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Field experiment reveals complex warming impacts on giant pandas' bamboo diet

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ABSTRACT

Understanding the impacts of global warming on keystone species is fundamental to addressing the threat of climate change to biodiversity. Understory bamboo species play a crucial role in many forest ecosystems and provide food and shelter for numerous animals, including the giant panda (*Ailuropoda melanoleuca*). While previous studies projected that global warming would cause substantial shrinkage of bamboo distribution and threaten giant pandas, substantial uncertainties persist due to an incomplete understanding of the impacts of warmer temperatures on both the quantity and quality of bamboo as the food source for giant pandas. To address this research gap, we conducted the first field experiment in giant panda habitats to assess the impacts of warmer temperatures on the population dynamics and dietary quality of arrow bamboo, a main food source of giant pandas. We observed that warming generated a nonlinear impact on bamboo survival, with a potential warming threshold between 1.5 °C and 3 °C, beyond which warmer temperatures substantially reduced the survival rate of bamboo. Additionally, our plant content analysis showed that warmer temperatures lowered bamboo's nutritional value but enhanced its palatability as food for giant pandas. Furthermore, we found that warming could jeopardize the bamboo food supply for giant pandas by intensifying aphid infections in bamboo. These findings advanced the understanding of food web dynamics under global warming and provided crucial information for effective giant panda conservation planning in the face of climate change.

1. Introduction

Earth is warming at a rate unprecedented in human history (IPCC, 2022). It is projected that without effective interventions to curb global warming, up to 15.7 % of species worldwide may become extinct due to climate change by the end of this century (Urban, 2015). This warming-induced species loss can profoundly alter the structure and processes of ecosystems, causing cascading effects on biodiversity and human societies (Weiskopf et al., 2020). For example, global warming is driving the population decline of bumble bees around the globe, jeopardizing ecosystem pollination and global food security (Soroye et al., 2020; Potts et al., 2020). Rising temperatures are also stressing corals worldwide, leading to more frequent coral bleaching and habitat loss for many marine species (Hughes et al., 2018). With an anticipated rise of 1.4 °C to 4.4 °C in global temperature within this century (IPCC, 2022), it is imperative to understand the impacts of warmer temperatures on the survival and function of species to prepare for the consequences of climate change. This is especially urgent for keystone species, which often play a critical role in maintaining the structure and processes of ecosystems (Paine, 1969). Changes in abundance, distribution, or

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behavior of keystone species due to climate change can have a disproportionally large impact on the entire ecosystem and the biodiversity it harbors (Morgan Ernest and Brown, 2001).

Understory plants are an essential component of many forests, comprising the majority of plant species and playing a key role in the decomposition, nutrient cycling, and successional development of forests (Gilliam, 2007; Taylor et al., 2004; Royo and Carson, 2006). However, many understory plant species are vulnerable to the effects of climate change, such as raised temperatures, altered precipitation patterns, and increased frequency of drought and wildfire (Gilliam, 2016). For example, previous studies projected that climate changes may generate adverse effects on the distribution, growth, and survival of the understory trilliums, epiphytic ferns, and rhododendrons (Sofi et al., 2022; Zotz and Bader, 2009; Kumar, 2012). Another example of this vulnerability that has attracted significant attention is understory bamboo species across the distribution ranges of giant pandas (*Ailuropoda melanoleuca*) in southwestern China. These bamboo species are an essential component of forest structural complexity and serve as a primary food source and shelter for animals, including giant pandas (Nie et al., 2015). Although the conservation status of giant pandas has been downgraded from “endangered” to “vulnerable”, climate change is projected to be a prominent threat to giant pandas in the future, mainly through impact on their bamboo food source (Tang et al., 2022). Understory bamboo species often have limited vegetative dispersal ability (Taylor et al., 1991), high sensitivity to water stress (Liu et al., 2017), and long sexual reproduction intervals (from 10 to 120 yr) (Janzen, 1976; Tian et al., 2019), which render them vulnerable to a changing climate (Tuanmu et al., 2013). Previous studies (e.g., (Tuanmu et al., 2013; Li et al., 2015; Songer et al., 2012)) projected that future climate change will result in a substantial reduction and spatial shift in the distribution of bamboo species that provide food for giant pandas, leading to cascading effects on giant pandas and other species that are trophically dependent on these bamboo species. For example, Tuanmu et al. (2013) estimated that 80–100 % of the current distribution range of giant pandas in the Qinling Mountains of China will become climatically unsuitable for understory bamboo species in this region by the end of this century, suggesting a high risk of food shortage for giant pandas in the future.

Although there have been many projections of how climate change will affect understory bamboo species, most were derived from species distribution models (SDMs, also called environmental niche models). These models use the correlations between a species' current distribution and current climate variables to project the species' future distribution under a changing climate (Wiens et al., 2009). While SDMs are widely used to project species distribution under changing climate (Urban et al., 2016), the assumptions of the models introduce uncertainty into these projections (Wiens et al., 2009; Moullec et al., 2022). For example, while SDMs typically assume that the climate-niche envelope (i.e., suitable climatic conditions) of a species does not change in a perturbed climate (Wiens et al., 2009), there is mounting evidence that many species can develop strategies to cope with unprecedented climate conditions (Root et al., 2003). For instance, some plants can shift their thermal optimum for photosynthesis upward to mitigate negative impacts of global warming (Way and Oren, 2010). Additionally, assessments using SDMs often assume that different species respond to climate change independently and overlook the complex interactions among species (e.g., plant-insect and predator-prey interactions) that may play an important role in the survival and health of species (Wiens et al., 2009; Moullec et al., 2022). Furthermore, SDMs cannot assess how climate change affects the quality of plants as food sources for wild animals. This is especially concerning since bamboo has low nutritional value and giant pandas have low efficiency in digesting bamboo (Wei et al., 2015; Zhang et al., 2017; Zhang et al., 2015). Reduction in the nutritional value of bamboo may lead to deficiencies in nutrient intake and be detrimental to the health of giant pandas (Wei et al., 2015). The reliance on SDMs to investigate climate change impacts on giant pandas' bamboo food contrasts with many other plants for which a larger arsenal of assessment tools, such as controlled experiments (e.g., growth chambers, open-top chambers, and field experiments) and process-based growth models (Kellner et al., 2019; Girardin et al., 2008), has been used to evaluate their biological responses to climate change. These tools have not been used to infer how global warming will affect understory bamboo species in giant panda distribution ranges, and the impacts of warmer temperatures on the quantity and quality of bamboo as a food source for giant pandas remain poorly understood.

