Climate Change Ecology 11 (2026) 100111

Contents lists available at ScienceDirect

Climate Change Ecology

journal homepage: www.journals.elsevier.com/climate-change-ecology

Handling the heat: Warming does not reduce alpine plant survival or reproduction under high precipitation conditions

Zoe A. Xirocostas [a,b,*], Angela T. Moles [a], Freya M. Brown [c], Zachary A. Brown [c], Giancarlo M. Chiarenza [a,d], Rosa Earle [a], Andy Leigh [b], Xuemeng Mu [a], Emma E. Sumner [e,f], Susanna E. Venn [e], Virginia G. Williamson [e], Karen Zeng [a], Inna Osmolovsky [a]

[a] Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, UNSW Sydney, NSW 2052, Australia
[b] University of Technology Sydney, School of Life Sciences, Faculty of Science, NSW 2007, Australia
[c] Division of Ecology and Evolution, Research School of Biology, Australian National University, Canberra, Australian Capital Territory, Australia
[d] ARC Training Centre for Healing Country, School of Molecular and Life Science, Curtin University, Perth, Australia
[e] School of Life and Environmental Sciences, Deakin University, Burwood, Victoria, Australia
[f] Western Sydney University, Hawkesbury Institute for the Environment, Richmond, NSW, Australia

ARTICLE INFO

Keywords:
Alpine
Climate change
Heat event
Plant community
Temperature

ABSTRACT

As a result of global climate change, ecosystems are facing increasingly long and intense heat events. While plant species may be able to tolerate, adapt, or shift their ranges in response to climate change, plants in alpine ecosystems are considered especially sensitive to the effects of climate change due to geographic constraints on uphill range expansions. We conducted a novel, *in-situ*, active warming experiment (under rainy conditions) on alpine plants growing near the summit of Mt Hotham, south-eastern Australia. Contrary to our predictions, we found no relationship between overall change in cover, survival, diversity, or reproductive effort with the intensity or duration of heat events. Additionally, there was no interaction between species' growth form (i.e., forb, shrub or graminoid) and change in cover in relation to the heat event intensity and duration. Thus, while climate change still poses substantial threats to alpine ecosystems, it is not clear how the intensity or duration of extreme heat events in conjunction with high precipitation might impact alpine communities, or favour particular plant forms. Improving our understanding of which aspects of climate change pose the largest threats to alpine ecosystems remains an important goal that can help us to understand how sensitive plant communities may be affected into the future.

Introduction

Unlike animals, plants cannot seek immediate refuge from the abiotic conditions they encounter; thus, they face immense pressure to tolerate or adapt to Earth's rapidly changing conditions, including longer and more intense heat events [1–4]. At the community level, heat events can induce changes in species composition and functional diversity, resulting in less diverse and less resilient ecosystems [5,6] or, in extreme cases, may lead to complete biome shifts (e.g., from tropical forests to savanna or salt marshes to mangroves) [7–10]. However, some ecosystems are more sensitive to extreme conditions than others. For example, plants in alpine regions may respond to extreme heat by making adjustments to their physiology [11], phenology [12], or phenotype [13]. Further, the availability of suitable habitats and opportunities to disperse to higher and cooler elevations becomes limited, particularly in areas such as high mountain peaks without nival zones [14–17]. While we know alpine communities are set to experience increasing intensities and durations of heat events, their longer-term responses remain poorly understood. It is uncertain whether alpine species can sustain optimal functionality for the entire extent of such events, even if maximum temperatures are within their tolerance limits, as tolerance assays are usually conducted within hours and heat events can span multiple days or weeks [18]. Understanding how these communities will respond to such climatic extremes is vital for informing

Manuscript prepared for submission to ***Climate Change Ecology*** as a Research Article

* Corresponding author.
E-mail address: zoe.xirocostas@uts.edu.au (Z.A. Xirocostas).

https://doi.org/10.1016/j.ecochg.2026.100111
Received 28 June 2025; Received in revised form 30 January 2026; Accepted 17 February 2026
Available online 18 February 2026

conservation and management strategies to safeguard their future survival. In this study, we performed an *in-situ* active warming experiment to quantify the ecological impacts of varying intensities and durations of heat events on an Australian alpine plant community.

Among field-based studies, there is a predominance of sustained warming experiments where open top chambers raise ambient temperatures by 1–2 °C across multiple years [19–23]. While there are issues with these experiments, including reliance on convection and being unable to provide heating at night, they provide invaluable insight into how plant communities might shift with ongoing warming temperatures [24,25]. The effects of extreme heat events, which are predicted to increase in frequency, intensity and length, are more commonly explored in a glasshouse setting [11,26–29]. Glasshouse experiments allow for greater control of high temperatures and improve our understanding of finer-scale physiological responses [29–31]; however, plants are typically grown in individual pots, and are divorced from many factors (e.g. plant-plant interactions) likely to influence responses [32], thus cannot be extrapolated to the field [33–35]. In this study, we used actively heated chambers to apply high temperatures in the field [36]. This *in-situ* approach enables elevated temperatures day and night so that plants can maintain their natural interactions, feedbacks, and access to soil moisture and nutrients, all of which are important in shaping responses to climate change at both the individual and ecosystem scale [6,36–41].

The effects of heat events are mostly explored at the peak of the growing season, testing the assumption that the change in resource allocation following exposure to extreme heat may affect species survival [42]. However, extreme heat events may occur throughout the year, and extreme heat events have consistently occurred in south-eastern Australia in March over the past decades [43–45]. Extreme heat may affect plants differently at the late stages of their growing season, as most resources have already been allocated for the upcoming year [46–48]. While late-season extreme climate events are suggested to have an overall lesser effect on plants [47], plants with shorter growing seasons may be more severely impacted [42,48]. Further, the reproductive output of alpine plants is influenced by the conditions experienced in the previous year, including extreme heat events (carry-over effects: [49]), suggesting that an immediate estimation of reproductive responses might be insufficient to fully gauge the impacts of climate change [50]. Thus, exploring how extreme heat occurring at the end of the growing season may influence plants' survival and reproductive success in the subsequent year may provide vital information on plant responses to climate change [51].

First, we test the hypothesis that with increasing intensity and duration of heat events, species' ground cover, survival, and community diversity will decrease. In alpine ecosystems, many species can tolerate a wide range of temperatures from harsh freezing winters to warm summers [52–55]. However, as heat events become more severe, alpine species may be at risk of increased mortality and, in extreme cases, local or complete extinction [5,56]. This dynamic is demonstrated through the 'press and pulse' framework, where extreme climatic events (e.g., extreme heat) may amplify the effects of the ongoing changes in climate [57]. Heat events can be defined as periods of abnormally high temperatures lasting from several days to weeks, typically identified when temperatures exceed a certain threshold in relation to local temperature records [4,58,59]. For example, regionally endemic plant species in central-western Italy experienced an overall mortality rate of 32 % following extreme heat events (defined as at least two consecutive days with maximum temperatures above the monthly mean maximum) that ranged from 8–18 days across 10 sites during one summer season [60]. In turn, responses to abrupt changes (e.g., increased mortality, changes in diversity, and biotic interactions) may persist into the future, even after the extreme event has passed [61]. Further, the intensity of the extreme climatic events affected the ability of biotic communities to recover; in marine environments for example, more extreme heat events lead to reduced reintroduction success of herbivore species [62]. We similarly expect that the duration of a heat event may impact the extent of change and the ability of a community to recover. Consequently, alpine communities may be moderately impacted by shorter heat events (e.g., up to 2 days), and detrimentally impacted by longer duration heat events (e.g., >2 days up to several weeks), as sustained exposure to high levels of heat may exceed plants' physiological limits and reduce their capacity for recovery [63,64]. While the literature is replete with studies investigating the effects of elevated temperature [65–68], or single-duration/intensity heat events on plant community dynamics [69–71], we are yet to uncover how diversity, cover and survival are shaped across communities over time in response to acute heat events of varying intensities and durations in situ. Our study collects detailed community-level data before and after applying heat to understand the finer-scale impacts of heat events on alpine communities.

Different plant growth forms within a community, such as graminoids, forbs, and shrubs, are not equally exposed to ambient heat [72]. Morphological traits associated with specific growth forms can influence plants' level of heat exposure and their ability to tolerate or recover from thermal stress [73–76]. For example, different growth forms can possess different metabolic rates, and differ in nutrient and water uptake efficiency, which may ultimately impact thermal tolerance [77–79]. This variation in thermal exposure across plant growth forms could lead to shifts in their relative abundance within a community, or changes in dominance following more intense and prolonged heat events. Meta-analysis by Fazlioglu and Wan [80]. incorporated data from 46 studies and found that shrubs responded more positively to warming, including greater fitness, growth, height, and biomass, compared to graminoids and forbs. However, these studies use open top chambers to demonstrate that long term warming can confer a fitness advantage to shrubs on an individual level. Therefore, it remains unclear whether more acute heat events, simulated through actively heated chambers, will elicit similar responses at the community scale. We predict that the magnitude of cover change following heat events will vary among growth forms.

