



# Warming-induced shifts on Tibetan Plateau: the overlooked ants and their ecological impacts

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## Abstract

**Context** Tibetan alpine ecosystems are among the world’s fastest-warming natural systems, and consequently, are expected to undergo dramatic changes in their ecological processes. However, despite the importance of ants in mediating these ecological processes, it remains unclear how they will respond to the rapid climate warming on the Tibetan Plateau.

**Objectives** In this perspective piece, we aim to establish a baseline understanding of the spatial distribution of ants on the Tibetan Plateau, to evaluate how these ants respond to climate change such as warming at both local and regional scales, and to identify future research avenues that can elucidate the impacts of warming-induced ant expansion.

**Methods** We first present the results of a long-term climate manipulation experiment on how ants respond to warming in a Tibetan alpine grassland. Next, we evaluated the current and future distribution of ants on the Tibetan Plateau using the MaxEnt model with data compiled from existing field survey of ant species in the region. Finally, we synthesize published studies to review the ecosystem functions in which ants are involved on the Tibetan Plateau and identify gaps in current research.

**Results** From our field warming experiment, we found that ant abundance significantly increased from 2017 to 2022. For our region-scale analysis, we found that the distribution of ants on the Tibetan Plateau will expand with future warming. Lastly, we identify a few key gaps in our knowledge of ants’ ecological impacts (*e.g.*, greenhouse gas emissions, trophic

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network, and the interplay between the different ecosystem properties).

**Conclusions** Our results suggest that ants are widespread on the Tibetan Plateau, and involved in several important ecosystem processes with significant impacts on soils, plants, microbes and Tibetan faunas. With rapid climate warming, their abundance, and ecological functions will further lead to unknown far-reaching impacts on the health of the ecosystem, food web dynamics, and nutrient cycling of Tibetan alpine ecosystems. We call for more research activities to address critical knowledge gaps that have not been explicitly assessed in this important geographic region.

**Keywords** Alpine grassland · Ants · Climate change experiment · Global warming · Regime shifts · Tibetan Plateau

## Introduction

The Tibetan Plateau, known as the “third pole” of the world (Yao et al. 2007), is one of the land areas most sensitive to global warming. It is currently warming 2–3 times faster than the global average, at a rate of 0.16 °C to 0.67 °C per decade (Kuang and Jiao 2016; Zhou and Zhang 2021), and this warming trend appears to be accelerating in recent decades (Duan and Xiao 2015). This rapid regional warming is reshaping vegetation growth on the plateau, which in turn will have cascading effects on the ecological functions and processes of the Tibetan alpine ecosystems (Li et al. 2016; Ma et al. 2017; Liu et al. 2018; He et al. 2021).

Ants are known to play a key role in maintaining a variety of ecological processes on the Tibetan Plateau (Hölldobler and Wilson 1990; Del Toro et al. 2012; Parker and Kronauer 2021). For example, ants redistribute soil and litter debris, which leads to changes in soil properties (temperature, humidity, pH, organic and mineral content) (Wang et al. 2017). At the local scale, these changes will indirectly affect plant community composition, for instance, by increasing the proportion of grasses close to the nest (Culver and Beattie 1983; Sebastià and Puig 2008; Meng et al. 2011; Xiang et al. 2016). At the landscape scale, it has been shown that, ants can enhance coexistence of plant species, in part by helping with seed dispersal