Here, we presented the findings of the first field experiment designed to examine the impacts of warmer temperatures on arrow bamboo (*Bashania fangiana*) – a primary food source for giant pandas in the study area. We exposed naturally grown arrow bamboo to ambient air temperature and to temperatures that were elevated by 1.5, 3, and 4.5 °C. We assessed the impact of warmer temperatures on the survival (quantity) of arrow bamboo by comparing the population dynamics and biomass of bamboo grown under ambient temperature and under varying degrees of warming. To assess the impact of higher temperatures on the dietary quality of bamboo as a food source for giant pandas, we analyzed the variation in the nutritional value (indicated by crude protein, crude fat, crude ash) and palatability (indicated by total tannins, total phenol, and crude fiber) of bamboo. We also examined the levels of aphid infection in bamboo exposed to the different treatment regimes to assess the potential threat of warming to bamboo through affecting bamboo-aphid interactions. Our findings provide insights into the complex impacts of warmer temperatures on both the quantity and quality of giant pandas' bamboo food supply, contributing essential information to support informed conservation planning.

2. Methods

2.1. Experimental site

We conducted the experiment in Wolong Nature Reserve (Wolong hereafter) in Sichuan Province, China. Wolong lies between the Sichuan Basin and the Tibetan Highlands (Fig. 1), and is a flagship protected area for the conservation of giant pandas with >100 giant pandas living in the reserve (Sichuan Forestry Administration, 2015). Giant panda habitats in Wolong have been transformed from long-term losses to recovery due to the implementation of conservation policies and subsequent reduction in human impacts since the early 2000s (Tuanmu et al., 2016; Yang et al., 2022; Yang et al., 2020; Yang et al., 2018). Along the altitudinal gradient, there are deciduous broad-leaved forests, mixed coniferous-deciduous forests, and subalpine coniferous forests (Wolong Nature Reserve, 2005). Arrow bamboo is one of the dominant understory species in these forests and the dietary staple of giant pandas in the region (Tuanmu et al., 2010). Although giant pandas forage on 34 different bamboo species in the wild, arrow bamboo is arguably their most important food source. According to the latest Giant Panda National Survey (Sichuan Forestry Administration, 2015), arrow bamboo provided over 20 % of giant pandas' diet across their range in Sichuan Province. In the Qionglai Mountain Range, where the Wolong is situated, 53 % of panda occurrence records were found in the arrow bamboo forest (Sichuan Forestry Administration, 2015). The mass flowering of arrow bamboo during 1983–1985 and consequent bamboo die-off in Wolong resulted in a 40–50 % decline in the local panda population (O'Brien and Knight, 1987), highlighting the critical importance of arrow bamboo for the survival of giant pandas.

The goal of our study was to infer the impacts of global warming, specifically from rising temperatures, on both the quantity and quality of arrow bamboo as a food source for giant pandas. Our Wolong site presented the ideal conditions for the experiment because it has the key features that are representative of suitable habitats for giant pandas, which allowed us to maximize the generalizability of our findings. These features include minimal human disturbance, flat terrain, overstory tree cover, and naturally-grown bamboo. The site is far from human

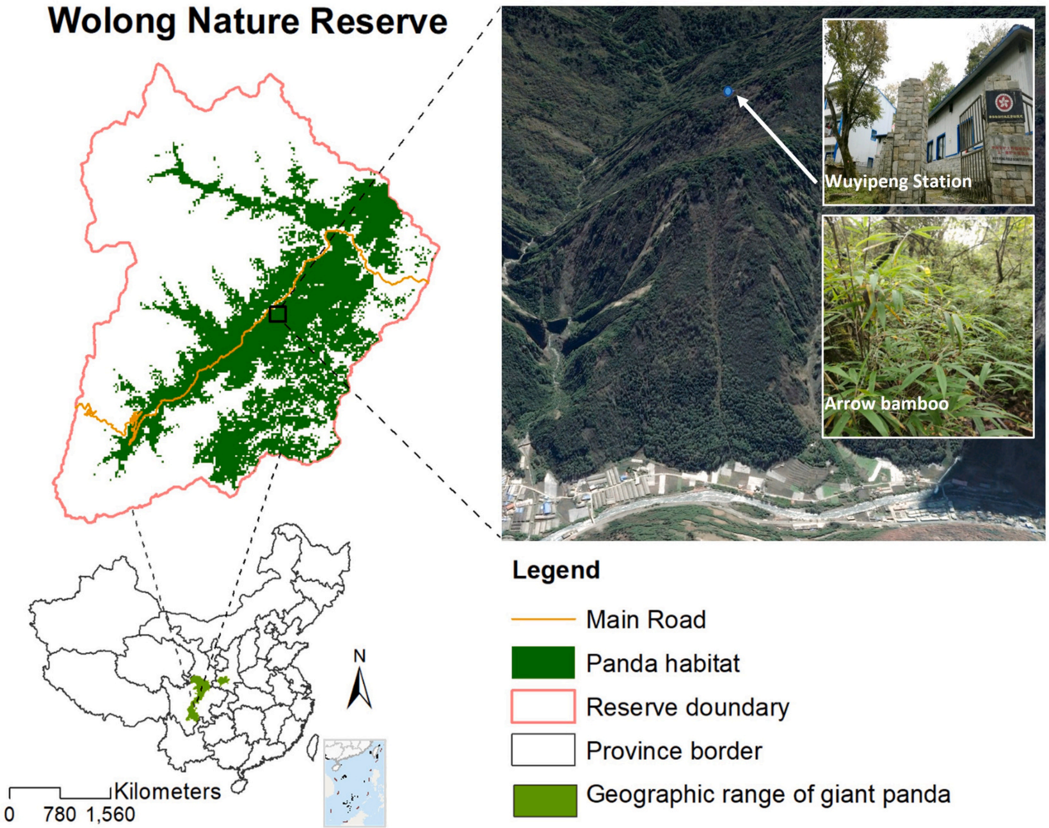

Fig. 1. The experimental site in Wolong Nature Reserve, Sichuan, China. The study site is located within the natural habitat of giant pandas and is about 5 km away from the nearest residential area. Arrow bamboo (*Bashania fangiana*) is the dominant understory plant species at the site and the average height is about 0.68 m. The Wuyipeng ranger station is about 300 m away from the experimental site and provides electricity for the warming treatments.