The success of ecological communities depends on not only species' survival, but also their ability to produce high-quality offspring in sufficient numbers that will comprise successive generations [81]. Therefore, it is important to consider how heat events impact plants' investment into their pre- and post-fertilisation reproductive structures. An extreme summer heat event in the Italian Alps reduced the number of flowers produced across two local species in comparison to subsequent years with no heat events [82]. Similarly, Li et al. [83]. observed a decrease in flower production in two aquatic macrophytes when exposed to fluctuating intensities of heat events. In crop species, heat events have varying impacts on offspring quality. For example, when subjected to heat events, lentils yield less grain overall, but with similarly sized seeds [84], whereas soybeans yield fewer and lighter seeds [85]. Less is known about the effects of heat events on offspring quality from non-crop species in natural field settings [5]. We finally predict that greater intensities and durations of heat events will be correlated with a decrease in plant reproductive units (i.e. flowers/inflorescences) and seed mass.

In summary, we hypothesise that:

1. Species' ground cover, survival, and community diversity will decrease with increasing intensity and duration of late-season heat events.
2. Different growth forms will have different magnitudes of cover change following heat events.
3. The number of species' reproductive units will decrease with increased intensities and durations of heat events.

Materials and methods

Site description

Our study took place close to the summit of Mount Hotham, south-eastern Australia (−36.97°, 147.13°, WGS 84 Web Mercator, EPSG: 3857), above the alpine tree line at an elevation of 1840 m [as in [36]]. The region is typically an open grassy herbfield, interspersed with patches of perennial shrubs. Peak flowering occurs during January, although some species flower as early as October (spring), through to March (early autumn). Snowfalls may begin any time and blanket the area from June with snowmelt starting around September and October, depending on the topography and elevation [86–88]. Mean summer maximum temperatures at Mt Hotham reach 19.2 °C while mean minimum winter temperatures fall to −1.3 °C (Australian Bureau of Meteorology; station 83085). Soils at the study site are shallow (typically <40 cm depth), and considered a skeletal, rocky alpine humus. One hundred and ninety-seven plant species have been recorded within a 1 km radius of our study site with 25 of these being introduced to the region (ala.org.au, accessed 31/08/2023 [based on species with at least two occurrence records]). The dominant plant families at the site include Asteraceae, Poaceae, and Apiaceae, with almost complete vegetation cover, which is unusual for mountain peaks elsewhere in the world.

Experimental design

We established seven experimental blocks, each containing five plots (one control and four heat treatments), with four blocks placed on the south-facing ridge and three on the north-facing ridge [as in [36]]. When selecting plot locations, we aimed for vegetation patches with high diversity and a large abundance of individual plants to maximise our ability to detect changes in community composition. Additionally, each plot was selected to maximise the inclusion of three native species: *Leptorhynchos squamatus* (Asteraceae), *Grevillea australis* (Proteaceae), and *Poa costiniana* (Poaceae) for concurrent studies. We also established three procedural control plots (hereby chamber controls) near the treatment blocks, in areas that maximised *L. squamatus, G. australis*, and *P. costiniana* coverage (Appendix A). All plots were marked with metal pegs at the northern and southern edges to identify and orient them during and after the experiment. We used a random number generator to assign the five plots within each block to heat treatments or to controls. No plots received continual heat, and we instead calculated the heat applied using temperature loggers (described below).

We placed 1.5 m diameter cylindrical chambers and lids onto plots that we identified as either heat-treated or chamber controls. Within each chamber, a central 1 *m* × 1 m quadrat was established and used to quantify mortality, cover change, and reproductive effort. Destructive sampling for parallel projects occurred within the 1.5 m chambers but outside the central quadrat [89,90]. Control plots had no chambers applied, and these were marked to avoid trampling or disturbance when taking measurements from adjacent plots.

Active heating was applied to our heat treatment plots as described in Arnold et al. [36]. To summarise, we used diesel-powered heaters (5 kW Caravan Heater; OnTrack Outdoor Pty Ltd., QLD, Australia) to direct warm air into the chambers through insulated ducting connected to the side of each chamber. A temperature actuator feedback system was deployed in each chamber to keep the inside air temperature at or near our set targets (described below), and three 12 V fans (AP120i, SilverStone Technology Co., Ltd, Taiwan) connected to the chamber lid were suspended above the plots to circulate warm air inside the chambers. No active heating was applied to chamber control plots. Thermocouples attached to data loggers (Onset HOBO UX120–014 M; Onset Computer Co., MA, USA) were deployed in the centre of all plots (including controls) and were programmed to take temperature measurements at one-minute intervals throughout the experiment.

We planned to apply continuous heat events ranging from 1 to 6 days in length to replicate plots, and aimed to keep all active heating chambers close to 32 °C during daylight hours (from 08:00 AM to 08:00 PM) and 22 °C overnight, for the entire duration of the experiment. These target temperatures were chosen as they represent 4 °C warmer than the highest daytime (28 °C) and night-time (18 °C) temperatures ever recorded at Mt Hotham, which might be expected with global warming reaching 2–3 °C [91]. However, due to substantial rain, wind, and an electrical storm, which necessitated the shutdown of heaters for 12 h due to safety concerns, temperatures did not always remain on target, and treatments did not always receive continuous heat [36]. To calculate the level of heat experienced by each plot (including controls and chamber controls), we used HOBOware software (https://www.onsetcomp.com/) to extract plot-level temperature from data loggers situated 100 mm above the vegetation [36]. While varying slightly from meteorological data in absolute terms, the temperature measured in the control plots was comparable to and closely tracked the simultaneous data reported by the nearest weather station [36]. From these data, we calculated two metrics:

1. **Heat event intensity:** the cumulative sum of degrees over the 90th percentile that was recorded in each 1-minute interval per plot [similar to [91]]. The 90th percentile threshold was based on data from the Australian Bureau of Meteorology (station 83085) for the entirety of March at Mt Hotham. The threshold was adjusted according to the time of day, where between 06:00 AM and 06:00 PM, plot temperatures needed to exceed 18.2 °C to add to its cumulative sum, whereas at night the threshold dropped to 10.5 °C. For example, if at any given 1-minute interval during daylight hours a plot recorded a temperature of 18.2 °C or below, the number added to that plot's cumulative sum of degrees over the 90th percentile was zero. But if that same plot recorded a daytime interval temperature of 20 °C, then 1.8 °C would be added to that plot's cumulative degree sum.
2. **Heat event duration** was computed as the number of instances (based on 1-minute intervals) when a plot reached a temperature greater than the 90th percentile (adjusted for time of day) [similar to [92,93]]. For example, if at any given 1-minute interval (during daylight hours) a plot recorded a temperature below the 18.2 °C threshold, the number added to that plot's number of instances over the 90th percentile would be zero. However, if that same plot recorded an interval temperature of 20 °C, then a value of 1 would be added.

Some plots reached temperatures above our thresholds either before or after their allotted heating time during the experimental period. To account for these natural heat fluctuations, we added an adjusted value of the cumulative sum of degrees and instances over the 90th percentile from control plots within the same block to each plot's total heat event intensity and duration (see Appendix B). This method ensured that temperature values for each minute of the entire experimental period (not just the heating period) were accounted for in each plot.

Community composition responses

Immediately prior to the experimental heating, and also one year after our heating experiment, we collected data from a total of 33 plant species (29 native and 4 introduced) from 38 plots. To detect any changes in the plant community across treatments, we:

1. Visually estimated the percent cover of all plant species (per 1 *m* × 1 m quadrat) immediately prior to and 1 year after the experiment. We estimated the exact (i.e., not binned) percentage of cover for each species, which has shown to be accurate, with a low measurement error, for experienced estimators [94,95].
2. Used the point-intercept method (1 *m* × 1 m grid divided into a hundred 10 cm × 10 cm cells) to identify plant species that were within a ~2 cm radius from the upper left corner of each grid cell before and 1 year after the experiment [96]. In the post-experiment observations, the presence/absence of each species, along with any new species that were present, were recorded.

Baseline measurements prior to the experiment were conducted between the 22nd to 25th February 2022 with the first day of the experimental heating treatments commencing on 2nd March 2022. Species names and growth form (forb, shrub or graminoid) were determined with the Flora of Victoria (VicFlora; https://vicflora.rbg.vic.gov.au/)

Reproductive responses

To evaluate how heat events may impact plant reproduction, we measured four aspects of reproductive effort in species that were actively flowering, fruiting, or seeding one year following the experiment, including:

(a) proportion of reproductive grid cells – We counted the number of grid cells (out of 100) in which each species was present (both wholly or part of) and then counted the number of those grid cells in which each species was seeding/fruiting/flowering (i.e. reproductive cells). We then divided the number of reproductive cells by the number of cells a species was present in to obtain the per-plot proportion of reproductive grid cells per species.
(b) reproductive units per unit cover – For each species, we used a random number generator to identify three cells in each plot. From here we estimated the percent cover of our species in the 10 cm × 10 cm cell (or the closest cell in which the species was present) and recorded the number of reproductive structures. The structures varied across species, as some were at different stages of development (e.g. some species were flowering, whereas others had fruit), but the units measured were held constant within a species. Details of the specific reproductive structures measured on each species are provided in Appendix A.
(c) reproductive units per cluster – We collected up to three reproductive clusters (e.g. grass spike, daisy capitulum, etc.) for each species from each plot (one from the top-right corner of each randomly chosen cell or nearby if none were present in the cell). For species that were not actively reproducing in any plots, no samples were collected. These reproductive clusters were stored in labelled paper bags and kept in a well-ventilated container prior to their reproductive units being counted in the laboratory 3 to 5 days following collection. Species-specific measurement details are provided in Appendix A.
(d) mean seed mass – Where mature seeds were available (c), they were oven-dried at 50 °C for 3 days and then placed into a desiccator (see Appendix A for species and structures measured). Once cooled, seeds were weighed, and means were calculated for each species per plot.