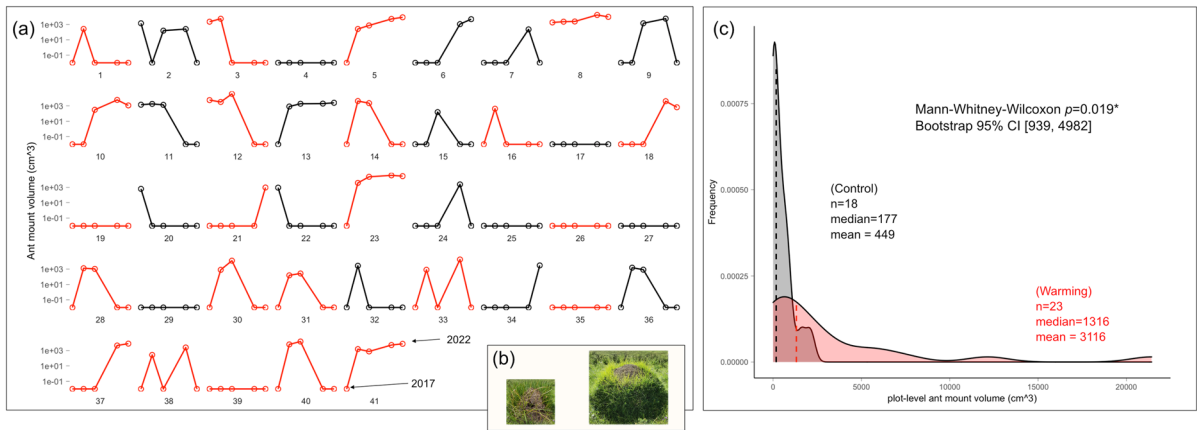
and germination (Xu et al. 2017). Additionally, ants were shown to promote the growth of graminoids and may promote patch quality in the alpine grassland ecosystems (Yu et al. 2010). Yet, despite the importance of ants in mediating these aforementioned processes, there remains a key knowledge gap in the understanding of how ants and their ecosystem services will respond to rapid warming on the Tibetan Plateau.

In this perspective piece, we first present local-scale empirical evidences of how ants responded to warming from a 12-year manipulation experiment (first experiment of its kind in the Tibetan grassland system). We then expand our analysis to the regional scale, by estimating the current habitable zone for ants and their future territories in response to warming. In the final section, we summarize existing studies of ant ecological impacts and points to avenues for future research efforts. It is our hope that the resulting conceptual framework can guide future research of ants on and beyond the Tibetan Plateau.

## Warming experiment reveals increasing ant abundance in a Tibetan alpine grassland

We used a long-term warming manipulation experiment (2011-present) to explore the response of the ant community to climate change on a Tibetan alpine grassland (Supplementary Note 1 for detailed experimental design). Within the study area, two ant species, *Formica candida* and *F. manchu*, are commonly observed (*F. candida* is a metropolitan species across the entire Tibetan Plateau (SI Appendix, Fig. S1), while *F. manchu* is a common alpine grassland species (Luo et al. 2023)). Based on our general observation, ant abundance was in general very low for the first 7 years after the experiment was set up, with ant mounds being sporadic and small. It is unclear whether this low abundance represent a long-term baseline, or a temporary state due to disturbance from the experimental setup.

We started to systematically track the ant population dynamics starting from 2017, counting the number of ant mounds within each experimental plot and measuring the volume of each mound. We adopted mound volume as a proxy to assess the population size of each colony given the robust positive association observed between the number of worker ants



**Fig. 1** Responses of ant abundance to warming. **a** Ant mound volume over time (2017–2022) across 41 individual experimental plots. In general, ant colonies emerge, expand, then decline in any given plot, with residence time ranging from 1 to 4 years. However, certain plots had no ant colonization throughout the observation period, while in a few plots, ant abundance keeps increasing for the entire 5-year period. Red indicates plots in the warming treatment while black indicates control plots. Here we are using ant mound volume as a

proxy for ant abundance as mound volume strongly correlate with the number of worker ants. **b** An overhead image of an ant mound and its change in size. **c** Warming significantly increased the average plot-level ant mound volume (Wilcoxon test,  $p=0.019^*$ , 95% CI for difference between control and warming [939  $\text{cm}^3$ , 4982  $\text{cm}^3$ ]). We derived average plot-level mound volume by integrating the temporal growth-phase curve in panel **a** and then averaging over 6 years of observation period

and the volume (the formula for calculating the volume is shown in Table S1) of ant nests at the colony level (Mikheyev and Tschinkel 2004). Adding up the volume of all mounds in each plot gives us the total mound volume at a given time point.

