phenotypic plasticity might have been affected by climatic variation, particularly in an experiment such as ours. For example, although the mean annual temperature has little changed during experiment, the rainfall was significantly higher in 2018 than usual (Extended Data Fig. 3), which might have contributed to the lower prey abundance relative to the other years in our study site.

Regardless of the proximate causes or evolutionary implications, the behavioural responses of the two spider species may have important ecological implications for future species diversity, community structure and ecosystem functioning. Specifically, the abundance of the large spider species *A. luosangensis* might further decrease due to demographic and/or environmental stochasticity without its attending behavioural responses, and an increased abundance of small prey species (including leaf hoppers) would result in an increase in plant herbivory. Thus, the adaptive responses of the predators observed in this study may help avoid species extinction and control pest outbreaks under warming conditions.

Warming is widely recognized to affect biodiversity, ecosystem functions and services. It is predicted that predator species will be the most sensitive and vulnerable species, whereas herbivores may become the prevailing species[51]. This study provides experimental evidence that predators may behaviourally adapt to warming-induced changes in community structure, which may contribute to buffering the magnitude of the effects of warming. Such adaptive behavioural responses and potential buffering effects might be more widespread. It is imperative, therefore, that future studies should consider the behavioural responses of predator species to warming in greater detail (for example, changes in territory size and group size in birds and mammals), and that these responses are incorporated into ecological modelling to gain a deeper insight into how communities and ecosystems respond to climate change. Subsequent studies should not only continue to consider the abundance and community structure of invertebrate communities, but should also explore trophic interactions and ecosystem functioning[52,53].

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-023-01918-8.

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Methods

Study site and species

This study was conducted at the Sichuan Zoige Alpine Wetland Ecosystem National Observation and Research Station located in an alpine meadow of the Qinghai-Tibet Plateau in Sichuan Province, China (32° 48′ N, 102° 33′ E, 3,500 m a.s.l). The records of the Hongyuan county meteorological station (5.5 km from the study site) showed that the annual mean air temperature was 1.7 °C and increased by +0.3 °C per decade (+0.27 °C in the summer and +0.5 °C in the winter) from 1960 to 2020. The annual mean precipitation was 760 mm (and ranged from 450 mm to 900 mm), most of which falls during the growing season (May–September).

The alpine meadow site is grazed by large herbivores (mainly yaks *Bos grunniens*, Hequ horses *Equus caballus* and Tibetan sheep *Ovis aries*). The meadow is mainly covered by forbs (including *Saussurea nigrescens*, *Polygonum viviparum* and *Anemone trullifolia* var. *linearis*), grasses (*Deschampsia caespitosa*, *Festuca ovina* and *Elymus nutans*) and sedges (*Kobresia setchwanensis* and *Carex* spp.)[24]. Typically, there are >30 plant species per m^2. Due to the diverse plant community, many arthropod species, such as herbivores[54], predators[55], parasitoids[56] and dung decomposers, coexist in the meadow.

Two locally dominant spider species were selected for our study, namely, *A. luosangensis* and *M. pusilla*. *A. luosangensis* (Araneidae) is an orb-weaving spider. A survey of the area indicates that the field density of this species is 2,000–2,500 ha^{-1} (https://doi.org/10.5281/zenodo.10380144). The body length of adult females is between 7.0 mm and 8.0 mm (ref. 57). This species produces egg sacs from the end of July to mid-August. The spiderlings emerge in late September. The orb web is constructed by attaching its silk to multiple plants between 40 cm and 60 cm above the ground. Its large vertical, flat orb web can easily be detected in the meadow[57]. Hence, their prey can be identified readily in the field. *M. pusilla* (Linyphiidae) spins a horizontal sheet web in low vegetation (13–20 cm aboveground). The local density is 5,000–9,000 ha^{-1} (https://doi.org/10.5281/zenodo.10380144), and the body length of adult females is between 2.5 mm and 5.0 mm. Female adults emerge in early May, with the density peak occurring from June to August[57]. Both species are generalists, consuming all potential prey species, including herbivores and even some predatory arthropods (for example, Reduviidae).

The warming experiment

Six OTCs (Supplementary Fig. 1a) were constructed in a winter pasture in October 2014. Each chamber measured 562.5 m^3 (15 m × 15 m × 2.5 m height) and was surrounded by a thin steel screen (Supplementary Fig. 1b). Three OTCs were warmed by surrounding them with transparent tempered glass, and their roofs were discontinuously covered by 1.5 m × 0.3 m (width) transparent glass strips with 0.6 m space between each other to prevent any strong airflow stack effect (Supplementary Fig. 1c)[58]. In 2015, all the OTCs were covered with gauze screen with a 0.2 mm × 0.2 mm mesh from May to September (Supplementary Fig. 1d), and only a few very mobile insects (for example, *Bombus friseanus*, *Apis mellifera, Apis cerana*, *Argynnis xipe* and *Peleteria versuta*) were found dead on the gauze screen. This is consistent with the observation that the flight boundary layers of >99% (except for one large-bodied moth species having a layer of 2.6 m) of insect species from seven orders are <2.5 m in an old-field grassland[59,60], and indicates that most of our study objects, including the spiders and their prey, are unlikely to enter and fly out of the chambers. Because the gauze screen may prevent rainfall and snowfall into the chambers, we removed the screens from all the OTCs after 2016. There was no significant limitation for the access of the dominant pollinator species (mostly *A. mellifera*). Consistently, the seed set ratio was not statistically different between the warmed and non-warmed chambers and between the field conditions (Extended Data Fig. 4), indicating no significant pollination limitation for the dominant dicot species that are naturally insect pollinated. Consequently, all six chambers served as seminatural ecosystem proxies.