Data analysis

We used RStudio version 4.4.2 to perform all data analyses [97]. For each statistical analysis, we visually inspected model residuals and calculated *p*-values, marginal R^2 values [98], and 95 % confidence intervals using the *model_parameters* function within the “parameters” package [99] unless otherwise stated.

To test for an association between changes in ground cover and the intensity and duration of heat events, we ran linear mixed-effects models using the *lmer* function in the “lme4” package [100]. The response variable, change in plant cover, was calculated as the difference between the cover abundance one year after the heating experiment and cover abundance immediately prior to the experiment. Our predictor variables (tested separately) were the cumulative sum of degrees over the 90th percentile (i.e., heat event intensity) and the number of instances where temperature was above the 90th percentile (i.e., heat event duration). To optimise our model fit across all proceeding analyses, both predictor variables were standardised using the *scale* function, as they spanned an extremely wide scale which was much larger than our response variable. Block and species were accounted for in our models as random effects terms.

To understand whether plant survival was affected by heat events, we calculated the proportion of plants that remained alive a year after the heating experiment for each species within each plot. We then ran linear mixed-effects models with the proportion of survivors as our response variable, heat event intensity or duration as our predictors, and species and block as random effects terms. We ran similar models to test for a correlation between change in community diversity and heat event intensity and duration. Community diversity both prior to and one year after the experiment were calculated using Shannon’s H-index [101] with the *diversity* function within the *vegan* package [102]. Change in diversity was therefore computed as the difference in H-indices one year after the experiment and immediately prior.

Next, we asked whether growth form affected change in cover in relation to heat event intensity or duration. First, we ran the aforementioned ground cover model with an additional predictor term of growth form and checked the variance inflation factor (VIF) using the *check_collinearity* function. The model showed low correlation (VIF = 1) between variables, so we proceeded with performing two separate ANCOVAs where cover change was always our response variable, along with species and block as random effects. Our predictor variables were either heat event intensity or duration, which was interacted with growth form. To determine statistical significance, we performed estimated marginal contrast analyses using the false discovery rate adjustment with the *estimate_contrasts* function [103].

Finally, to quantify the relationship between reproductive traits and heat event intensity and duration, we performed separate linear mixed-effects models. Our response variables were either the proportion of reproductive cells, reproductive units per unit cover (square-root transformed), reproductive units per cluster (square-root transformed), or mean seed mass ($\log_{10}$-transformed). Heat event duration and intensity were our predictor variables, and species and block were included as random effects terms.

For most of our analyses (exceptions below), we amalgamated records of *Deyeuxia monticola* and *Poa costiniana* (two graminoids in the Poaceae) as it was not possible to reliably differentiate them in their non-reproductive states in the field. For reproductive units per unit cover, we removed records of *D. monticola* as they could not be amalgamated with *P. costiniana* because measured cells differed across species. *P. costiniana* and *D. monticola* records were kept separate when analysing reproductive units per cluster and mean seed mass, as we were confident in distinguishing reproductive structures between the species.

Results

Across all plots, heat event intensity ranged from 478 to 112,374 cumulative degrees Celsius above the 90th percentile threshold, while heat event duration ranged from 275 min (~0.2 days) to 10,156 min (~7 days) above the 90th percentile threshold. Overall change in species cover per plot was not related to the intensity (Fig. 1a; $p = 0.99$) or duration of heat events (Fig. 1b; $p = 0.63$). There were no significant relationships between the proportion of surviving plants per species per plot and the intensity (Fig. 1c; $p = 0.33$) or duration (Fig. 1d; $p = 0.52$) of heat events. We found no evidence for a correlation between changes in plot diversity (Shannon’s H-index) and the intensity (Fig. 1e; $p = 0.23$) or duration of heat events (Fig. 1f; $p = 0.18$). Marginal R^2 values and confidence intervals for all models are presented in Appendix C.

We did not find an interaction between species growth form (forb, graminoid or shrub), and change in species cover per plot, with increasing heat event intensity (Fig. 2a; $p > 0.51$ across all contrasts) and duration (Fig. 2b; $p > 0.50$ across all contrasts) of heat events.

We found no evidence for a correlation between the proportion of grid cells in which plants were reproducing (i.e., flowering, fruiting, or seeding) and the intensity (Fig. 3a; $p = 0.63$) or duration (Fig. 3b; $p = 0.87$) of heat events. Similarly, we found no relationship between the proportion of reproductive units per unit cover and heat event intensity

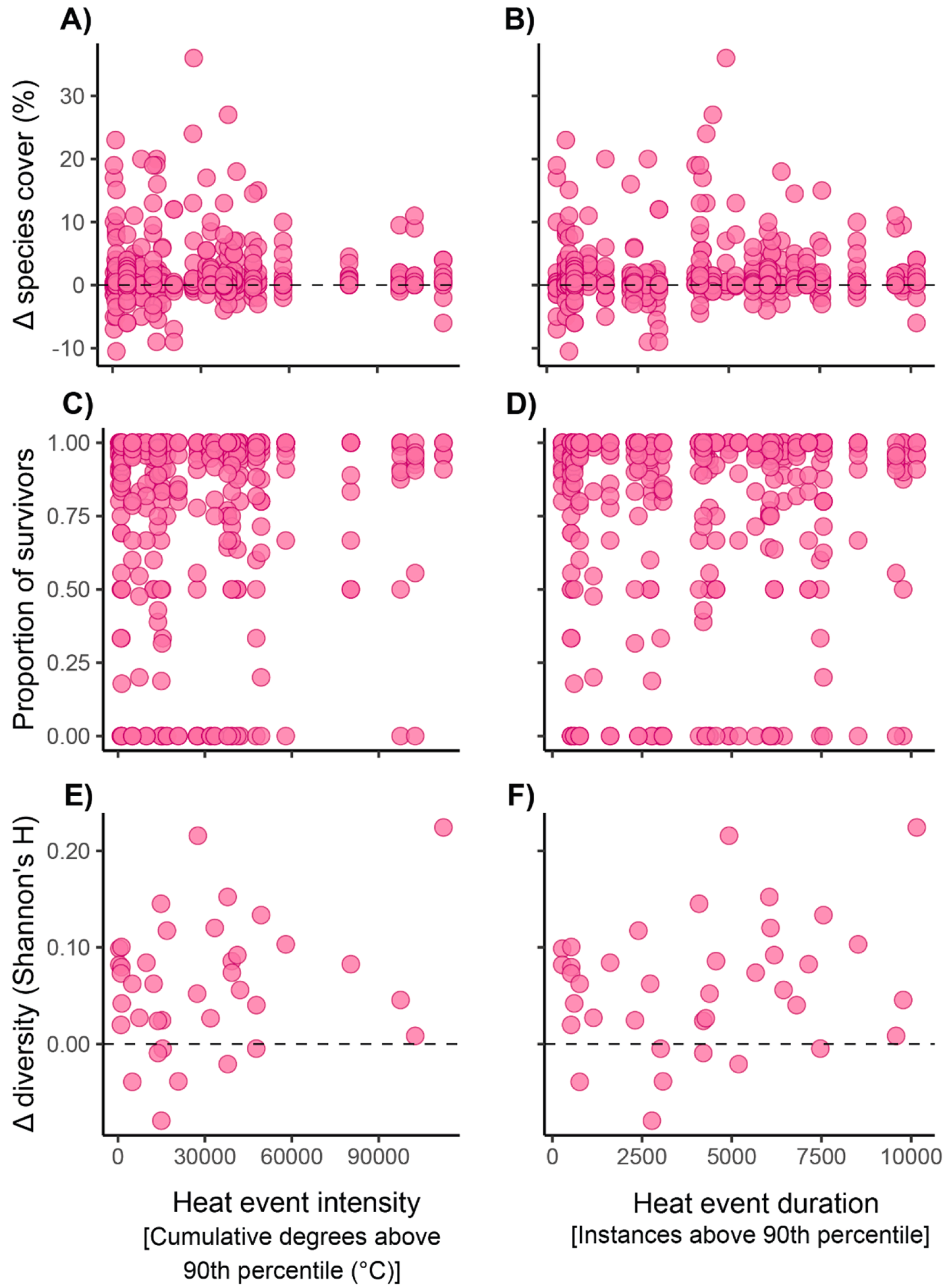

Fig. 1. Effects of heat event intensity (a, c, e) and duration (b, d, f) on per cent change in species cover per plot (a, b), proportion of survivors for each species per plot (c, d), and change in diversity per plot (e, f). Positive and negative values (a, b, e, f) represent increases or decreases relative to baseline measurements. Horizontal dashed black lines at zero (a, b, e, f) indicate no change.

(Fig. 3c; $p = 0.09$) or duration (Fig. 3d; $p = 0.15$). Reproductive units per cluster were not correlated with the intensity (Fig. 3e; $p = 0.10$) or the duration of heat events (Fig. 3f; $p = 0.07$). Finally, we found no relationship between seed mass and heat event intensity (Fig. 3g; $p = 0.45$) or heat event duration (Fig. 3h; $p = 0.22$).