Typically, the lifecycle of ant nests consists of multiple stages, including establishment, expansion, contraction, and eventual disappearance, with the duration ranging from 1 to 4 years (Fig. 1a, b). During this process, the volume of mounds undergoes temporal changes, giving rise to a growth-phase curve over time (Fig. 1a). To obtain the average plot-level mound volume, we integrated the temporal growth-phase curve depicted in panel a and calculated the mean value based on 6 years of continuous observation (Fig. 1c).

When comparing the group difference of plot-level mound volume between control and warming plots, we found that the two groups are significantly different (Fig. 1c, Mann–Whitney–Wilcoxon test,  $p=0.019^*$ , Supplementary Note 1). Specifically, warming plots on average contains 939–4982  $\text{cm}^3$  (bootstrap CI) more mound volume than the control plots (Supplementary Note 1). Our result is consistent with previous reported observations in other cold systems (Youngsteadt et al. 2017; Høye et al.

2021; Illich and Zuna-Kratky 2022). Our finding can potentially be explained by the positive effect of warming on various phases of ant colony development. For instance, researchers have demonstrated that elevated temperatures can accelerate ant colony development by promoting the maturation of ant larvae and extending the foraging duration of workers (Porter 1988; Diamond et al. 2012; Shik et al. 2019).

Another proxy for ant abundance is the number of ant mounds within each plot (ignoring the volume of these mounds). In many cases, multiple ant nests can be identified in a single plot. We asked the simple question of whether warming treatment will increase the number of ant mound at the plot level. The occurrence of ant mounds can be approximated by Poisson distribution, but in our specific case with an inflated zero component. Our analysis shows that warming significantly increases ant mound count (equivalent to mound density per area) at the plot level ( $p=0.047^*$ , generalized linear mixed model, Supplementary Note 1).

Together, our results suggest that at the local scale, warming will increase the population size of ants. However, these local-scale findings raised a very important question: *how will ants respond to warming*

across the entire Tibetan Plateau? While it is tempting to simply scale up local experimental understanding to a much bigger area, the geographical distribution of ants at regional scale is a complex function of many other factors that our local-scale experiment could not manipulate: species identity and their dispersal traits, other climatic factors, geographic isolation and vegetation types, etc. In the following section, we evaluate warming-induced ant responses at the region level.

### Warming expands ant distribution across the Tibetan Plateau

It is valuable to estimate future response of ants to warming across the entire Tibetan region, given ants' extensive impacts on their host ecosystems. Yet, thus far, knowledge of ant distribution relies on various small-scale surveys. To address this knowledge gap, we treated the geographical distribution of ants as a black-box, and used statistical tools to unpack the key factors that give rise to the current distribution pattern. From there, we venture to extrapolate future ant distribution based on how these external factors will change under Tibetan warming scenario. We acknowledge that this phenomenological approach is less mechanistic (especially when compared with the local-scale manipulation experiment) and can be problematic should the underlying mechanisms shift. However, for this perspective piece, we believe this approach can be useful in offering us first-hand coarse-gained insight.

We first compiled the published literature between 2000 and 2022 from Web of Science and the China National Knowledge Infrastructure (CKNI) using the keyword combination 'ants' or 'Formicidae', with geographical regions, such as 'Tibetan Plateau', 'Qinghai-Tibetan Plateau', 'Tibet', 'Qinghai', 'Xinjiang', 'Yunnan'. To ensure data accuracy, we included only sampling data in which ants are identified to the level of genus. In total, we collected 26 primary research articles and one review (SI Appendix, Table S2).