settlement and located within the core zone of the nature reserve where human development activities are banned. The flat terrain of the site reinforces its suitability as habitat for giant pandas because flat terrain facilitates movement of giant pandas for more efficient foraging (Zhang et al., 2015). The forest overstory is dominated by tall, mature trees with a few scattered saplings and understory shrubs. Arrow bamboo is the dominant understory plant, with an average height of 0.68 m, an average base diameter of 3.64 mm, and an average stem density of 33.5/m^2. There were no symptoms of plant illness (withered leaves, pests) observed on arrow bamboo at the start of the experiment. Furthermore, the site is about 300 m away from the Wuyipeng ranger station, which provided access to the electricity needed to warm the chambers (Fig. 1). At an altitude of 2560 m, the site is near the lower end of the elevation range (2500 m – 3100 m) of arrow bamboo (Schaller et al., 1985); consequently, the temperature is likely near the upper thermal limits for arrow bamboo. By exposing the bamboo to warmer temperatures, we

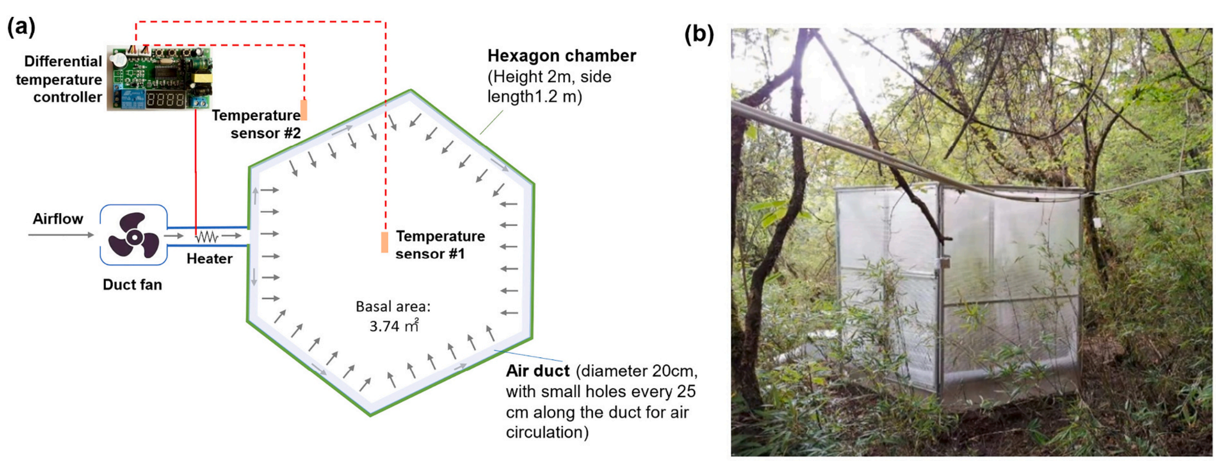

Fig. 2. The design (a) and appearance (b) of the improved hexagon open-top chamber system. Fresh air was pumped into the chamber constantly. An air duct with small holes was installed inside the chamber to distribute air within the chamber. The temperature difference between inside and outside the chamber is maintained by a differential temperature controller which has two sensors monitoring air temperatures inside and outside the chamber. The controller manages the power of a heater placed in the air duct based on the temperature difference inside and outside the chamber. When the difference is higher than intended, the heater shuts off; otherwise, the heater warms the air flowing into the chamber.

can study the species' responses to conditions beyond their current thermal range.

2.2. Open-top chambers for warming simulation

We deployed an improved hexagon open-top chamber system (OTC, Fig. 2) to simulate different degrees of warming, and compared arrow bamboo's biological responses to warmer temperatures. OTCs are a widely used tool for generating warmth while keeping vegetation relatively intact to allow species interactions, responses to environmental stimuli, and other ecological processes to unfold in a natural manner (Norby et al., 1997). OTCs often passively increase air temperature inside the chamber by allowing sunlight to enter and warm the air (Hollister et al., 2022), but sunlight under the forest canopy is often too weak to sufficiently increase the temperature for warming experiments. We followed previous studies (Norby et al., 1997; Messerli et al., 2015) and addressed this warming limitation by adding an active warming control system to provide the warming effect inside the OTC (Fig. 2). In this system, an in-line duct fan pumps fresh air constantly into the chamber (Fig. 2a). The temperature difference between the inside and outside of the chamber is maintained by a fixed amount using a differential temperature controller equipped with two sensors, which monitor the air temperature inside and outside the chamber. The controller adjusts the power of a heater according to the temperature difference inside and outside the chamber. If the difference is higher than the intended warming level, the heater stops working; otherwise, the heater warms the air flowing into the chamber. We tracked the temperature inside and outside the improved OTCs and the results showed that our warming simulation system can maintain a temperature that is warmer by fixed amounts than the ambient temperature (Fig. 3).

2.3. Experimental design

We deployed 16 OTCs, each covering a hexagon plot of arrow bamboo. The area of each plot is 3.7 m^2 and the distance between neighboring bamboo plots ranged from 2 to 5 m. Bamboo is a clonal plant and different bamboo individuals (ramets) could exchange nutrients via shared underground rhizomes. We cut the rhizomes along the edge of the plot and established an underground partition that extends from the surface to a 25 cm depth using solid plastic panels to isolate the bamboo within the boundary of each plot. To minimize the potential edge effects of the treatment, we only analyzed bamboo 20 cm away from the plot edge.

We divided the 16 bamboo plots into 4 groups with each group comprised of 4 randomly selected plots. All plots were rainfed only. The annual precipitation in this area is 882 mm and the annual average relative humidity is 86 %. Soils at the experimental site have a dark, humus-rich surface layer and a lighter subsoil layer, with a pH of 5.02 ± 0.16 and an organic matter of 12.9 % ±1.85 %. To capture the uncertainty of future temperature increases, we exposed 3 experimental groups to different levels of elevated temperatures (Winkler, 2016). Specifically, the temperature was maintained at 1.5, 3, and 4.5 °C warmer than the ambient temperature. We selected these three warming levels in accordance with the projected warming over the region under different greenhouse gas emissions scenarios outlined in the sixth report of the Intergovernmental Panel on Climate Change (IPCC) (IPCC, 2022). The remaining group of 4 bamboo plots without warming treatment constituted our control group. The randomness of treatment assignment ensures observations across experiment groups are independent from one another. All experiment groups were set in the relatively stable habitat with similar states of arrow bamboo, including the number of bamboo individuals, bamboo base diameter, and bamboo height (Fig. S1), which ensured a sound comparability in the responses of bamboo in different groups to warmer temperatures.