Discussion

Contrary to our predictions, neither heat event intensity nor duration impacted the survival, composition or reproductive effort of these alpine plant communities (Fig. 1, 3). This is potentially welcome news, as it provides hope that some of the world's most sensitive plant communities may be able to withstand the inevitable periods of prolonged heat brought on by climate change. Several factors may explain the lack of impact we observed. First, our experiment was carried out when a high rainfall event (50 mm) occurred on day 3, which may have enabled plants to respond to the increased heat through transpirational cooling [36,104–107]. Second, we exposed plants to heat events at the end of their growing season, which supports evidence from other studies on the reduced impact of late-season extreme climatic events on plant survival and fitness [46,47]. While late-season drought can negatively affect plants [48], late-season heat events appear to be less damaging [46,47]. The combination of increased precipitation and late-season timing likely contributed to the minimal responses we observed. Running similar experiments during periods of naturally low soil moisture and in different stages of the growth season (early and/or peak) would be a

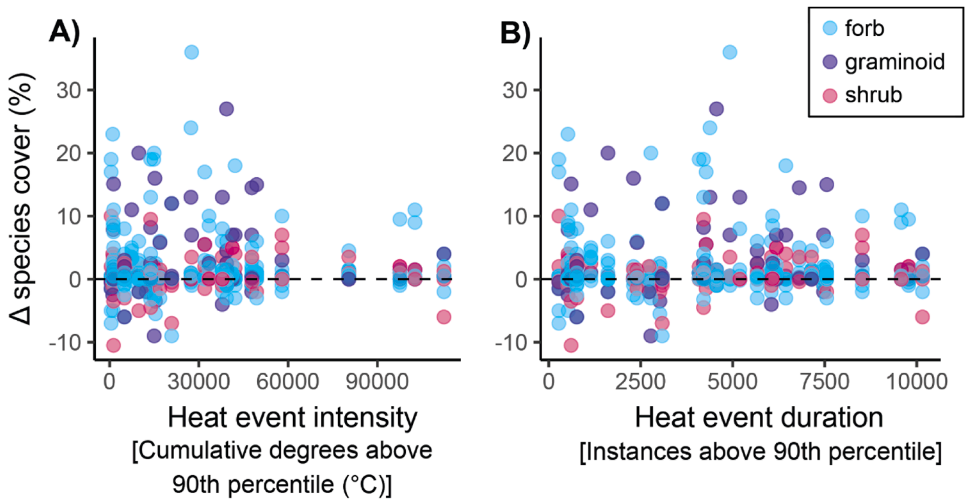

Fig. 2. The relationship between heat event intensity (a) and duration (b) to per cent change in cover of forb (blue), graminoid (purple) and shrub (pink) species per plot. Positive and negative values represent increases or decreases relative to baseline measurements. Horizontal dashed black lines at zero indicate no change.

worthwhile future direction. However, it is also possible that these alpine communities are simply resistant to periods of warming [52,89,108].

Alpine plant species can exhibit a wide range of thermal tolerance [54,109–111]. A study comparing thermal tolerance thresholds across multiple biomes, including alpine, found that all species exhibited thermal tolerance breadths that exceeded the range of local temperature variation [109]. Further, many alpine species display maximum thermal tolerance thresholds far beyond local maximum temperatures [55]. Although our plots experienced varying intensities and durations of heat events at or above the 90th percentile for March, these temperatures may not have reached or exceeded species' maximum thermal tolerance thresholds, as demonstrated in a concurrent study [89]. Using the same experimental design but focusing on thermal tolerance, plants subjected to heat events exhibited a 1.34 °C increase in heat tolerance by day three of the treatment [89]. Different life forms exhibit different tolerances to extreme temperatures, often leading to different responses to climate change [89,112,113]; however, our results suggest that diverging thermal tolerance might not be reflected in the response to extreme heat events (Fig. 2). While thermal tolerance might shape species' response to climate change, with species with lower tolerance displaying faster response to climate change [114], many of these studies correlate short-term thermal tolerance with long-term observed responses (e.g., range shifts and extinction risk [114,115]). In contrast, our study highlights the capacity for rapid physiological acclimation, which likely enhances thermal resilience under short-term heat stress.

Our study suggests that multi-day heat stress events may not lead to shifts in plant community composition, contradicting evidence suggesting that extreme heat events may exacerbate the ongoing effects of climate change and lead to irreversible changes in community composition [57,62,116]. However, rapid adjustments in thermal tolerance can buffer individuals against high temperature stress and promote rapid recovery [117]. Overall, our results suggest that alpine ecosystems have increased species' resistance in the face of extreme heat events, particularly when combined with high soil moisture conditions [117]. However, the timing of heat events may be more critical, particularly when they coincide with sensitive ontogenetic stages such as flowering, seed set, or seedling establishment, which are known to be more vulnerable to thermal extremes [118–120].

Plant growth form did not mediate changes in species cover one year after our experiment (Fig. 2). This outcome was unexpected as shrubs are generally considered more resilient to rising temperatures than other growth forms, with several studies documenting their uphill expansion [121], advancement of tundra ecotones [122], and increased dominance under warming conditions [23,123]. However, it is important to note that these findings are largely based on responses to gradual, sustained warming, whereas our study examined plant responses to more extreme climatic anomalies, which may explain the contrasting outcomes. Further, the differences in heat exposure experienced between growth forms may not have been substantial enough to drive relative shifts in cover. A simultaneous study within our experimental plots found that, overall, all growth forms had increased their thermal tolerance in response to applied heat events, but forbs less so than shrubs and graminoids [89]. It is possible that community-level shifts in growth form dominance may take longer to emerge following acute heat events, especially for slower-growing shrub species, or may only become apparent after repeated episodes of extreme heat.

A worthwhile direction for future research could explore how different frequencies of heat events (either standalone or in conjunction with varying duration and intensity) may impact alpine plant communities [124]. The frequency at which plants are subjected to heat stress could be more important in eliciting structural and reproductive changes at a community level than the effects of heat intensity and duration alone. Global forecasting has predicted that extreme heat events are likely to become more frequent under a changing climate [3,4,58,125]. Reduced intervals between heat events may be a driving factor of alpine biodiversity loss, as plants may not have enough time to fully recover from physiological stress or damage [26,30]. We encourage further research into this topic to better understand their risk to alpine ecosystems.

Whilst we did not uncover any immediate effects of heat events on the Mt Hotham alpine plant community, it is unknown whether potential consequences exist for consecutive generations. Parental environmental conditions can alter the phenotypic outcomes or fitness of an organism [126–128]. Studies exposing parent plants to higher temperatures have shown varied effects on offspring outcomes, including decreased [129]. and increased germination success [130], and earlier [131,132] and delayed emergence [129]. Future research could explore the viability or fitness of seedlings harvested from parent plants exposed to varying intensities, frequencies and durations of heat events to gain a clearer understanding of how current climate extremes will affect successive plant generations and ecosystems.

In this study, we have comprehensively assessed the relative impact of the intensity and duration of heat events on the composition, survival, diversity, and reproductive success of a sensitive alpine plant community using novel, *in-situ*, active warming methods [36]. The enormity of effort that is required to execute studies of this kind (i.e. remote areas, challenging conditions, extensive personnel, constant monitoring, and