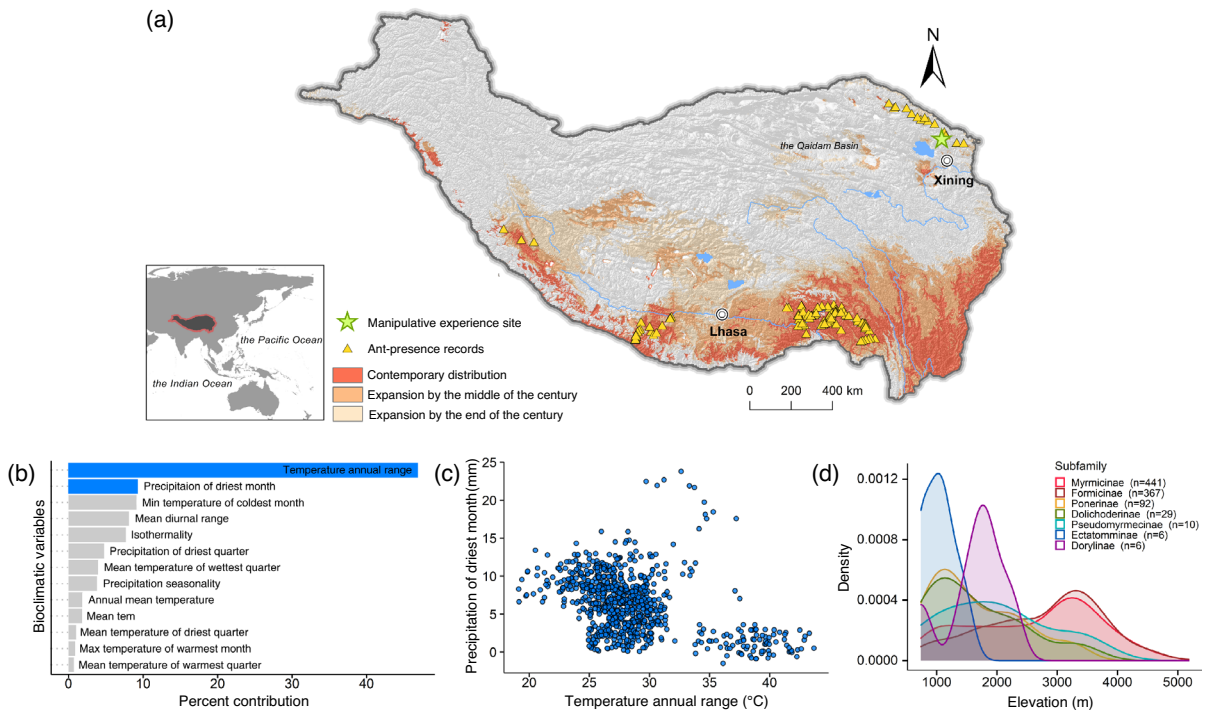
In total, we compiled data from 213 ant species belonging to 60 genera and nine subfamilies (SI Appendix, Table S3). To infer the total biodiversity from these sampling data, we fitted species

accumulation curves at the scale of sampling site (SI Appendix, Fig. S2a) and landscape type (SI Appendix, Fig. S2b). We found that with the increase of sampling sites and landscape types, the total number of species observed gradually saturated, indicating that our synthesis gives a sound estimate of the total ant biodiversity on the Tibetan Plateau.

For external factors, we obtained the contemporary bioclimatic data (19 climatic data collated for species distribution model by WorldClim) from the World Climate Data website (<http://www.worldclim.org/>, Fick and Hijmans 2017). We then used MaxEnt model ([http://biodiversityinformatics.amnh.org/open\\_source/Maxent/](http://biodiversityinformatics.amnh.org/open_source/Maxent/), version 3.4.4) to evaluate the contemporary ant distribution across the Tibetan Plateau (see Supplementary Note 3 for detailed methods). We next mapped the contemporary distribution of Tibetan ants (Fig. 2a, red area) and predicted the future distribution as a function of future climate warming (Fig. 2a, the middle of this century, 2030–2050: orange area; the end of this century, 2080–2100: light orange area).