Recorded climatological data showed that the mean annual air temperature ranged annually from 4.77 °C to 5.63 °C at 30 cm aboveground in the warmed chambers, and from 4.07 °C to 5.18 °C in the non-warmed chambers, that is, the temperatures in the warmed chambers were from 0.45 °C to 0.70 °C higher than in the non-warmed chambers (Extended Data Fig. 5 and Supplementary Table 5). Such a temperature differential is consistent with the predicted increase in temperatures for the next two to three decades in the Tibetan Plateau according to SSP1–1.9 scenarios[61] (Extended Data Fig. 6 and Supplementary Table 5). The warming effect was stronger in the winter (November–January, +0.95 °C) than in the summer (June–August, +0.43 °C). The vapour pressure deficit was 40.7% in the non-warmed chambers, higher than that in the warmed chambers (45.0%) in the growing season from April to September. The relative humidity was on average 71.15% in the warmed chambers and 72.99% in the non-warmed chambers. Additionally, in the growing season the soil moisture at −5 cm was 20.2% v/v on average in the warmed chambers and 22.4% v/v in the non-warmed chambers (for details, see refs. 24,62). Possibly because of the variation in precipitation intensity and timing (Extended Data Fig. 3), the minimum soil moisture differed greatly among years (Extended Data Fig. 2). All the aboveground plant parts were clipped and distributed evenly within chambers after the growing season (early October) for each experimental year to simulate typical autumnal senescent conditions for nutrient recycling and detritivore behaviour and feeding.

The biotic environments of spiders

Plant community. Plant species abundance was investigated using a quadrat sampling method[63]. We harvested aboveground plant parts in sixteen 1 m × 1 m quadrats randomly located in each chamber during mid-August of each experimental year, when most plant species had completed reproduction. The aboveground parts were sorted into two functional groups (that is, graminoids including Poaceae and Cyperaceae species, and forbs including all of the remaining species). The aboveground parts were subsequently dried and weighed[24].

Arthropod abundance and body size. Light muslin sweep nets (38 cm in diameter with 180-cm-long handles) were used to survey the arthropod community within all six chambers every ten days (weather permitting) from June to August each year from 2017 to 2020 (seven surveys each year). For each sampling, a total of 96 sweeps were performed in each chamber to uniformly cover the entire chamber on sunny days from 11:30 to 15:30 (Beijing time), when most arthropods were active. For each sweep, the net moves ~120° along an angle of ~45° between the net and the ground. All of the arthropods collected within the nets were identified using morphological traits, recorded and subsequently released back into the chambers from which they were removed. Samples of the unidentified species were taken to the laboratory for identification using molecular techniques (see below). For each arthropod species, at least three individuals (except two individuals for very rare species, that is, *Ceraeochrysa* sp. and *Tetanocera* sp.) were collected, and then photographed and measured, dried, and weighed to determine dry body mass. The body length of each arthropod species was measured from their photographic images using ImageJ (https://imagej.nih.gov/ij/index.html) from the anterior tip of the head to the posterior end of the abdomen (Helicon Focus 6.3.0 with a Canon DS126271 camera).

Response of spiders

Spider abundance and body size. Species abundance was recorded for both spider species in the early mornings of late July to late August of each year (2017–2020), when their webs were visible. Species abundance was measured as the number of webs in each chamber as determined one to three times each year, because field observations indicated that each web is typically occupied by only one individual spider.

At least three female spiders (depending on their abundance) were collected from each chamber each year and subsequently dried and weighed. Mean body mass was calculated for both non-warmed and warmed chambers for each species.

Observed prey identity and body size. A minimum of 20 webs (depending on their abundance) were randomly marked using stake flags for each spider species in each chamber to subsequently determine prey community composition in 2020. The investigations of prey community were conducted from June to August, with a frequency of two or three times a month. In each investigation, we recorded the prey in each web as thoroughly as possible and carefully removed unidentified arthropod residues using forceps. Specimens were preserved in absolute ethanol and identified to species or genus using DNA barcodes. DNA was extracted using the Chelex-100 method[64], and the universal barcodes primers COI (LCO1490 and HCO2198) were used to amplify a 650 bp segment[65].

To investigate the range of prey body size for each of the two spider species, we recorded the species identity of 250 prey items in non-warmed chambers, and we recorded the species identity of 200 prey items in warmed chambers for the large spider *A. luosangensis*. Likewise, we recorded the species identity of 240 prey items in the non-warmed chambers and 381 prey items in the warmed chambers of the small spider *M. pusilla*. We calculated the weighted average of observed prey body length in each chamber for each spider species.

The prey species body length of *A. luosangensis* ranged between 2.3 mm (that is, Ephydridae: *Psilopa* sp.) and 16.0 mm (that is, Geometridae: *Epirrhoe pupillata*) in the non-warmed chambers. The prey species size of *M. pusilla* ranged between 1.5 mm (for example, Chironomidae: *Chironomus novosibiricus*) and 9.0 mm (for Tortricidae: *Celypha flavipalpana*) in the non-warmed chambers (Supplementary Table 2). The body lengths of the prey of the two spider species overlapped within the 2.3 mm to 9.0 mm range, which was consistent with previous studies[66,67]. The abundance of the observed prey species of the two spider species was significantly and positively correlated with the abundance of the potential prey species collected from sweep nets (GLMM: $\chi^2 = 43.21$, d.f. = 1, $P < 0.0001$), indicating that the prey abundance deduced using sweep nets reflected the abundance of prey species.