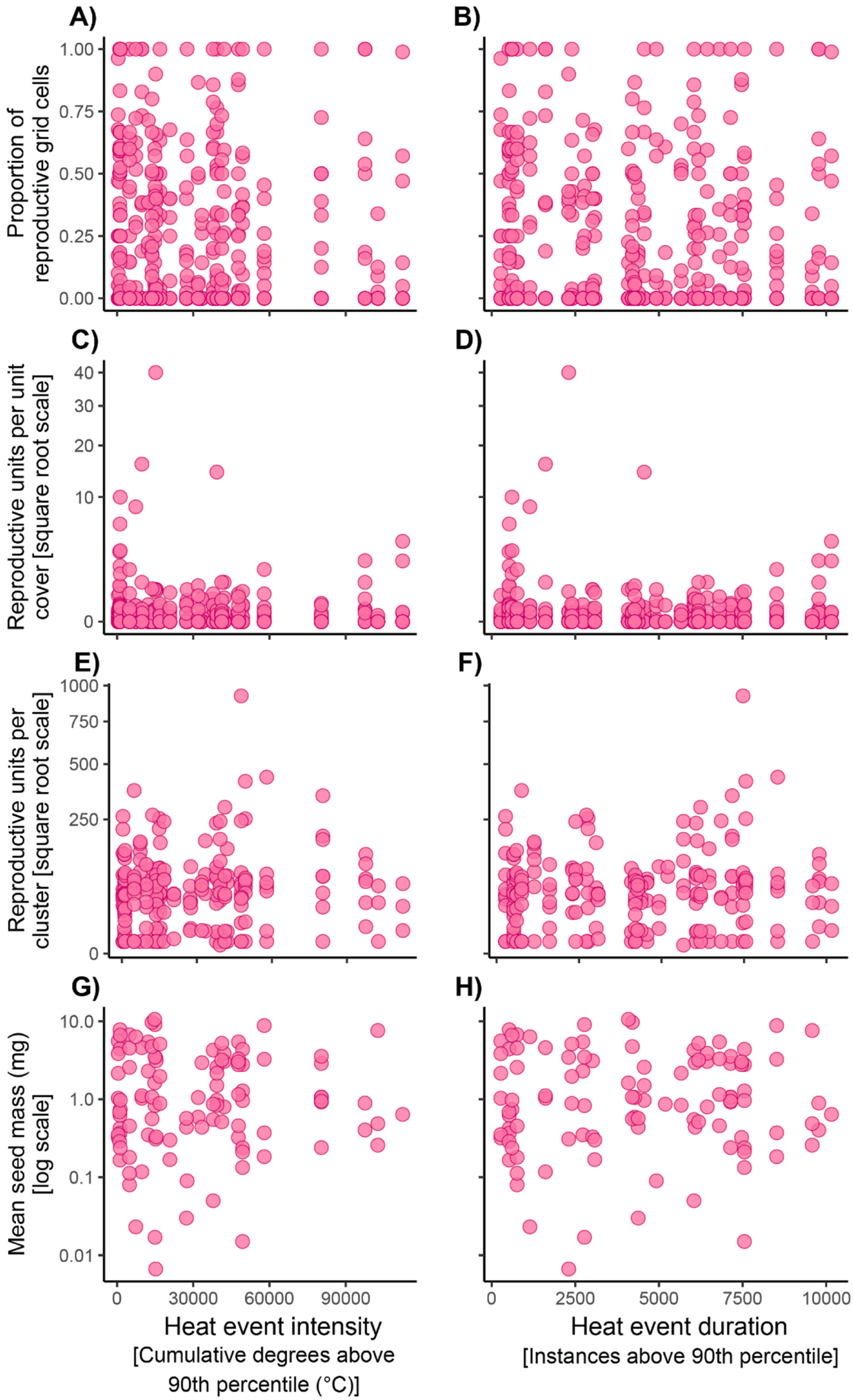

Fig. 3. Effects of heat event intensity (a, c, e, g) and duration (b, d, f, h) on: the proportion of reproductive grid cells (i.e. flowering, fruiting, or seeding) (a, b); the number of reproductive units per unit of cover (i.e. flowers, inflorescences, or fruits) (c, d); the number of reproductive units per cluster (as outlined in Appendix A) (e, f); and seed mass (g, h).

unforgiving terrain) is not to be understated, but it is far outweighed by the urgency and importance of understanding how at-risk ecosystems will respond to, and be shaped by, extreme climatic events.

Author contributions

ZAX: investigation, methodology, project administration, data curation, formal analysis, visualisation, writing - original draft, writing –

review and editing. **ATM:** conceptualisation, methodology, supervision, investigation, funding acquisition, writing – review and editing. **FMB:** investigation, writing – review and editing. **ZAB:** investigation, writing – review and editing. **GMC:** formal analysis, visualisation, writing – review and editing. **RE:** investigation, writing – review and editing. **AL:** investigation, funding acquisition, writing – review and editing. **XM:** investigation, writing – review and editing. **EES:** investigation, writing – review and editing. **SEV:** investigation, funding acquisition, writing – review and editing. **VGW:** investigation, writing – review and editing. **KZ:** investigation, writing – review and editing. **IO:** investigation, methodology, project administration, writing – review and editing.

CRediT authorship contribution statement

Zoe A. Xirocostas: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Angela T. Moles:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Freya M. Brown:** Writing – review & editing, Investigation. **Zachary A. Brown:** Writing – review & editing, Investigation. **Giancarlo M. Chiarenza:** Writing – review & editing, Visualization, Formal analysis. **Rosa Earle:** Writing – review & editing, Investigation. **Andy Leigh:** Writing – review & editing, Investigation, Funding acquisition. **Xuemeng Mu:** Writing – review & editing, Investigation. **Emma E. Sumner:** Writing – review & editing, Investigation. **Susanna E. Venn:** Writing – review & editing, Investigation, Funding acquisition. **Virginia G. Williamson:** Writing – review & editing, Investigation. **Karen Zeng:** Writing – review & editing, Investigation. **Inna Osmolovsky:** Writing – review & editing, Project administration, Methodology, Investigation.

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.

Acknowledgements

We pay our respects to the Gadigal, Bedegal, Gunaikurnai and Taungurung Peoples who are the Traditional Custodians of the Lands on which our research was conducted. We thank Thomas Hanley and Adrienne Nicotra for their valuable conceptual and field contributions, Mark Hovenden and Sarah Perkins-Kirkpatrick for project design expertise, Madelon Cruickshank, Bettina Ignacio, and Charlotte Simpson-Young for assistance with data collection and data input, and the Mt Hotham Alpine Resort for allowing us access to their property. This work was funded by an ARC Discovery grant (DP180103611) to Moles, an ARC Linkage Infrastructure Equipment and Facilities grant to Nicotra et al. (LE190100039), and a University International Postgraduate Award to Osmolovsky. Xirocostas is currently supported by a Chancellor's Research Fellowship from the University of Technology Sydney and Chiarenza is currently employed by the ARC ITTC Healing Country.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2026.100111.

Data availability

Data and code related to this study are availablevia this link (https://doi.org/10.6084/m9.figshare.29430113).

References

[1] R.T. Corlett, D.A. Westcott, Will plant movements keep up with climate change? Trends Ecol. Evol. (Amst.) 28 (2013) 482–488, https://doi.org/10.1016/j.tree.2013.04.003.

[2] R.M. Horton, J.S. Mankin, C. Lesk, E. Coffel, C. Raymond, A review of recent advances in research on extreme heat events, Curr. Clim. Change Rep. 2 (2016) 242–259, https://doi.org/10.1007/s40641-016-0042-x.

[3] S.E. Perkins, L.V. Alexander, J.R. Nairn, Increasing frequency, intensity and duration of observed global heatwaves and warm spells, Geophys. Res. Lett. 39 (2012), https://doi.org/10.1029/2012GL053361.

[4] S.E. Perkins-Kirkpatrick, S.C. Lewis, Increasing trends in regional heatwaves, Nat. Commun. 11 (2020) 3357, https://doi.org/10.1038/s41467-020-16970-7.

[5] D.D. Breshears, J.B. Fontaine, K.X. Ruthrof, J.P. Field, X. Feng, J.R. Burger, D. J. Law, J. Kala, G.E.St.J. Hardy, Underappreciated plant vulnerabilities to heat waves, New Phytologist. 231 (2021) 32–39, https://doi.org/10.1111/nph.17348.

[6] G.R. Walther, E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, F. Bairlein, Ecological responses to recent climate change, Nature 416 (2002) 389–395, https://doi.org/10.1038/416389a.

[7] C. Bonannella, T. Hengl, L. Parente, S. de Bruin, Biomes of the world under climate change scenarios: increasing aridity and higher temperatures lead to significant shifts in natural vegetation, Peer. J. 11 (2023) e15593, https://doi.org/10.7717/peerj.15593.

[8] T.E. Lovejoy, C. Nobre, Amazon tipping point, Sci. Adv. 4 (2018) eaat2340, https://doi.org/10.1126/sciadv.aat2340.

[9] N. Saintilan, N.C. Wilson, K. Rogers, A. Rajkaran, K.W. Krauss, Mangrove expansion and salt marsh decline at mangrove poleward limits, Glob. Chang. Biol. 20 (2014) 147–157, https://doi.org/10.1111/gcb.12341.

[10] L.F. Salazar, C.A. Nobre, M.D. Oyama, Climate change consequences on the biome distribution in tropical South America, Geophys. Res. Lett. 34 (2007), https://doi.org/10.1029/2007GL029695.

[11] R.F. Notarnicola, A.B. Nicotra, L.E.B. Kruuk, P.A. Arnold, Tolerance of warmer temperatures does not confer resilience to heatwaves in an alpine herb, Front. Ecol. Evol. 9 (2021). https://www.frontiersin.org/articles/10.3389/fevo.2021.615119 (accessed June 27, 2023).

[12] Z. Zhao, X. Wang, R. Li, W. Luo, C. Wu, Impacts of climate extremes on autumn phenology in contrasting temperate and alpine grasslands in China, Agric. For. Meteorol. 336 (2023) 109495, https://doi.org/10.1016/j.agrformet.2023.109495.

[13] P.A. Arnold, S. Wang, A.A. Catling, L.E.B. Kruuk, A.B. Nicotra, Patterns of phenotypic plasticity along a thermal gradient differ by trait type in an alpine plant, Funct. Ecol. 36 (2022) 2412–2428, https://doi.org/10.1111/1365-2435.14128.

[14] J. Auld, S.E. Everingham, F.A. Hemmings, A.T. Moles, Alpine plants are on the move: quantifying distribution shifts of Australian alpine plants through time, Divers. Distribution. 28 (2022) 943–955, https://doi.org/10.1111/ddi.13494.

[15] S. Dullinger, A. Gattringer, W. Thuiller, D. Moser, N.E. Zimmermann, A. Guisan, W. Willner, C. Plutzar, M. Leitner, T. Mang, M. Caccianiga, T. Dirnböck, S. Ertl, A. Fischer, J. Lenoir, J.-C. Svenning, A. Psomas, D.R. Schmatz, U. Silc, P. Vittoz, K. Hülber, Extinction debt of high-mountain plants under twenty-first-century climate change, Nat. Clim. Chang. 2 (2012) 619–622, https://doi.org/10.1038/nclimate1514.