At a species level, we observed great difference in the ants' abilities to cope with various environmental conditions. For example, there are ant species that can cope with an annual temperature range of 42.84 °C, and an annual maximum temperature as low as 2.43 °C, barely above freezing. In particular, *Myrmicinae* and *Formicinae* species tend to occupy the most challenging ecological niche, allowing them to be widely distributed across the plateau (SI Appendix, Fig. S3). In comparison, other subfamilies such as *Pseudomyrmecinae*, *Ectatomminae*, and *Dorylinae* are less abundant and are only observed in environments where the annual temperature range is < 27.55 °C.

In our data, the diversity of ants decreased significantly with increasing elevation, and the survival fitness of ants decreased as expected (temperature decrease and annual temperature range increase with increasing elevation). We found that these ant species are distributed from 740 to 5183 m above sea level (Fig. 2d), across a variety of ecosystems including alpine grasslands, alpine shrublands, and alpine forests, and alpine tundra. Note that *F. candida* maintained the highest vertical distribution record on the Tibetan Plateau, at an altitude of 5183 m, where alpine grasslands are found. *F. candida* is the most widely distributed species in the Tibetan Plateau, and



**Fig. 2** The suitable area and niche-analysis of ants on the Tibetan Plateau. **a** Based on the data of field survey in literature (yellow triangle), we evaluated the contemporary distribution area of ants (red) and predicted the distribution area of ants at the middle (orange) and end (light orange) of this century by using the MaxEnt model. The white areas hold a lower fitness in results. The green star indicates the location of the experimental warming site, i.e., Haibei Research Station.

**b** The importance of environmental variables in the MaxEnt model. **c** The ecological niches of ants on the Tibetan Plateau by analyzing the temperature annual range and the driest quarter precipitation of all ants under the contemporary environment (x-axis jitter × degree, y-axis jitter × mm). Each dot represents a species record. **d** Distribution of different subfamilies along the altitudinal gradient

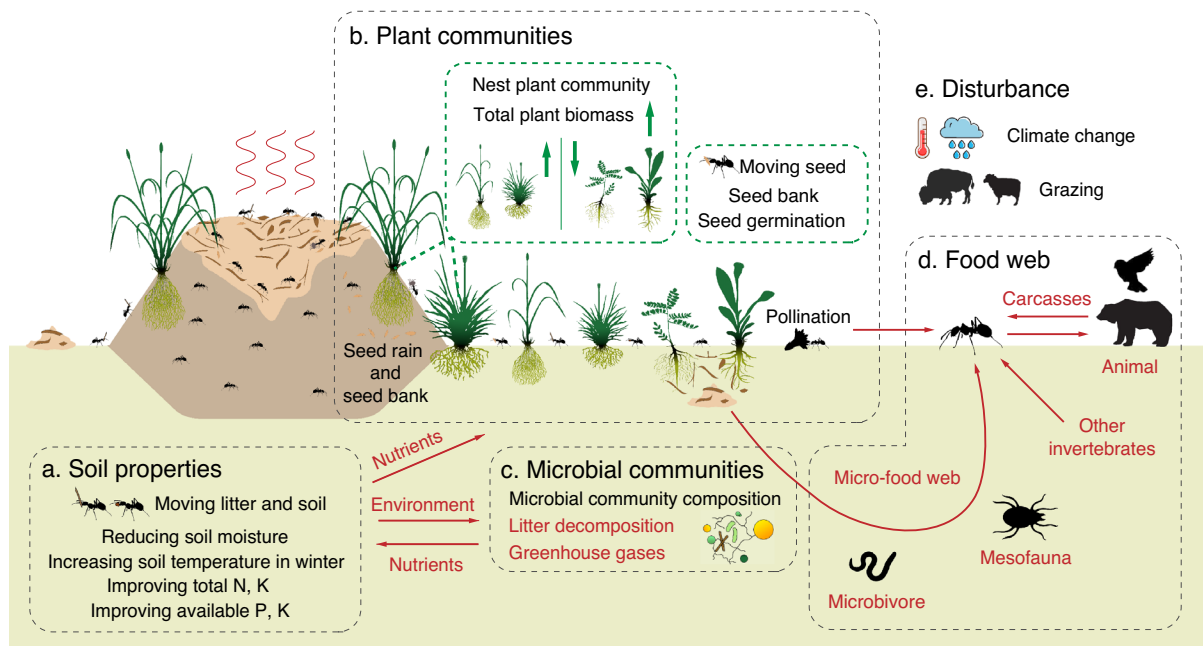
its distribution can almost represent the limit of the distribution range of any single species of ants on the plateau (SI Appendix, Fig. S1).