2.4. Measurements and data analysis

We evaluated the impact of warmer temperatures on the quantity of arrow bamboo by comparing population dynamics and biomass of bamboo grown under different experimental groups. We assessed the impact of warming on the dietary quality of bamboo by analyzing the variations in the nutritional indicators (crude protein, crude fat, crude ash) and palatability indicators (total tannins, total phenol, and crude fiber) of bamboo across different groups. Furthermore, we assessed the potential impact of warming on bamboo-aphid interactions by examining the levels of aphid infection and the content of total flavonoids (a compound in plants that often enhances plant defense against insect infection) in bamboo exposed to the different treatment regimes.

Specifically, we tracked bamboo population dynamics and measured bamboo biomass at the end of the experiment. We counted the number of live bamboo individuals and calculated the percent change of bamboo population in each plot at four different time intervals: April 2019 (the start of the experiment), October 2019 (after 6 months of the experiment), October 2020 (after 18 months of the experiment), and April 2021 (after 24 months of the experiment). In April 2021, we collected all aboveground biomass components, including stems, leaves, and branches. The collected biomass was then dried to remove moisture and weighed using sensitive scales to determine the dry weight of the stems,

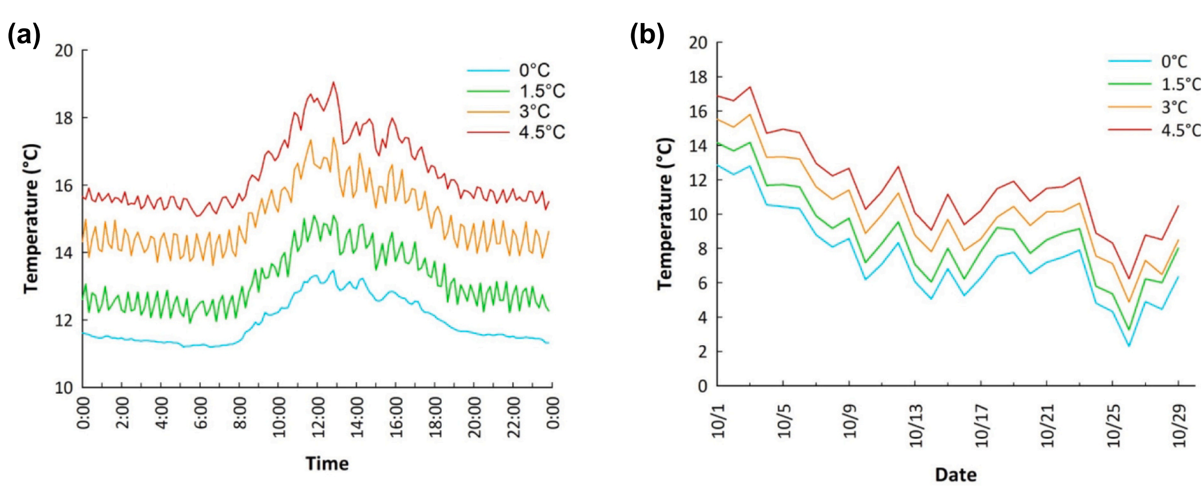

Fig. 3. Temporal dynamics in air temperature across the open-top chambers for the control (0 °C, no warming) and 1.5 °C, 3 °C, and 4.5 °C warming experiments. (a) Temporal variations within a sample day (October 5, 2020) with temperature recorded every 10 min. (b) Variations of daily average temperature for a sample month (October 2020).

leaves, and branches. We recorded the total above ground biomass of each plot by summing the dry weight of the stems, leaves, and branches. We did not measure the belowground biomass of bamboo because of the nature reserve's regulations, which prohibit major disturbances to the habitats of giant pandas.

For the bamboo samples collected in April 2021, we also measured the contents of crude protein, crude fat, and crude ash, which are the common indicators of the nutritional value of bamboo (Yuan et al., 2015). Crude protein in bamboo provides essential amino acids necessary for growth, tissue repair, and overall health of pandas while crude fat can help fulfill pandas' energetic and metabolic needs. Crude ash is another common nutritional indicator and represents the inorganic mineral content of a plant, such as iron, manganese, zinc, and copper. A previous study (Yuan et al., 2015) shows that pandas often avoid consuming bamboo with a high content of crude ash as high ash content may indicate the presence of mineral compounds that are not easily digestible or usable by pandas. We measured crude protein using the Kjeldahl method (Kjeldahl, 1883) and crude fat using the Soxhlet technique (von Soxhlet, 1879) – both are standard techniques to extract analytes from plant tissues. To measure the crude ash content, we heated bamboo samples at high temperatures to remove the organic materials, leaving behind the ash residue (plant's mineral content) which was then weighed and recorded. We selected three indicators to evaluate the impacts of warmer temperatures on the palatability of bamboo as food for pandas, including total phenol, total tannin, and crude fiber. Tannins and phenols are secondary metabolites found in plants, including bamboo. They often have a bitter and astringent taste that can be unappealing to animals (Okuda and Ito, 2011). Additionally, tannins and phenols can bind to proteins and other nutrients, reducing their availability for absorption by pandas and leading to reduced nutrient intake from their bamboo diet (Reed, 1995). Crude fiber is a component of plant cell walls that provides structural support to the plant. It is not easily digestible by pandas because they lack the necessary enzymes to break it down (Schaller et al., 1985). As a result, bamboo with high contents of tannins, phenols, and fiber are less palatable for giant pandas, which aligns with previous observations that giant pandas often avoid foraging on bamboo with high phenol, tannin, or fiber content (Yuan et al., 2015). We measured tannin using a ferric ammonium citrate method (Price et al., 1978), total phenol using Folin's phenol reagent method (Folin and Ciocalteu, 1927), and fiber using the acid-based digestion approach (Van Soest et al., 1991). More details on the various measurements (crude protein, crude fat, total tannin, total phenol, and crude fiber) can be found in the Supplementary Materials.

We also examined the level of aphid infection in bamboo exposed to varying levels of warming at our experimental site for evaluating the warming impact on bamboo-aphid interactions. The aphid (*Chaitoregma tattakana*) feeds on the bottom of bamboo leaves where the plant sap is stored. When feeding on this sap, the aphids produce excrement called honeydew that can facilitate fungus growth in the form of black, sooty mold, which will cause the bamboo leaves to yellow, wilt, and wither (Chia-Chi et al., 2002). We noticed the presence of bamboo aphids in our study site for the first time in October 2019. At that time, no bamboo in the control group was affected. In the group where the temperature increased by 1.5 °C, we detected aphids in two of the four bamboo plots. Aphids occurred in all bamboo plots with temperatures elevated by 3 °C and 4.5 °C, but they only affected a few leaves in each bamboo plot. In October 2020, aphid infection prevalence had increased substantially in bamboo plots. We counted the number of aphid individuals on the leaves of 10 randomly selected bamboo ramets in each of the bamboo plots and calculated the number of aphid individuals per leaf as the measurement of infection level. We did not apply insecticide during the experimental period to ensure that the aphid and bamboo could interact in a natural manner. To examine the potential reason for the prevalence of aphid infection, we used the spectrophotometry technique (Hortsense, 2024) to measure the content of total flavonoids in bamboo (see more details on the procedure in the Supplementary Materials), which are often known as a component that can enhance the resistance of plants to insect infection (Ramaroson et al., 2022).