[16] H. Pauli, M. Gottfried, G. Grabherr, Effects of climate change on mountain ecosystems – upward shifting of alpine plants, World Resour. Rev. 8 (1996). https://www.osti.gov/biblio/379668 (accessed June 26, 2023).

[17] M.S. Sritharan, F.A. Hemmings, A.T. Moles, Few changes in native Australian alpine plant morphology, despite substantial local climate change, Ecol. Evol. 11 (2021) 4854–4865, https://doi.org/10.1002/ece3.7392.

[18] S.R. Geange, P.A. Arnold, A.A. Catling, O. Coast, A.M. Cook, K.M. Gowland, A. Leigh, R.F. Notarnicola, B.C. Posch, S.E. Venn, L. Zhu, A.B. Nicotra, The thermal tolerance of photosynthetic tissues: a global systematic review and agenda for future research, New Phytologist. 229 (2021) 2497–2513, https://doi.org/10.1111/nph.17052.

[19] J.M.G. Hudson, G.H.R. Henry, High Arctic plant community resists 15 years of experimental warming, J. Ecol. 98 (2010) 1035–1041, https://doi.org/10.1111/j.1365-2745.2010.01690.x.

[20] P. Liancourt, L.A. Spence, D.S. Song, A. Lkhagva, A. Sharkhuu, B. Boldgiv, B. R. Helliker, P.S. Petraitis, B.B. Casper, Plant response to climate change varies with topography, interactions with neighbors, and ecotype, Ecology. 94 (2013) 444–453, https://doi.org/10.1890/12-0780.1.

[21] S.L. Pelini, F.P. Bowles, A.M. Ellison, N.J. Gotelli, N.J. Sanders, R.R. Dunn, Heating up the forest: open-top chamber warming manipulation of arthropod communities at harvard and duke forests, Methods Ecol. Evol. 2 (2011) 534–540, https://doi.org/10.1111/j.2041-210X.2011.00100.x.

[22] H.M. Prather, A. Casanova-Katny, A.F. Clements, M.W. Chmielewski, M. A. Balkan, E.E. Shortlidge, T.N. Rosenstiel, S.M. Eppley, Species-specific effects of passive warming in an Antarctic moss system, R. Soc. Open. Sci. 6 (2019) 190744, https://doi.org/10.1098/rsos.190744.

[23] M.D. Walker, C.H. Wahren, R.D. Hollister, G.H.R. Henry, L.E. Ahlquist, J. M. Alatalo, M.S. Bret-Harte, M.P. Calef, T.V. Callaghan, A.B. Carroll, H.E. Epstein, I.S. Jónsdóttir, J.A. Klein, B. Magnússon, U. Molau, S.F. Oberbauer, S.P. Rewa, C. H. Robinson, G.R. Shaver, K.N. Suding, C.C. Thompson, A. Tolvanen, Ø. Totland, P.L. Turner, C.E. Tweedie, P.J. Webber, P.A. Wookey, Plant community responses to experimental warming across the tundra biome, Proceed. Nat. Acad. Sci. 103 (2006) 1342–1346, https://doi.org/10.1073/pnas.0503198103.