These areas that we deemed unsuited for ant presence mainly consists of two land-cover types: the cold alpine ecosystems of the Himalayas in the south and Kunlun Mountain in the north, and the dry desert ecosystem within Qaidam Basin in the north. In these environments, the warm period each year is too short for the ant populations to accumulate enough food and energy to maintain a positive population growth rate.

Taken together, our analysis suggested that at least 12% of the Tibetan Plateau is contemporary potential ants’ habitat, overlapping with all vegetated types (grassland, shrublands, forest, etc.). This suggest that ants are a metropolitan presence on the Tibetan Plateau and likely play key roles in maintaining

ecosystem processes across all Tibetan alpine ecosystems. In particular, the MaxEnt model identified ant presence in the alpine meadow ecosystems near our experiment sites, which is consistent with our field observations. By in large, ants were mostly found in the southeast edge of the Tibetan Plateau, which feature relatively warm weather, with smaller temperature annual range, due to lower latitude and lower elevation compared to the central and northern part of the Plateau.

However, we should note our model prediction of current ant distribution might be conservative. The model is based on existing ant-presence data, and it is likely that the fit area will be larger when more ant diversity surveys are conducted in the northwest part of the Tibetan Plateau (for example, the area south of the Taklamakan Desert and the area in and around the Qaidam Basin). The region is likely hospitable for



**Fig. 3** Ant-mediated interaction network in ecosystems. **a** By moving the litter and soil, ants affect soil physicochemical properties. **b** The burial of soil and the alteration of soil properties change the plant community around the ant nest. Ants as seed dispersers also affect the distribution and germination rate of plant seeds. **c** Changes of soil physical and chemical proper-

ties will affect the composition and structure of soil microorganisms; in turn, these will accelerate the change of soil properties. **d** By decomposition of litter, a unique ant-centric food web structure forms around the ant nest. **e** Disturbance factors, such as climate change, and grazing activities all could impact these ant-mediated processes

some other ant species despite thus far no field-observations have been made, which will further expand the plausible ant distribution area (both contemporary and future) within the model.

Under the strong climate warming scenario (ssp 5–8.5 UKESM1-0-LL), distribution for ants on the plateau will expand inward and northward. Total habitable area will cover 21% of the entire region by mid-century and to 34% by the end of the century. This expansion is largely driven by increasing temperature (and consequently decreasing temperature annual range) across the region. While the spatial and temporal resolution of our prediction is rather limited, the overall trend is clear and robust. Our particular prediction of warming-induced ant expansion to higher latitudes (and altitude) is consistent with predictions of termite expansion from a recent study (Zanne et al. 2022).

The ecological implications of ant expansion for their host ecosystems are rather unclear and demand more research attention. In the next section, we review existing studies of ant-induced impacts on

ecosystem processes and point to future avenues of research efforts.

### Ants' ecological impacts on alpine ecosystems: missing links and future avenues

Ants are integral components of most ecosystems on Earth (Wilson 2020). Through foraging and nesting, ants interact with plants, animals, microbes and the abiotic environment (Parker and Kronauer 2021). This myriad of ecological interactions ultimately forms an interaction network, the processes of which are mediated by ant activities. A unified understanding of this network might allow us to better understand and better predict the future states of ecosystems.

Here we review this ant-mediated interaction network by looking into its subcomponents: (a) soil properties, (b) plant communities, (c) microbial communities, and (d) the food web (Fig. 3a–d). In addition, we included disturbance factors (for example, grazing, warming, change of precipitation) that can

impact the interaction network as external forcings (Fig. 3e). We denote in black these ant-mediated processes (text and arrows) that have been reported in studies of Tibetan ecosystems. In order to highlight potential future direction of research efforts, we denote in red these processes that have been reported from ecosystems elsewhere (*e.g.*, tropical forests) but have not been studied on the Tibetan Plateau.