In addition, we surveyed and recorded the number of spiders that were feeding for a minimum of six spiders during 10 min in each chamber from 12:00 to 16:00 on five sunny days in 2020. We calculated the foraging success as the number of webs with feeding spiders divided by the total number of webs for each of the two spider species.

Spider web properties. For each of the two spider species, webs were randomly selected and photographed (with a ruler as a scale) to determine web area and mesh size (Supplementary Fig. 2) using ImageJ (https://imagej.nih.gov/ij/index.html). The web diameter was calculated as the mean of three measurements transverse to the spiral tread of the web. The mesh size of *A. luosangensis* is the mean space between the adjacent sticky spirals; the mesh size of *M. pusilla* is the mean area of 10–15 meshes (Supplementary Fig. 2).

Data analysis

All analyses were performed in R 4.1.2[68]. The spider–prey bipartite network was visualized using the plotweb function in the bipartite package (v.2.16)[69]. After testing for the error distribution of data, we used GLMMs (R package lme4[70]) with warming, year and their interactions as fixed factors, and chamber identity and 'chamber identity × year' as random factors to determine the warming effect on the variables having multiple data from a single chamber per year, including spider abundance (with negative binomial error) and mesh size of small spider (gamma error with log link function). Similarly, LMMs with warming, year and their interactions as fixed factors, and chamber identity and 'chamber identity × year' as random factors, were used to determine the warming effect on the variables having multiple data from a single chamber per year, including plant aboveground biomass, relative biomass of graminoids (that is, Poaceae and Cyperaceae), spider body size, mesh size of the large spider and web diameter, to account for the non-independence of data derived from the same chamber within each year (Supplementary Table 6).

GLMMs (with negative binomial error structure) with warming, year and their interaction as fixed factors, and chamber identity as a random factor, were used to determine the warming effect on the variables having data for the whole chamber in each year (that is, prey abundance per chamber per year). The data on prey abundance (including the specialized prey of each spider, and shared prey) were summed across sweeps and across time points for each chamber and for each year (Supplementary Table 6).

The difference in the prey body mass at the species level was determined using a GLMM (gamma error with log link function) with species and chamber identity as random factors, and warming as a fixed factor. The difference of the foraging success between treatments was determined using the Fisher–Pitman permutation test in the R package coin (v.1.4-2)[71], because the number of replicates ($n = 3$) was small for each treatment.

In addition, we conducted an SEM analysis in the R package piecewiseSEM (v.2.1.2)[72] to explore the mechanisms underlying the warming effect on spider behaviour (as reflected by the change in web diameter and mesh size of each of the two spider species). As noted, warming may directly affect plant and prey communities, and spider abundance and behaviour, and it may also indirectly affect spider abundance and behaviour by altering plant community structure, which in turn can affect the prey community. Thus, we set the air temperature as a driving (exogenous) variable, minimum soil moisture in the growing season, plant aboveground biomass, relative biomass of graminoids, the abundance of prey (including the specialized prey of each spider species and the prey shared by both spider species) as intermediate (endogenous) variables, and the abundance and behaviour of spiders as dependent (endogenous) variables. The residual correlations among the endogenous variables were also estimated (Extended Data Fig. 6). In addition, we set year as a random factor because the SEM identified warming as the most important putative cause. Moreover, we also set chamber identity as a random factor to account for non-independence of data coming from the same chamber across different years. The data on plant aboveground biomass, the relative biomass of graminoids, and the abundance and behaviour of spiders were averaged for each chamber and for each year for the SEM analysis to avoid any pseudoreplication.

From an initial model following a priori knowledge of interactions with all hypothesized effects, we used a backward stepwise elimination process based on the Akaike information criterion (AIC) to remove non-significant links and variables. We used Fisher's *C*-test to assess the goodness of fit of the SEM ($0 \leq$ Fisher's C/d.f. ≤ 2 and $0.05 < P \leq 1.00$). We report both the marginal (R^2_{marginal}, fixed effects only) and the conditional ($R^2_{\text{conditional}}$, all effects) coefficients of determination for linear mixed models incorporated in the SEM after the variables were *Z*-score transformed because of the different dimensions (decostand function in the package vegan v.2.5-7)[73]. Thus, although the resulting SEM may be currently and provisionally the best, it is possible that additional information could lead to model modifications and improvement.