We followed previous experimental studies (e.g., *59*) and performed ANOVA followed by the Duncan Multiple Range test (Duncan's test; (Duncan, 1955)) to examine whether the difference in the mean responses of bamboo across different groups in our experiment was statistically significant. The ANOVA followed by Duncan's test is an efficient method for conducting multi-group comparisons. With ANOVA, we compared and identified significant differences in the mean responses of arrow bamboo across different groups to warmer temperatures. Subsequently, we performed pairwise comparisons between specific bamboo groups using Duncan's test to obtain detailed insights into the differences among groups. For comparison of each of the outcome indicators using the ANOVA, we tested assumptions of normality and equal variance using Shapiro-Wilk test and Bartlett's test, respectively. All the comparisons passed the assumption examinations except for the comparison of the percent change of bamboo population measured in April 2021. For this comparison, we instead performed the Kruskal-Wallis test followed by Dunn's test, which are the non-parametric equivalents to ANOVA and Duncan's test and do not require the assumptions of normality and equal variance. For each of the comparisons, we had four observations (replicates) from each experimental group. We performed the comparisons in R, using the R package, 'agricolae' (de Mendiburu and de Mendiburu, 2019) to perform the ANOVA and the Duncan's test, and using the package 'dunn.test' (Dinno and Dinno, 2017) to perform the Dunn's test.

3. Results

3.1. Impacts on population dynamics and biomass of bamboo

The results of arrow bamboo population dynamics suggest that the impact of warming on bamboo survival is nonlinear across different degrees of warming (Fig. 4a, b). Bamboo in the control group and the 1.5 °C-warmer group exhibited similar changes in population size after 6, 18, and 24 months of the experiment, suggesting that a temperature increase of 1.5 °C did not have a significant impact on the bamboo population. For example, the control group achieved a 28.8 % net increase in population size after 24 months, which was similar to that found in the 1.5 °C-warmer group (19.4 % increase; $p > 0.05$). These results contrast with the substantial population shrinkage observed in the 3 °C- and 4.5 °C-warmer groups (Fig. 4a, b). After 24 months of the experiment, bamboo population sizes in the 3 °C- and 4.5 °C- warmer groups decreased by 67.5 % and 93.2 %, respectively (Fig. 4a, b), suggesting that a temperature increase of 3 °C or more could pose a significant threat to bamboo survival.

The results of bamboo biomass across different groups also indicate a nonlinear impact of warming on bamboo as temperature increase (Fig. 4c, d). At the end of the experiment, the total aboveground biomass of bamboo per unit area was similar between the control group (727.6 g per m^2) and the 1.5 °C-warmer group (801.6 g per m^2) ($p > 0.05$). In the groups where temperatures were elevated by 3 and 4.5 °C, the total aboveground biomass per unit area was 258.7 g per m^2 and 47.0 g per m^2, respectively, representing a 65.5 % and 93.5 % reduction compared to the control group. This pattern of total aboveground bamboo biomass across different groups remained consistent when different parts of the bamboo were analyzed separately (Fig. 4d). The biomass of bamboo stems, branches, and leaves in the control group and 1.5 °C-warmer group were similar ($p > 0.05$) but significantly greater than the biomass observed in the 3 °C- and 4.5 °C-warmer groups ($p < 0.05$; Fig. 4d). These results provide evidence that warming has a nonlinear impact on bamboo quantity, with a potential tipping point between 1.5 and 3 °C. Warming at or above 3 °C may have a significant impact on bamboo population size and biomass, threatening the sufficiency of the food supply for giant pandas.

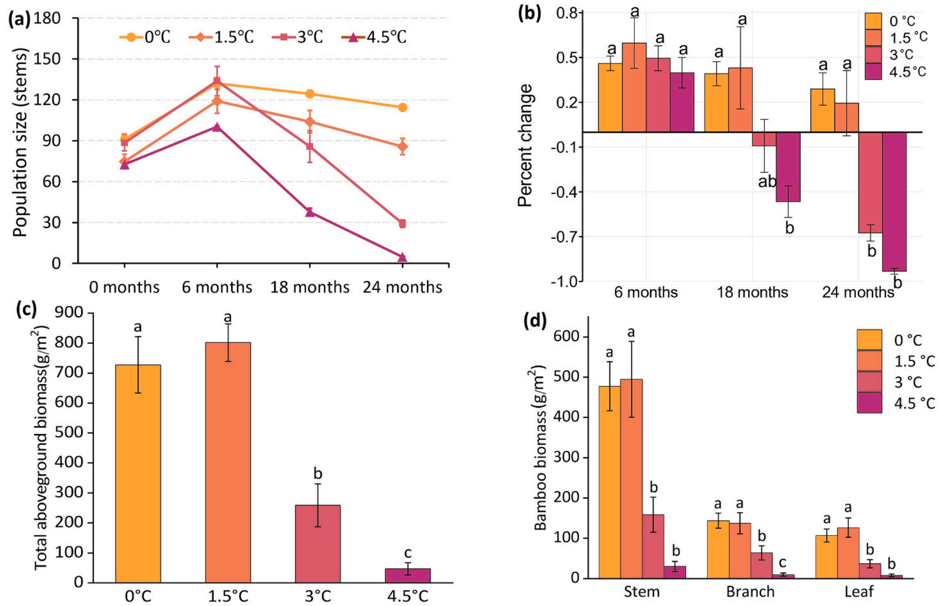

Fig. 4. Bamboo population dynamics and biomass across different groups where the temperature was elevated by 0, 1.5, 3, and 4.5 °C. (a) Bamboo population sizes that were measured at the beginning and after 6, 18, and 24 months of the experiment. (b) Percent change of bamboo population sizes after 6, 18, and 24 months. (c) The total aboveground biomass of bamboo per unit area across different groups after 24 months of the experiment. (d) Biomass of bamboo stem, branch, and leaf per unit area after 24 months of the experiment. The mean values were calculated by averaging across different plots in each treatment or control group. The error bars represent the standard error. The significance of the differences in the means of percent change in bamboo population sizes measured after 24 months of the experiment was tested using the Kruskal-Wallis follow by Dunn's test. The significance of the differences in the means of other outcome variables was tested using ANOVA followed by Duncan's test. Means with the same letter are not significantly different. Means with different letters are significantly different ($p < 0.05$).