In general, much work has been done on the Tibetan Plateau to reveal the impacts of ants on soil properties (Fig. 3a) and plant communities (Fig. 3b), while processes related to microbial communities (Fig. 3c), the food web (Fig. 3d), and the effects of external disturbance factors (Fig. 3e) remain poorly studied.

Ant activities—in the form of foraging and nesting—can greatly impact soil properties at both local and landscape levels (Fig. 3a). As a result of ant activities, soils near the ant nest in general differ greatly from ambient soil in their physicochemical properties (Yu et al. 2010; Wang et al. 2017; Yang et al. 2017). Bare ground created by ant nests will absorb more solar radiation, and consequently maintain a higher soil temperature, lower soil moisture, excellent conditions for the ants within the nest (Yu et al. 2010; Meng et al. 2011; Chen et al. 2013).

Ant activities can also impact the plant communities (Fig. 3b), both directly through ants foraging for plant materials and indirectly through ants impact on the soil properties described above. In general, ant activities can increase total plant biomass (for instance, via enriching soil nutrients), shift plant communities, and reduce local plant species diversity on and around nests (Meng et al. 2011; Chen et al. 2013). Meanwhile, farther away from ant nests, ant activities such as seed dispersal and pollination can impact plant community composition (Puterbaugh 1998; Hou et al. 2009; Xu et al. 2017; Zhao et al. 2020).

As a consequence of the ant-induced changes in soil properties (Fig. 3a) and plant communities (Fig. 3b), studies have identified that ant activities can affect microbial communities in the soil (Yang et al. 2017; Wang et al. 2017; Fig. 3c). Future research should shed more light on the interaction between subcomponents of the ant-mediated interaction network, for example effects of nesting activity on greenhouse gases, effects of changing plant

communities on belowground carbon storage and microbial respiration.

Another research area that represents a knowledge gap is the study of food webs (Fig. 3d). Ant species are omnivorous and consequently serve as hubs for the material and energy flow, connecting the food web. The foraging activities of ants may have a top-down control to the soil micro-food web, affecting the diversity of soil fauna and microbial metabolism, ultimately affecting litter decomposition. The effects of ants on soil fauna and other arthropods, especially those involved in processes such as pollination and soil loosening, are also important gaps that can lead to fruitful future discoveries.

Last but not least, the external forcings from disturbance factors (Fig. 3e) can modify the entire interaction network. In addition to the effects of climate factors (*e.g.*, warming), grazing represents another important factor that can interact with ant activity and impact ecosystem health on the Tibetan Plateau (Dong and Sherman 2015). It has been shown that ant diversity and abundance are often affected by both grazing intensity and site productivity (Schmidt et al. 2012). In particular, moderate grazing pressure seems to co-occur with highest ant diversity and ant nest densities in grasslands (Usnick and Hart 2002). High grazing intensity tends to cause grasslands degradation but will nevertheless favor the population growth of a few specific ant species (Eldridge et al. 2020). It is unclear whether the overrepresentation of these ant species in degraded landscapes will create positive feedbacks that further degrade the ecosystem or instead prevent a runaway collapse of the system. With a booming economy and dynamic demography, the Tibetan region is bound to experience more frequent human-mediated disturbances (grazing included); therefore, research efforts along this dimension will not only be important from an economic viewpoint, but crucial for the ecosystem stability of the entire region.

## The missing scale: discussion and conclusion

A fundamental pursuit in ecology is connecting emergent ecological patterns to their underlying processes (Wu and Loucks 1995). A challenge though is that a number of processes might be contributing to the emergence of a single phenomenon, and these

processes are often nested within a range of spatial and temporal scales (Levin 1992). This challenge gives rise to the fundamental constraint when we try to scale up local understandings to processes and properties at much larger scale.