Analyses showed a large decrease in soil moisture at 5 cm depth in the warmed chambers particularly in the late growing season (August; Extended Data Fig. 2), which might affect plant community composition and structure. Although soil moisture is associated with temperature, air relative humidity and vapour pressure deficit, it is hard to dissect the individual effect of each of these variables on soil moisture. Thus, we set the minimum soil moisture (as a representative of relative humidity and vapour pressure deficit) in the late growing season as an intermediate factor affected by temperature because (1) we set the OTCs to increase temperatures but not decrease soil moisture and

(2) it is more reasonable to assume that temperature directly affects soil moisture rather than the converse. Because of a logger malfunction in 2020, we used the average soil conditions of 2017–2019 as a proxy. Moreover, we used the abundance of the prey of the large spider species and the shared prey of the two spider species (ranging between 2.317 mm and 9.037 mm) as predictors of the abundance and behaviour of the large spider species, and the abundance of the prey of the small spider species, and the shared prey as predictors for the abundance and behaviour of the small spider species, using the observed prey size spectrum for the two different spider species. We did not incorporate body mass into the SEM, because significant changes in body mass with warming were observed for hardly any prey species (Supplementary Table 3). In addition, because the shared prey (for example, Glyphipterygidae sp. and *Empoasca* sp.) mostly feed on graminoids (Poaceae and Cyperaceae), we used the relative biomass of the species in these two families as an indicator of plant community change and as a predictor for the abundance of shared prey[68].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Source data on physical environment, abundance and body size of spiders and their prey resulting from the warming experiment have been deposited in Zenodo (https://doi.org/10.5281/zenodo.10379963). Source data on spider density and web height resulting from an independent field survey have been deposited in Zenodo (https://doi.org/10.5281/zenodo.10380144).

Code availability

R scripts for statistical analyses have been deposited in Zenodo (https://doi.org/10.5281/zenodo.103799421).

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Author contributions

S.S. and X.W. conceived and designed the methodology. X.H. and Q.Z. collected the data. X.H. and S.S. analysed the data. K.J.N., P.B.R., L.J. and N.E. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