[24] G.m. Marion, G.h.r. Henry, D.w. Freckman, J. Johnstone, G. Jones, M.h. Jones, E. Lévesque, U. Molau, P. Mølgaard, A.n. Parsons, J. Svoboda, R.a. Virginia, Open-top designs for manipulating field temperature in high-latitude ecosystems, Glob. Chang. Biol. 3 (1997) 20–32, https://doi.org/10.1111/j.1365-2486.1997.gcb136.x.
[25] K.B. Welshofer, P.L. Zarnetske, N.K. Lany, L.A.E. Thompson, Open-top chambers for temperature manipulation in taller-stature plant communities, Methods Ecol. Evol. 9 (2018) 254–259, https://doi.org/10.1111/2041-210X.12863.
[26] C.W. Ahrens, A. Challis, M. Byrne, A. Leigh, A.B. Nicotra, D. Tissue, P. Rymer, Repeated extreme heatwaves result in higher leaf thermal tolerances and greater safety margins, New Phytologist. 232 (2021) 1212–1225, https://doi.org/10.1111/nph.17640.
[27] S.C. Andrew, P.A. Arnold, A.K. Simonsen, V.F. Briceño, S.C. Andrew, P.A. Arnold, A.K. Simonsen, V.F. Briceño, Consistently high heat tolerance acclimation in response to a simulated heatwave across species from the broadly distributed Acacia genus, Function. Plant. Biol. 50 (2022) 71–83, https://doi.org/10.1071/FP22173.
[28] R.M. Marchin, D. Backes, A. Ossola, M.R. Leishman, M.G. Tjoelker, D. S. Ellsworth, Extreme heat increases stomatal conductance and drought-induced mortality risk in vulnerable plant species, Glob. Chang. Biol. 28 (2022) 1133–1146, https://doi.org/10.1111/gcb.15976.
[29] E.E. Sumner, V.G. Williamson, R.M. Gleadow, T. Wevill, S.E. Venn, Acclimation to water stress improves tolerance to heat and freezing in a common alpine grass, Oecologia 199 (2022) 831–843, https://doi.org/10.1007/s00442-022-05245-1.
[30] P.R. Alvarez, R.J. Harris, A.M. Cook, V.F. Briceño, A.B. Nicotra, A. Leigh, Native Australian seedlings exhibit novel strategies to acclimate to repeated heatwave events, Oecologia 207 (2025) 84, https://doi.org/10.1007/s00442-025-05704-5.
[31] P.A. Arnold, M.J. White, A.M. Cook, A. Leigh, V.F. Briceño, A.B. Nicotra, Plants originating from more extreme biomes have improved leaf thermoregulation, Ann. Bot. (2025) mcaf080, https://doi.org/10.1093/aob/mcaf080.
[32] J.B. Passioura, The perils of pot experiments, Function. Plant. Biol. 33 (2006) 1075–1079, https://doi.org/10.1071/FP06223.
[33] A. Canto, R. Pérez, M. Medrano, M.C. Castellanos, C.M. Herrera, Intra-plant variation in nectar sugar composition in two Aquilegia species (Ranunculaceae): contrasting patterns under field and glasshouse conditions, Ann. Bot. 99 (2007) 653–660, https://doi.org/10.1093/aob/mcl291.
[34] J. Limpens, G. Granath, R. Aerts, M.M.P.D. Heijmans, L.J. Sheppard, L. Bragazza, B.L. Williams, H. Rydin, J. Bubier, T. Moore, L. Rochefort, E.a.D. Mitchell, A. Buttler, L.J.L. van den Berg, U. Gunnarsson, A.-J. Francez, R. Gerdol, M. Thormann, P. Grosvernier, M.M. Wiedermann, M.B. Nilsson, M.R. Hoosbeek, S. Bayley, J.-F. Nordbakken, M.P.C.P. Paulissen, S. Hotes, A. Breeuwer, M. Ilomets, H.B.M. Tomassen, I. Leith, B. Xu, Glasshouse vs field experiments: do they yield ecologically similar results for assessing N impacts on peat mosses? New Phytologist. 195 (2012) 408–418, https://doi.org/10.1111/j.1469-8137.2012.04157.x.
[35] K. Mokany, J. Ash, Are traits measured on pot grown plants representative of those in natural communities? J. Vegetat. Sci. 19 (2008) 119–126, https://doi.org/10.3170/2007-8-18340.
[36] P.A. Arnold, F.M. Brown, Z.A. Brown, S.M. Aitken, L.M. Danzey, T.C. Hanley, J. L. King, X. Mu, I. Osmolovsky, E.E. Sumner, V.G. Williamson, Z.A. Xirocostas, A. Leigh, A.T. Moles, S.E. Venn, A.B. Nicotra, Effective heating chamber design to simulate acute heatwaves and night-time warming for ecological communities under natural field conditions, Methods Ecol. Evol. 16 (2025) 1935–1947, https://doi.org/10.1111/2041-210X.70114.
[37] M.Y. Bader, E. Moureau, N. Nikolić, T. Madena, N. Koehn, G. Zotz, Simulating climate change in situ in a tropical rainforest understorey using active air warming and CO2 addition, Ecol. Evol. 12 (2022) e8406, https://doi.org/10.1002/ece3.8406.
[38] R.W. Brooker, Plant–plant interactions and environmental change, New Phytologist. 171 (2006) 271–284, https://doi.org/10.1111/j.1469-8137.2006.01752.x.
[39] J.E. Drake, M.G. Tjoelker, A. Vårhammar, B.E. Medlyn, P.B. Reich, A. Leigh, S. Pfautsch, C.J. Blackman, R. López, M.J. Aspinwall, K.Y. Crous, R.A. Duursma, D. Kumarathunge, M.G. De Kauwe, M. Jiang, A.B. Nicotra, D.T. Tissue, B. Choat, O.K. Atkin, C.V.M. Barton, Trees tolerate an extreme heatwave via sustained transpirational cooling and increased leaf thermal tolerance, Glob. Chang. Biol. 24 (2018) 2390–2402, https://doi.org/10.1111/gcb.14037.
[40] P.-O. Hedwall, J. Brunet, H. Rydin, Peatland plant communities under global change: negative feedback loops counteract shifts in species composition, Ecology. 98 (2017) 150–161, https://doi.org/10.1002/ecy.1627.
[41] P. Pandey, M. Senthil-Kumar, Plant-pathogen interaction in the presence of abiotic stress: what do we know about plant responses? Plant Physiol. Rep. 24 (2019) 541–549, https://doi.org/10.1007/s40502-019-00483-7.
[42] K.V. Milner, K. French, D.W. Krix, S.M. Valenzuela, A. Leigh, K.V. Milner, K. French, D.W. Krix, S.M. Valenzuela, A. Leigh, The effects of spring versus summer heat events on two arid zone plant species under field conditions, Function. Plant. Biol. 50 (2023) 455–469, https://doi.org/10.1071/FP22135.
[43] J. Gergis, L. Ashcroft, P. Whetton, A historical perspective on Australian temperature extremes, Clim. Dyn. 55 (2020) 843–868, https://doi.org/10.1007/s00382-020-05298-z.
[44] Bureau of Meteorology. Special Climate Statement 55 – Prolonged March Heatwave Affects Many Parts Of Australia, Australian Government, 2016. https://www.bom.gov.au/climate/current/statements/scs55.pdf.
[45] Bureau of Meteorology, Special Climate Statement 45 - a prolonged autumn heatwave for southeast Australia, Australian Government, 2013. https://www.bom.gov.au/climate/current/statements/scs45.pdf.
[46] O.L. Cope, L.N. Zehr, A.A. Agrawal, W.C. Wetzel, The timing of heat waves has multiyear effects on milkweed and its insect community, Ecology. 104 (2023) e3988, https://doi.org/10.1002/ecy.3988.
[47] E. Cinto Mejía, W.C. Wetzel, The ecological consequences of the timing of extreme climate events, Ecol. Evol. 13 (2023) e9661, https://doi.org/10.1002/ece3.9661.
[48] C. Wu, J. Peng, P. Ciais, J. Peñuelas, H. Wang, S. Beguería, T.Andrew Black, R. S. Jassal, X. Zhang, W. Yuan, E. Liang, X. Wang, H. Hua, R. Liu, W. Ju, Y.H. Fu, Q. Ge, Increased drought effects on the phenology of autumn leaf senescence, Nat. Clim. Chang. 12 (2022) 943–949, https://doi.org/10.1038/s41558-022-01464-9.
[49] L.V. Jahn, S.R. Carrino-Kyker, D.J. Burke, Interannual variation in spring weather conditions as a driver of spring wildflower coverage: a 15-year perspective from an old-growth temperate forest, AoB Plants. 15 (2023) plad078, https://doi.org/10.1093/aobpla/plad078.
[50] C. Körner, Plant reproduction, in: C. Körner (Ed.), Alpine Plant life: functional plant ecology of high mountain ecosystems, Springer, Berlin, Heidelberg, 2003, pp. 259–290, https://doi.org/10.1007/978-3-642-18970-8_16.
[51] X. Mu, R.F. Notarnicola, P. Arnold, P. Pollo, W.K. Cornwell, Systematic review of heatwave experiments on plant health and survival, (preprint). https://doi.org/10.32942/X2Q93C.
[52] O. Buchner, G. Neuner, Variability of heat tolerance in alpine plant species measured at different altitudes, Arct. Antarct. Alp. Res. 35 (2003) 411–420, https://doi.org/10.1657/1523-0430(2003)035[0411:VOHTIA]2.0.CO;2.
[53] W. Larcher, C. Kainmüller, J. Wagner, Survival types of high mountain plants under extreme temperatures, flora - morphology, distribution, Function. Ecol. Plant. 205 (2010) 3–18, https://doi.org/10.1016/j.flora.2008.12.005.
[54] I.V. Leon-Garcia, E. Lasso, High heat tolerance in plants from the Andean highlands: implications for paramos in a warmer world, PLoS. One 14 (2019) e0224218, https://doi.org/10.1371/journal.pone.0224218.
[55] E.E. Sumner, S.E. Venn, Thermal tolerance and growth responses to in situ soil water reductions among alpine plants, Plant Ecol. Divers. 15 (2022) 297–308, https://doi.org/10.1080/17550874.2022.2160674.
[56] R. Teskey, T. Wertin, I. Bauweraerts, M. Ameye, M.A. Mcguire, K. Steppe, Responses of tree species to heat waves and extreme heat events, Plant Cell Environ. 38 (2015) 1699–1712, https://doi.org/10.1111/pce.12417.
[57] R.M.B. Harris, L.J. Beaumont, T.R. Vance, C.R. Tozer, T.A. Remenyi, S.E. Perkins-Kirkpatrick, P.J. Mitchell, A.B. Nicotra, S. McGregor, N.R. Andrew, M. Letnic, M. R. Kearney, T. Wernberg, L.B. Hutley, L.E. Chambers, M.-S. Fletcher, M. R. Keatley, C.A. Woodward, G. Williamson, N.C. Duke, D.M.J.S. Bowman, Biological responses to the press and pulse of climate trends and extreme events, Nat. Clim. Chang. 8 (2018) 579–587, https://doi.org/10.1038/s41558-018-0187-9.
[58] D.I.V. Domeisen, E.A.B. Eltahir, E.M. Fischer, R. Knutti, S.E. Perkins-Kirkpatrick, C. Schär, S.I. Seneviratne, A. Weisheimer, H. Wernli, Prediction and projection of heatwaves, Nat. Rev. Earth. Environ. 4 (2023) 36–50, https://doi.org/10.1038/s43017-022-00371-z.
[59] J. Park, J. Kim, Defining heatwave thresholds using an inductive machine learning approach, PLoS. One 13 (2018) e0206872, https://doi.org/10.1371/journal.pone.0206872.
[60] A. Coppi, L. Lazzaro, F. Selvi, Plant mortality on ultramafic soils after an extreme heat and drought event in the Mediterranean area, Plant Soil. 471 (2022) 123–139, https://doi.org/10.1007/s11104-021-05179-2.
[61] G. Martínez-De León, M.P. Thakur, Ecological debts induced by heat extremes, Trends Ecol. Evol. (Amst.) 39 (2024) 1024–1034, https://doi.org/10.1016/j.tree.2024.07.002.
[62] L.I. Seifert, G. Weithoff, M. Vos, Extreme heat changes post-heat wave community reassembly, Ecol. Evol. 5 (2015) 2140–2148, https://doi.org/10.1002/ece3.1490.
[63] A.M. Cook, E.L. Rezende, K. Petrou, A. Leigh, Beyond a single temperature threshold: applying a cumulative thermal stress framework to plant heat tolerance, Ecol. Lett. 27 (2024) e14416, https://doi.org/10.1111/ele.14416.
[64] D.E. Marias, F.C. Meinzer, C. Still, Impacts of leaf age and heat stress duration on photosynthetic gas exchange and foliar nonstructural carbohydrates in Coffea arabica, Ecol. Evol. 7 (2017) 1297–1310, https://doi.org/10.1002/ece3.2681.
[65] S.M. Munson, R.H. Webb, J. Belnap, J.Andrew Hubbard, D.E. Swann, S. Rutman, Forecasting climate change impacts to plant community composition in the Sonoran Desert region, Glob. Chang. Biol. 18 (2012) 1083–1095, https://doi.org/10.1111/j.1365-2486.2011.02598.x.
[66] C.S. Sheppard, J.M. Alexander, R. Billeter, The invasion of plant communities following extreme weather events under ambient and elevated temperature, Plant Ecol. 213 (2012) 1289–1301, https://doi.org/10.1007/s11258-012-0086-5.
[67] Z. Shi, R. Sherry, X. Xu, O. Hararuk, L. Souza, L. Jiang, J. Xia, J. Liang, Y. Luo, Evidence for long-term shift in plant community composition under decadal experimental warming, J. Ecol. 103 (2015) 1131–1140, https://doi.org/10.1111/1365-2745.12449.
[68] K. Wangchuk, A. Darabant, H. Nirola, J. Wangdi, G. Gratzer, Climate warming decreases plant diversity but increases community biomass in high-altitude grasslands, Rangel. Ecol. Manage 75 (2021) 51–57, https://doi.org/10.1016/j.rama.2020.11.008.
[69] L. Li, Z. Zheng, J.A. Biederman, R. Qian, Q. Ran, B. Zhang, C. Xu, F. Wang, S. Zhou, R. Che, J. Dong, Z. Xu, X. Cui, Y. Hao, Y. Wang, Drought and heat wave impacts on grassland carbon cycling across hierarchical levels, Plant Cell Environ. 44 (2021) 2402–2413, https://doi.org/10.1111/pce.13767.
[70] F.L. Marchand, S. Mertens, F. Kockelbergh, L. Beyens, I. Nijs, Performance of High Arctic tundra plants improved during but deteriorated after exposure to a