In our work, we elaborated on how ants respond to warming at the site scale. At this end of the scale spectrum, what matters for ant ecology and ecosystem process are ant physiology, behavioral adaptation, foraging behavior, etc. However, these processes might become less important as we zoom out to the entire region. A crucial link that connects local scale processes and regional pattern are ants and ant-mediated activities at the scale of landscapes (a range of tens to hundreds of kilometers; Wu 2001). At that level, species identity, biodiversity, dispersal ecology, inter-specific competition, and large-scale geographical constraints will become increasingly more important.

Our study focused on alpine grasslands, which is one of the most important landscape components of Tibetan Plateau (above 60% by vegetation area, Chen et al. 2014; Dong and Sherman 2015). However, alpine forests, alpine shrublands, and alpine tundra are also important alpine ecosystems that host a diversity of wild animals and rare plants found nowhere else (*i.e.*, endemic). What roles do ants play in these alpine ecosystems, and how will their activity respond to the rapid warming? In the context of global warming, the entire Tibetan Plateau is facing conditions such as large-scale permafrost freezing and thawing, treeline rise, and changes in plant communities (Guo et al. 2012; Wang et al. 2022). These landscape-scale shifts will very likely provide ants with an expanded ecological niche, growing abundance, and increasing species diversity. A natural prediction is that the ant species might move up along the altitude gradient with the change of the plant community that they associate with.

From our ant-distribution dataset, we found that the same ant species can inhabit a broad range of vegetation types, such as grassland (meadow, steppe), scrub (*Rhododendron* shrub land, *Salix cupularis fruticosa* shrub land, *Dasiphora fruticosa* shrub land etc.), and forest (various broad-leaf, coniferous and mixed coniferous forests). This observation indicates that migration and dispersal within and across landscapes might be common, yet it is unclear how ant dispersal will be impacted

by warming (despite our analysis demonstrates an enlarging habitable area). To fill this gap, we need to census ants at the hectare scale to analyze the effects of different landscape (*e.g.*, mudflats, bare ground, artificial grassland, natural grassland, grazing land, ditches, and town buildings, etc.) indices, hydrological indices, and vegetation indices on ant dispersal. Ultimately, we should aim for an integrated understanding of ant response to warming across local, landscape and regional scale.

But more broadly, we further argue the importance of studying ants in ecosystems similar to the Tibetan plateau, such as the Arctic tundra, and the alpine tundra of the Andes. These ecosystems feature high biodiversity and high endemism, but at the same time, their perennially low annual temperature will be most dramatically modified by global warming. Ants and their activities may play a disproportionately important role in these ecosystems that have previously been underexplored. For historical and logistic reasons, observational efforts on ants have been largely limited to warmer places and places that were more accessible (*e.g.*, temperate grasslands). Large-scale ant monitoring and ecosystem monitoring are needed to test our predictions. Furthermore, predicting ants' response to climate warming based on the optimal temperature is reliable (Diamond et al. 2013). Conducting a comprehensive survey of the optimal temperature for ants in the Tibet Plateau is necessary. Such foundational research is lacking in the Qinghai-Tibet Plateau, as ant surveys cannot be conducted on a large scale using remote sensing techniques, as is the case with plants (Chen et al. 2021).

In this perspective piece, we call for more empirical observations and experiments to quantify the change across a broader range of alpine ecosystem types. Our study on understanding the warming-induced response of ants represents a small step towards a better understanding how external forcings will influence ants and in turn the entire alpine ecosystems on the Tibetan Plateau. We call for more mechanistic research that can elucidate the response of ant communities to various disturbance factors, and the consequent cascading impacts on the whole ecosystem.

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**Author contributions** JL, ML, XJ, and J-SH designed the research. JL compiled the data, analyzed the data, and designed visualization with input from ML, XJ, and J-SH. HG collected most of the ant mound data. JL wrote the first draft and all authors contributed to revisions.

## Declarations

**Conflict of interest** The authors declare no competing interests.

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