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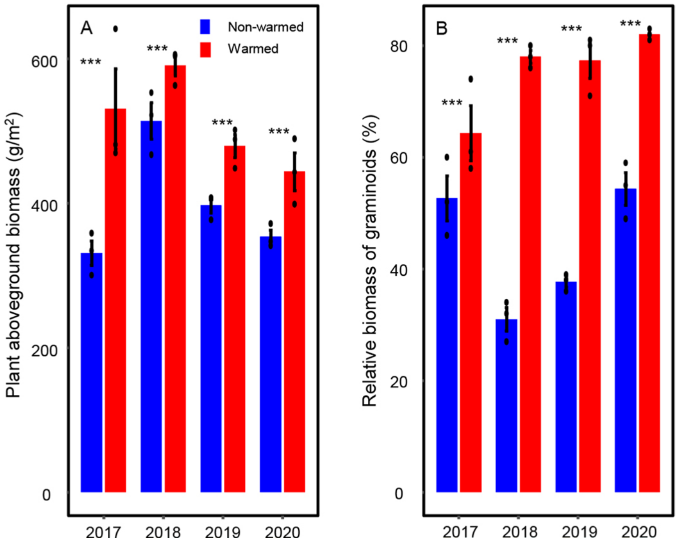
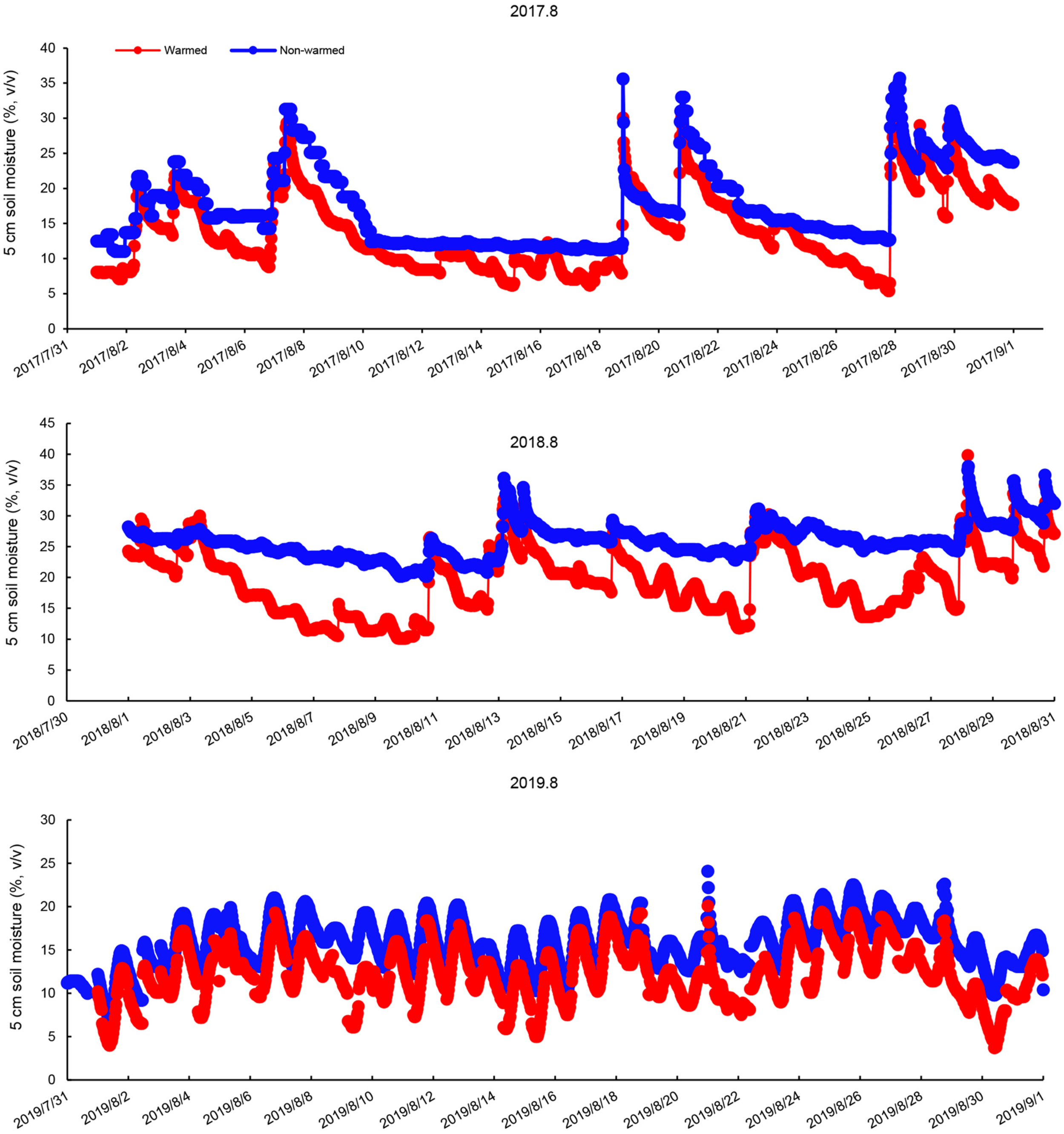
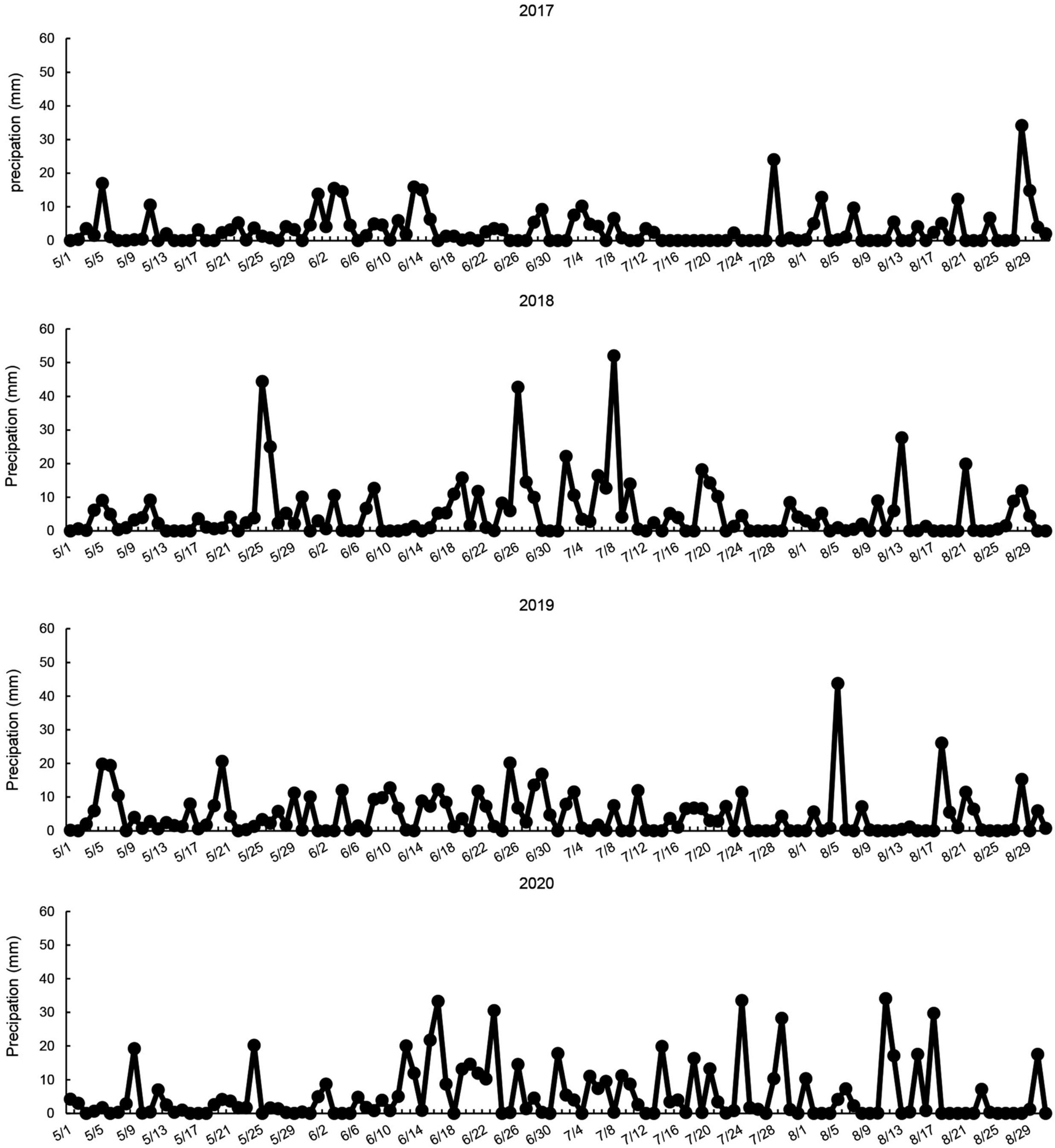