3.2. Impacts on nutrition and palatability of bamboo

The comparisons of crude protein, crude fat, and crude ash in bamboo across different experimental groups suggest that warmer temperatures can degrade the nutritional value of arrow bamboo as a food source for giant pandas (Fig. 5). The macronutrients of crude protein and crude fat in bamboo across different groups exhibited a declining trend as bamboo were exposed to warmer temperatures. The crude protein in bamboo declined from 5.3 % in the control group to 4.5 % in the 4.5 °C-warmer group, while the crude fat declined from 0.96 %

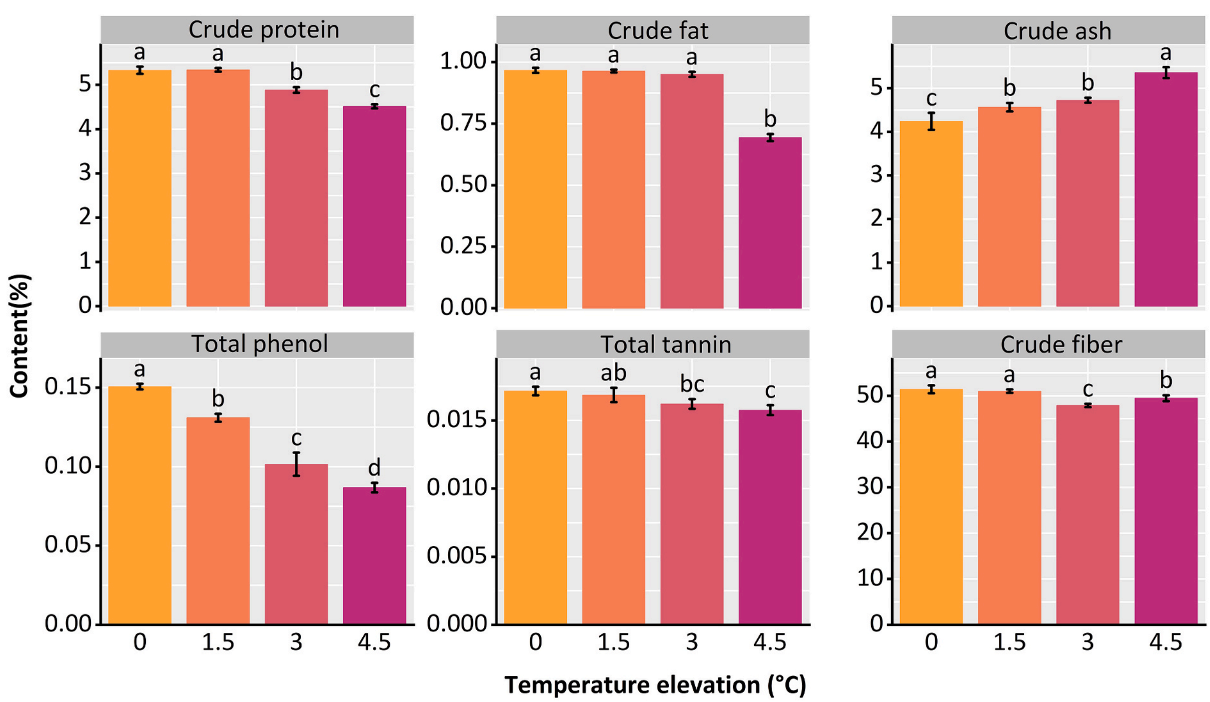

Fig. 5. The content of crude protein, crude fat, crude ash, total phenol, total tannin, and crude fiber in bamboo across groups exposed to temperatures elevated by 0, 1.5, 3, and 4.5 °C, respectively. The values were measured after 24 months of the experiment. The significance of the differences in the means was tested using ANOVA followed by Duncan's test. Means with the same letter are not significantly different ($p > 0.05$). Means with different letters are significantly different ($p < 0.05$).

in the control group to 0.69 % in the 4.5 °C-warmer group. The content of crude ash, which is negatively associated with the nutritional value of bamboo (Barh et al., 2021), increased from 4.2 % in the control group to 5.4 % in the 4.5 °C-warmer group. These results show that warmer temperatures can negatively impact bamboo's nutritional value as food for pandas. We noted that crude protein and crude fat of bamboo in the 1.5 °C-warmer group did not differ significantly from that of the control group ($p > 0.05$), suggesting that a temperature increase of 1.5 °C did not significantly change the crude protein and crude fat content in bamboo. The patterns of change in crude protein, crude fat, and crude ash in the different parts of bamboo (stem, branch, and leaf) as temperature increase were similar (Fig. S2).

Despite the negative impact of warming on bamboo's nutritional value, the results of total phenol, tannin, and crude fiber across the different groups of bamboo indicate that warmer temperatures can enhance the palatability of arrow bamboo as a food source for pandas. As discussed previously, pandas often avoid foraging on bamboo with high phenol, tannin, or fiber content (Barh et al., 2021). We found these three components all exhibited a declining trend as bamboo was exposed to warmer temperatures (Fig. 5), suggesting improvements in the palatability of bamboo with increased temperatures. For example, the total phenol of bamboo decreased by nearly half from 1.51 mg/g in the control group to 0.87 mg/g in the 4.5 °C-warmer group. Total phenol, tannin, and crude fiber in bamboo stems, branches, and leaves across different groups exhibited a similar pattern, though some variations exist among the different parts (Fig. S3). For example, total tannin in leaves decreased significantly from 0.27 mg/g in the control group to 0.18 mg/g in the 4.5 °C-warmer group ($p < 0.05$) but total tannin did not change significantly in the stems ($p > 0.05$).

3.3. Impacts on aphid infection of bamboo

We found that warming was positively associated with the prevalence of aphid infection in bamboo at our experimental site. The aphid infection was lowest for the control group with an average of 0.16 aphid individuals found on each randomly selected bamboo leaf (Fig. 6a). This number significantly increased to 4.73 in the 1.5 °C-warmer group, 8.6 in the 3 °C-warmer group, and 17.87 in the 4.5 °C-warmer group ($p < 0.05$). We observed a significant decrease in the total flavonoid content, a compound commonly associated with plant defense against insect infestation, in bamboo stems, branches, and leaves as temperature increased ($p < 0.05$) (Fig. 6b). Among different parts of bamboo, the most pronounced decline in total flavonoids was observed in the leaves, where the content dropped from 14.2 mg/g in the control group to 7.98 mg/g in the 4.5 °C-warmer group ($p < 0.05$). These results suggest that warmer temperatures may weaken bamboo's resistance to insect infection and exacerbate aphid infestations, forming a potential pathway for degradation in the quality of giant pandas' bamboo diet.