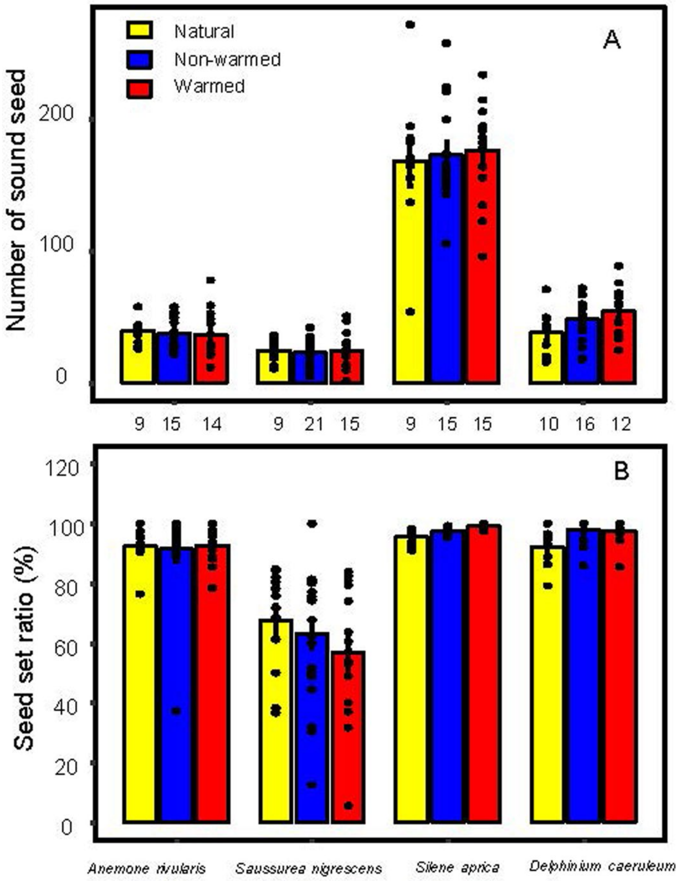
Extended Data Fig. 1 | The warming effect on plant aboveground biomass and relative biomass of graminoids. Aboveground biomass (**a**), relative biomass of Graminoids (**b**) in both non-warmed (blue) and warmed (red) chambers from 2017 to 2020. The data are shown as mean ± s.e.m.; $n = 3$. The linear mixed model with treatment as fix effect and chamber identity as random effect was used for statistical analysis. The asterisk represents significant differences (*** $P < 0.001$). The statistical parameters (t and P value) were shown in Supplementary Table 4. The data from 2017 to 2018 were published in Frontiers in Ecology and Evolution (Hu et al. [24]).



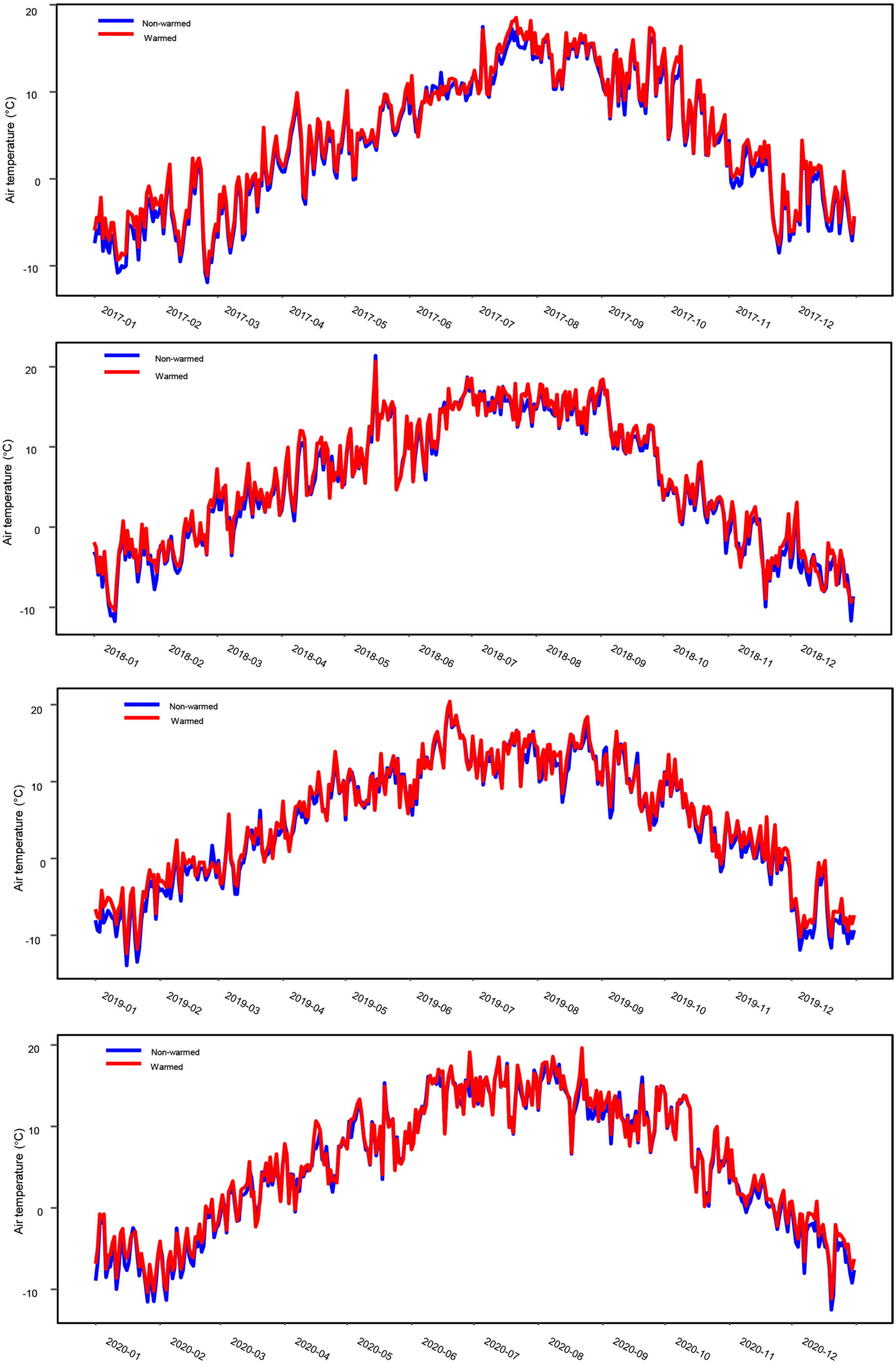
Extended Data Fig. 2 | The variation in soil moisture during the experimental period. The soil moisture (−5 cm) in the August (the driest month each year) of 2017 to 2019 (data deficiency in 2020 because of the logger malfunctioning).



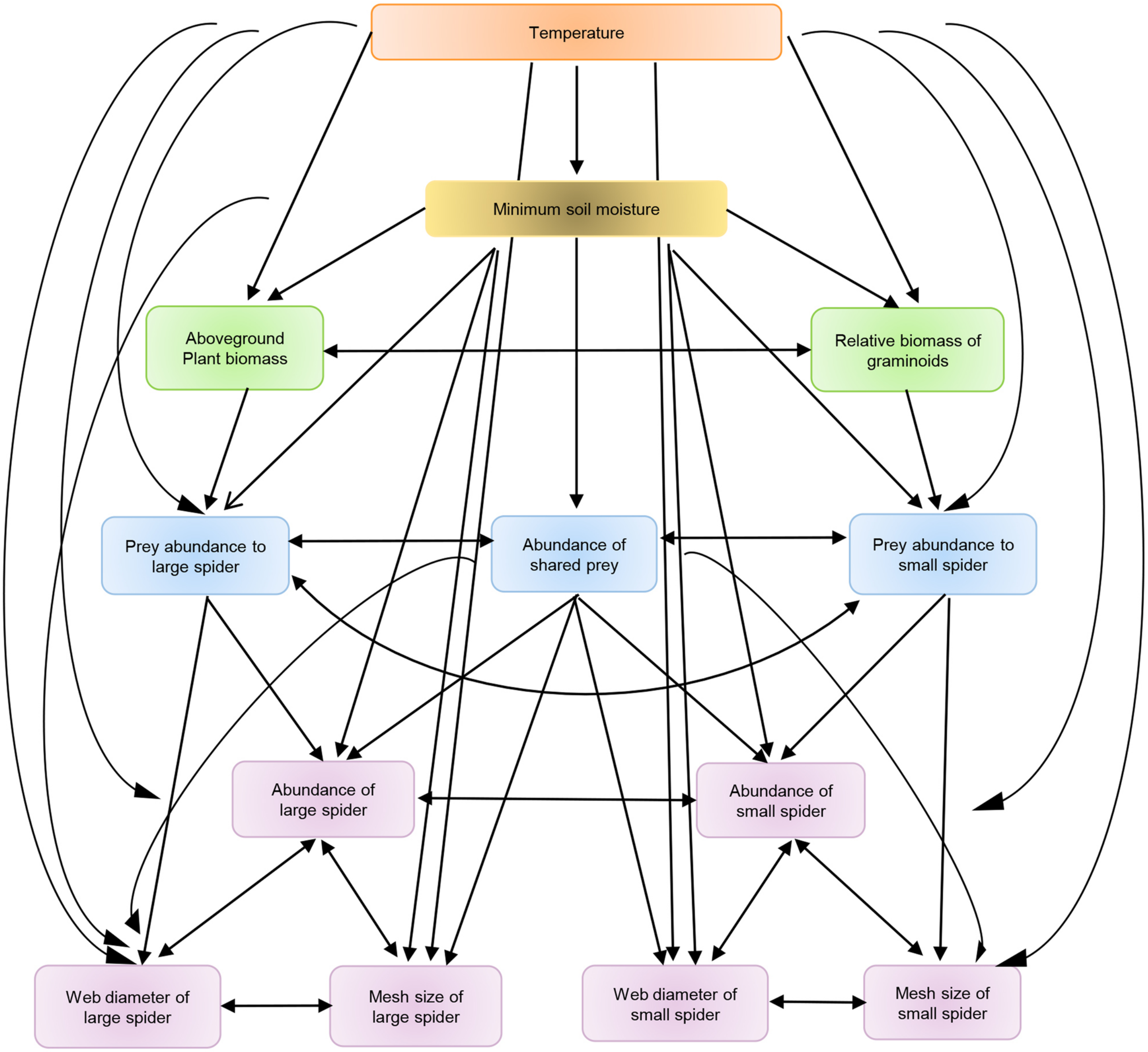
Extended Data Fig. 3 | The variation in precipitation intensity during the experimental period. The precipitation in May to August during experimental period from 2017 to 2020.