4. Discussion

To address the threat of climate change to global biodiversity, policymakers, scientists, and conservation practitioners need a better understanding of climate change impacts on keystone species and their functions. Although both field experiments and SDMs are common approaches to infer global warming impacts on species (Elmendorf et al., 2015), our study demonstrates that field experiments have some unique strengths in revealing the complex responses of species to warmer temperatures. First, unlike evaluations based on correlative SDMs, the results of field experiments can better capture the effects of species' resilience to changing climate conditions. Our experiments showed that an increase in temperature by 1.5 °C did not generate a significant impact on the population dynamics of arrow bamboo. This aligns with a growing body of evidence showing that many plant species can tolerate some changes beyond their current climate-niche envelope (Way and Oren, 2010; Craine et al., 2013), an important biological process overlooked in previous assessments of climate change impact on understory bamboo and giant panda habitats using SDMs. Therefore, it is important to reassess previous projections that suggested even modest climate change could pose a high risk to giant pandas' bamboo food supply (Tuanmu et al., 2013; Songer et al., 2012). Field experiments also enable evaluations of climate change impact on the dietary quality of a species, which are often difficult to assess using SDMs. Understanding the impacts of climate change on the dietary quality of plants is essential for reliable predictions of their functional change in providing food for the fauna. Our study found that a 3 °C and 4.5 °C temperature increase not only reduced the population size of arrow bamboo but also decreased the content of crude protein and crude fat in bamboo, degrading the nutritional value of bamboo and exacerbating the threat of warming to giant pandas' food supply. An additional benefit of field experimentation is that it allows us to observe changes in species interactions under simulated climatic conditions. Species interactions can affect species' responses to climate change, and many species extinctions due to climate change so far have involved altered species interactions (e.g., predator-prey interactions) (Urban et al., 2016; Cahill et al., 2013). Our study indicates that warmer temperatures have lowered the compound of total flavonoids in bamboo. This reduction may have contributed to the observed high prevalence of aphid infection in bamboo exposed to warmer temperatures, representing a novel pathway through which warming could adversely affect bamboo. We noted that the occurrence

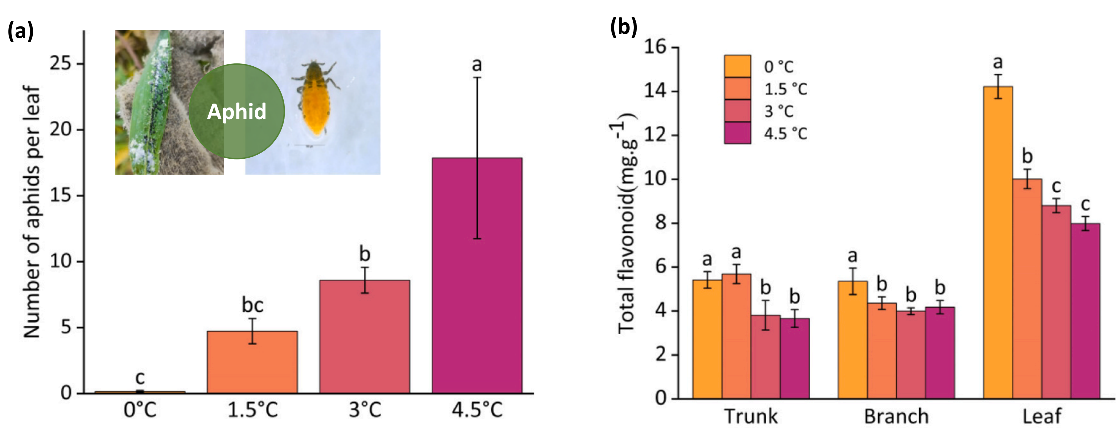

Fig. 6. Aphid infection and content of flavonoid in different parts of bamboo across groups exposed to temperatures elevated by 0, 1.5, 3, and 4.5 °C, respectively. (a) Number of aphids per leaf in bamboo plots across different groups. (b) Total flavonoids in bamboo stems, branches, and leaves across different groups. The values were measured after 24 months of the experiment. The significance of the differences in the means was tested using ANOVA followed by Duncan's test. Means with the same letter are not significantly different ($p > 0.05$). Means with different letters are significantly different ($p < 0.05$).

of aphids may attract their natural enemies to appear and predate them, which would require a longer period to monitor.

In recent decades, dozens of manipulative warming experiments have been conducted and provided unparalleled insights into how ecosystems respond to climate change, but they have not yet been implemented for various keystone species. By revealing the complex warming impacts on both the quantity and quality of giant pandas' bamboo diet, our study made valuable contributions to the experimental assessment of global warming impacts on species. For example, previous global warming experiments have mostly focused on assessing the impacts of warmer temperatures on plant physiology (e.g., heat tolerance, photosynthesis, and respiration rates) while the role of the plants in supporting wildlife and biodiversity has rarely been considered. Our experiment addresses this research need and reveals potential global warming impacts on the bamboo food supply for giant pandas, which advances the understanding of food web responses to global warming. Furthermore, the identification of nonlinear responses of species to global warming is crucial as these nonlinear responses suggest complex, potentially abrupt, changes in ecosystems. However, such pattern in species responses to global warming remains poorly understood (Kreyling et al., 2018). Our experiment illustrated the nonlinearity in arrow bamboo's responses to warmer temperatures, shedding light on the tipping points that can lead to irreversible impacts on giant pandas in the face of global warming.