Extended Data Fig. 4 | Plant seed production unchanged by the chamber setting. Number of sound seeds per fruit (**a**) and seed set ratio (**b**) of four dicot species (that is, *Anemone rivularis*, *Saussurea nigrescens*, *Silene aprica*, and *Delphinium caeruleum*) in the field (yellow), non-warmed (blue) and warmed chambers (red). The data are shown as mean ± s.e.m. Sample size (n) is the same for both panels A and B, as provided under the panel A for each treatment and each species. The treatment effects (natural, non-warmed and warmed) was determined by generalized linear mixed model with treatment as fixed effect as well as 'species' and 'chamber identity' as random effects. The treatment (that is chamber setting) did not significantly affected the number of sound seed (GLMM with negative binomial error distribution: $\chi^2 = 0.89$, $d.f = 2$, $P = 0.64$) and seed set ratio (GLMM with binomial error distribution: $\chi^2 = 4.44$, $d.f = 2$, $P = 0.11$).



Extended Data Fig. 5 | The variation in air temperature during the experimental period. The temperature variation (daily mean) during the experimental period (2017–2020).



Extended Data Fig. 6 | Hypothesized structural equation model. Full hypothesized structural equation models used in the AIC model selections.

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Reporting Summary

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n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used to collect data.
Data analysis	The “lme4”, “picewiseSEM”, “coin”, "bipartite" and "vegan" package of the R software version 4.1.2 are used in this paper.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

The data is available on the GitHub Repository at https://github.com/Botanicalzoe/Spider_behavior_data

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study conducted a field warming experiment using six large open-top chambers (OTCs) to study how predators (large-bodied and small-bodied orb-weaver spider) will behaviorally respond to climate warming. Each chamber measuring 562.5 m3 (15 × 15 × 2.5 m (height)) was surrounded by a thin steel screen. The three warmed OTCs were also surrounded by transparent tempered glass, and their roofs were discontinuously covered by 1.5 m × 0.3 m (width) transparent glass strips to prevent a strong airflow stack effect. Recorded climatological data showed that the mean annual air temperature was 0.45-0.70°C higher at 30 cm aboveground in the warmed chambers. The abundance of two spider species (Aculepeira luosangensis and Microlinyphia pusilla) and their prey was monitored in four consecutive years from 2017 to 2020. The web diameter, mesh size and the body length of their prey were also measured during experimental periods.
Research sample	Surveys and measurements are made using established methods in the Ecology. Plant species abundance was investigated using a quadrat sampling method. The mesh size, web diameter and prey body length were measured using ImageJ (https://imagej.nih.gov/ij/index.html). The abundance of prey species to both spider was investigated by light muslin sweep nets. The species identification of unidentified prey residues identified to species or genus using DNA barcodes .
Sampling strategy	Our sample area was confined to the area of the six chambers. To explore how two spiders behaviorally respond to climate warming, we recored all the spider individuals in each chamber one to three times in the early mornings of late July to late August of each year (2017 to 2020), when the webs are visible. The webs were randomly selected and photographed to determine web area and mesh size using ImageJ (https://imagej.nih.gov/ij/index.html). The prey abundance was monitored with a total of 96 sweeps uniformly covered the entire chamber on sunny days from 11:30 AM to 15:30 PM each observational time, when most arthropods were active. To minimize the disturbance, all the arthropods of the sweep nets were identified and recorded as soon as possible, and then released them back in situ.
Data collection	Data from field survey was collected by Xiaoli Hu, Qingping Zhou, Shucun Sun and trained field assistants. Face-to-face training were undertaken by the researchers.
Timing and spatial scale	In an alpine meadow located in eastern Tibetan Plateau, quantitative data were collected in four consecutive years from 2017 to 2020. The prey abundance species was observed seven time during growing season (June-September) of each year. The each Open-top chambers is 562.5 m3 ((15 m× 15 m× 2.5 m (height)).
Data exclusions	The very mobile dispersers (e.g., Bombus friseanus, Apis cerana, Argynnis xipe, and Peleteria versuta) could escape from or enter the chambers and hence was excluded in the analyses. The analyses indicated that these data did not change our results when they are included.
Reproducibility	The experiment includes three replicates for each treatment, and they were surveyed for four years. Thus the effects of warming on prey community and spider behaviors leading to the results shown in the manuscript for spider and prey dynamics have been replicated 4 times. Our statistical analysis accounts for this experimental design where the three chamber level responses are nested within the year-level effect.
Randomization	The experimental facilities were constructed in homogeneous alpine meadow with similar initial plant and arthropods community. All chambers are randomly set in the similar environmental conditions excepted temperature.
Blinding	Blinding was not relevant to our study.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	In the study site, the annual mean air temperature had been 1.7°C, and has increased by +0.3°C per decade (+0.27°C in the summer and +0.5°C in the winter) from 1961 to 2020; The annual mean precipitation was 760 mm (and ranged from 450 to 900 mm), most of which falls during the growing season (May to September).
Location	The study was conducted in Hongyuan county located in an alpine meadow of the Qinghai-Tibet Plateau in Sichuan Province, China (32°48′N, 102°33′E, 3500 m a.s.l).
Access & import/export	We cooperated with Qinghai-Tibetan Research Base of Southwest University of Nationalities to do our research. All our experiment can be accessed.
Disturbance	No disturbance in our experiment.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	No laboratory animals were used.
Wild animals	One to ten individuals of each species (depending on their abundance) were captured to measure their body size.
Reporting on sex	No sex was consider in our experimental design.
Field-collected samples	Specimens were preserved in absolute ethanol after measuring.
Ethics oversight	All animal experimental procedures were in compliance with Directive 2010/63/EU on the protection of animals used for experimental purposes and were approved by the related ethical regulations of Nanjing university.

Note that full information on the approval of the study protocol must also be provided in the manuscript.