The complex impacts of warmer temperatures on arrow bamboo revealed in this study can have important implications for the conservation of giant pandas. On the one hand, our study confirmed that future temperature increases could threaten arrow bamboo, a major species that provides food for giant pandas. This is substantiated by our finding that arrow bamboo exposed to temperatures elevated by 3 °C and 4.5 °C experienced a significant decline in population size and degradation in nutritional value as food for giant pandas. Decreases in the quantity and nutritional value of bamboo could cause cascading effects on the health and survival of giant pandas. As a species in the order of Carnivora, the giant panda retains the simple stomach and short gastrointestinal tract, and consequently has a low efficiency in digesting bamboo (Schaller et al., 1985). To meet their energy requirements, giant pandas must feed during a large portion of each day (10 to 16 h) and consume large quantities of bamboo relative to their body mass to obtain sufficient nutrition (Schaller et al., 1985). If the nutritional value and quantity of bamboo decreases, pandas may struggle to find enough suitable food to obtain the necessary nutrients and energy, leading to malnutrition and population decline. On the other hand, bamboo may tolerate moderate global warming and maintain its function as a source of food for giant pandas, as there was little difference between bamboo grown under 1.5 °C warmer conditions and those under control conditions, both in terms of population dynamics and contents of crude protein and crude fat. Although further efforts are needed to validate this finding over an extended experimental period (e.g., 5 years or more), our results provide evidence that temperature increases may not generate cascading impacts on giant pandas' bamboo food if we can achieve the goal of limiting global warming to 1.5 °C under the Paris Agreement.

Results of the impacts of warming on bamboo quantity and quality also provide essential information for the development of process-based models (e.g., *33*) to project future changes in bamboo populations, distributions, and nutrients at the landscape scale to support conservation planning. For example, conservation planners can use such information to prioritize bamboo habitats that are especially vulnerable to future climate change for connectivity restoration efforts. While making it easier for giant panda subpopulations in those areas to crossbreed, enhanced panda habitat connectivity could increase the potential of bamboo species and giant pandas to disperse to other areas where they can survive in the future.

While arrow bamboo contributes the most to giant pandas' food supply, we noted that there are 33 other bamboo species in 7 genera distributed across the natural habitats of giant pandas in the wild (Sichuan Forestry Administration, 2015). Arrow bamboo and the other bamboo species share some commonalities that may render them vulnerable to temperature increases, such as shallow root, long sexual reproduction intervals, and limited seed and vegetative dispersal ability (Tuanmu et al., 2013). However, bamboo species, especially across different genera, can have varying characteristics, such as heat tolerance (Fadrique et al., 2022) and phenology (Tang et al., 2020), which may influence their responses to warmer temperatures. Therefore, a more comprehensive assessment of the impacts of warmer temperatures on different bamboo species is necessary to better infer the threat of global warming to the food source of giant pandas. Moreover, like the dependence of giant pandas on understory bamboo for food, many other plant species play a critical role in ecosystems by providing the essential food sources for other threatened animal species. Examples include the koala (*Phascolarctos cinereus*), which relies on specific eucalyptus tree species for food, and the Karner blue butterfly (*Plebejus melissa samuelis*), whose caterpillars exclusively feed on wild lupine. Approaches similar to what we have demonstrated in our study may be applied to reveal potential global-warming-driven effects on the survival and dietary quality of those plants. This knowledge can provide critical information for the conservation of not only the plant species, but also the threatened animals that are trophically dependent on them.

Like other assessments of global warming impact on species using field experiments, the present study has several limitations that could be addressed by future research. First, it is important to run the experiment over an extended period because time-lag and -accumulation effects may exist in the responses of plants to global warming. Some ecological processes, such as the decomposition of plant residues and the release of nutrients, may respond slowly to global warming, resulting in delayed impacts on plant species (Alexander et al., 2018). Therefore, running an experiment for a longer period (e.g., 5 to 10 years) would be beneficial in detecting effects that may take years to fully emerge. Second, more research is needed to better identify the tipping point in the nonlinear impacts of warmer temperatures on bamboo survival rate. Our initial assessment indicates that warming has a nonlinear impact on arrow bamboo survival, with a potential tipping point between 1.5 °C and 3 °C. Future experiments may expose arrow bamboo to a range of warmer temperatures with smaller intervals, such as 0.5 °C increments, to more accurately determine the temperature threshold beyond which warming will generate substantial impacts on bamboo's population and nutritional value. Third, although temperature increase is a major dimension of global warming, changes in other facets of climate, such as precipitation and frequency of heat waves, could pose additional threats to bamboo's survival and function as a food source for giant pandas. More experiments are needed to assess the impacts of changes in multiple climatic factors on bamboo species. Lastly, our experiments would benefit from expanded monitoring of factors other than bamboo's population dynamics and dietary quality to reveal the mechanisms underlying the impacts of warmer temperatures on bamboo. For example, studies showed that climate change has altered soil carbon, nitrogen, and the structure and function of soil microbial communities, often with profound impacts on biogeochemical cycling and plant species (Jansson and Hofmockel, 2020). Monitoring the dynamics of soil-related properties may help reveal the various pathways via which climate change affects bamboo.

5. Conclusion

Our study represents an important step to understanding the impacts of global warming on both the quantity and quality of giant pandas' bamboo food. The findings from our two-year study revealed two complexities in the warming impacts on giant pandas' bamboo diet. Firstly, we observed that warmer temperatures generated a nonlinear impact on the survival of arrow bamboo and there is a warming threshold beyond which warmer temperatures can substantially reduce bamboo survival rates and threaten giant pandas' food supply. Secondly, we found that warming had a biphasic impact on the dietary quality of bamboo. On the one hand, warming increased the content of hardly digestible crude ash in bamboo and decreased the macronutrients of crude protein and crude fat, resulting in a degradation of bamboo's quality as a nutrient source for giant pandas. On the other hand, warming reduced the content of tannin, phenol, and fiber in bamboo, thereby enhancing the palatability of bamboo as a food for giant pandas. Furthermore, our study shed light on a novel pathway through which warming adversely affect bamboo. We found that warming intensified aphid infection in arrow bamboo, jeopardizing bamboo health and posing a further threat to food supply for giant pandas. These findings advanced our understanding of the impacts of global warming on giant pandas and provide crucial insights for informed conservation planning in the face of climate change.

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CRediT authorship contribution statement

Hongbo Yang: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Dongyao Zhang:** Writing – original draft, Investigation, Data curation. **Julie Ann Winkler:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Qiongyu Huang:** Writing – review & editing, Writing – original draft, Supervision, Formal analysis, Conceptualization. **Yuanbin Zhang:** Writing – original draft, Methodology, Data curation, Conceptualization. **Jianguo Liu:** Writing – review & editing, Writing – original draft, Conceptualization. **Zhiyun Ouyang:** Writing – review & editing, Writing – original draft, Supervision. **Weihua Xu:** Writing – original draft, Data curation. **Xiaodong Chen:** Writing – review & editing, Writing – original draft, Project administration, Conceptualization. **Daifu Wu:** Writing – original draft, Project administration, Data curation. **Jindong Zhang:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Melissa Songer:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110635.

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