simulated extreme temperature event, Glob. Chang. Biol. 11 (2005) 2078–2089, https://doi.org/10.1111/j.1365-2486.2005.01046.x.
[71] Z. Ratajczak, A.C. Churchill, L.M. Ladwig, J.H. Taylor, S.L. Collins, The combined effects of an extreme heatwave and wildfire on tallgrass prairie vegetation, J. Vegetat. Sci. 30 (2019) 687–697, https://doi.org/10.1111/jvs.12750.
[72] C. Körner, Significance of temperature in plant life. Plant growth and climate change, John Wiley & Sons, Ltd, 2006, pp. 48–69, https://doi.org/10.1002/9780470988695.ch3.
[73] P. Sklenář, Kučerová, Andrea, Macková, K. Jana, Romoleroux, Temperature microclimates of plants in a tropical alpine environment: how much does growth form matter? Arct. Antarct. Alp. Res. 48 (2016) 61–78, https://doi.org/10.1657/AAAR0014-084.
[74] P.K. Groom, Lamont, B. Byron, Leighton, Sylvia, Leighton, C. Pattie, Burrows, Heat damage in sclerophylls is influenced by their leaf properties and plant environment, Écoscience 11 (2004) 94–101, https://doi.org/10.1080/11956860.2004.11682813.
[75] W.K. Smith, A.K. Knapp, J.A. Pearson, J.H. Varman, J.B. Yavitt, D.R. Young, Influence of microclimate and growth form on plant temperatures of early spring species in a high-elevation prairie, Am. Midl. Nat. 109 (1983) 380–389, https://doi.org/10.2307/2425419.
[76] J.A. Thompson, J.C. Zinnert, D.R. Young, Immediate effects of microclimate modification enhance native shrub encroachment, Ecosphere 8 (2017) e01687, https://doi.org/10.1002/ecs2.1687.
[77] W.D. Bowman, T.A. Theodose, M.C. Fisk, Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: implications for differential community response to environmental change, Oecologia 101 (1995) 217–227, https://doi.org/10.1007/BF00317287.
[78] E.O. Box, Plant functional types and climate at the global scale, J. Vegetat. Sci. 7 (1996) 309–320, https://doi.org/10.2307/3236274.
[79] E. Dorrepaal, Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? J. Ecol. 95 (2007) 1167–1180, https://doi.org/10.1111/j.1365-2745.2007.01294.x.
[80] F. Fazlioglu, J.S.H. Wan, Warming matters: alpine plant responses to experimental warming, Clim. Change 164 (2021) 56, https://doi.org/10.1007/s10584-021-02996-3.
[81] E. Fernández-Pascual, E. Mattana, H.W. Pritchard, Seeds of future past: climate change and the thermal memory of plant reproductive traits, Biol. Rev. 94 (2019) 439–456, https://doi.org/10.1111/brv.12461.
[82] T. Abeli, G. Rossi, R. Gentili, M. Gandini, A. Mondoni, P. Cristofanelli, Effect of the extreme summer heat waves on isolated populations of two orophitic plants in the north Apennines (Italy), Nord. J. Bot. 30 (2012) 109–115, https://doi.org/10.1111/j.1756-1051.2011.01303.x.
[83] Z. Li, L. He, H. Zhang, P. Urrutia-Cordero, M.K. Ekvall, J. Hollander, L.-A. Hansson, Climate warming and heat waves affect reproductive strategies and interactions between submerged macrophytes, Glob. Chang. Biol. 23 (2017) 108–116, https://doi.org/10.1111/gcb.13405.
[84] M. Bourgault, M. Löw, S. Tausz-Posch, J.G. Nuttall, A.J. Delahunty, J. Brand, J. F. Panozzo, L. McDonald, G.J. O'Leary, R.D. Armstrong, G.J. Fitzgerald, M. Tausz, Effect of a heat wave on Lentil grown under free-air CO2 enrichment (FACE) in a semi-arid environment, Crop. Sci. 58 (2018) 803–812, https://doi.org/10.2135/cropsci2017.09.0565.
[85] D. Soba, C. Arrese-Igor, I. Aranjuelo, Additive effects of heatwave and water stresses on soybean seed yield is caused by impaired carbon assimilation at pod formation but not at flowering, Plant Sci. 321 (2022) 111320, https://doi.org/10.1016/j.plantsci.2022.111320.
[86] S.E. Venn, J.W. Morgan, P.T. Green, Do facilitative interactions with neighboring plants assist the growth of seedlings at high altitudes in Alpine Australia? Arct. Antarct. Alp. Res. 41 (2009) 381–387, https://doi.org/10.1657/1938-4246-41.3.381.
[87] L.J. Wearne, J.W. Morgan, Floristic composition and variability of subalpine grasslands in the Mt Hotham region, north-eastern Victoria, Aust. J. Bot. 49 (2001) 721–734, https://doi.org/10.1071/bt01025.
[88] R.J. Williams, Patterns of air temperature and accumulation of snow in subalpine heathlands and grasslands on the Bogong High Plains, Victoria, Australian J. Ecol. 12 (1987) 153–163, https://doi.org/10.1111/j.1442-9993.1987.tb00936.x.
[89] V.G. Williamson, P. Waryszak, S.E. Venn, J. Vázquez-Ramírez, Z.A. Xirocostas, P. A. Arnold, S.M. Aitken, I. Osmolovsky, X. Mu, Z.A. Brown, F.M. Brown, T.C. Hanley, A. Leigh, A.B. Nicotra, A.T. Moles, E.E. Sumner, The heat is on: acclimation of alpine plants to water stress and thermal tolerance under an experimentally-induced heat event, (in review).
[90] T.C. Hanley, P.A. Arnold, Z.A. Brown, A. Leigh, V.G. Williamson, S.E. Venn, A. B. Nicotra, Acclimation and de-acclimation of photosystem heat tolerance of alpine plants in response to multiday heat exposure in the field, J. Veg. Sci. 37 (1) (2026) e70109.
[91] S.E. Perkins-Kirkpatrick, P.B. Gibson, Changes in regional heatwave characteristics as a function of increasing global temperature, Sci. Rep. 7 (2017) 12256, https://doi.org/10.1038/s41598-017-12520-2.
[92] W. Zhou, F. Yan, Y. Fan, C. Zhang, F. Yang, Q. Liu, T. Wang, B. Li, Y. Chen, F. Deng, J. Hu, X. Lei, Y. Tao, H. Cheng, W. Ren, Accumulated temperature and allocation of photo-thermal resources are key meteorological factors affecting rice cadmium content, European J. Agronom. 142 (2023) 126674, https://doi.org/10.1016/j.eja.2022.126674.
[93] A. Vitali, A. Felici, A.M. Lees, G. Giacinti, C. Maresca, U. Bernabucci, J. B. Gaughan, A. Nardone, N. Lacetera, Heat load increases the risk of clinical mastitis in dairy cattle, J. Dairy. Sci. 103 (2020) 8378–8387, https://doi.org/10.3168/jds.2019-17748.
[94] K.A. Kennedy, P.A. Addison, Some considerations for the use of visual estimates of plant cover in biomonitoring, J. Ecol. 75 (1987) 151–157, https://doi.org/10.2307/2260541.
[95] M.M. Cruickshank, A.T. Moles, S.A. Debono, Z.A. Xirocostas, COVERater—A free application for training researchers to accurately estimate species cover in terrestrial and aquatic ecosystems, Ecol. Evol. 14 (2024) e70447, https://doi.org/10.1002/ece3.70447.
[96] C.D. Bonham, Measurements for terrestrial vegetation, John Wiley & Sons, 2013.
[97] R Core Team, R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria, 2022. https://www.R-project.org/.
[98] S. Nakagawa, H. Schielzeth, A general and simple method for obtaining R2 from generalized linear mixed-effects models, Methods Ecol. Evol. 4 (2013) 133–142, https://doi.org/10.1111/j.2041-210x.2012.00261.x.
[99] D. Lüdecke, M.S. Ben-Shachar, I. Patil, D. Makowski, Extracting, computing and exploring the parameters of statistical models using R, J. Open. Source Softw. 5 (2020) 2445, https://doi.org/10.21105/joss.02445.
[100] D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4, J. Stat. Softw. 67 (2015) 1–48, https://doi.org/10.18637/jss.v067.i01.
[101] C.E. Shannon, A mathematical theory of communication, Bell Syst. Tech. J. 27 (1948) 379–423, https://doi.org/10.1002/j.1538-7305.1948.tb01338.x.
[102] J. Oksanen, G.L. Simpson, F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, P. Solymos, M.H.H. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M.D. Caceres, S. Durand, H.B.A. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M.O. Hill, L. Lahti, D. McGlinn, M.-H. Ouellette, E.R. Cunha, T. Smith, A. Stier, C.J.F.T. Braak, J. Weedon, vegan: community Ecology Package, 2022. https://CRAN.R-project.org/package=vegan.
[103] Y. Benjamini, Y. Hochberg, Controlling the false discovery rate: a practical and powerful approach to multiple testing, J. Royal Statist. Soc.: Series B (Methodological) 57 (1995) 289–300, https://doi.org/10.1111/j.2517-6161.1995.tb02031.x.
[104] H.J. De Boeck, S. Bassin, M. Verlinden, M. Zeiter, E. Hiltbrunner, Simulated heat waves affected alpine grassland only in combination with drought, New Phytologist 209 (2016) 531–541, https://doi.org/10.1111/nph.13601.
[105] D.L. Hoover, A.K. Knapp, M.D. Smith, Resistance and resilience of a grassland ecosystem to climate extremes, Ecology. 95 (2014) 2646–2656, https://doi.org/10.1890/13-2186.1.
[106] L.M. McDonald, A. Scharnagl, A.K. Turcu, C.M. Patterson, N.J. Kooyers, Demographic consequences of an extreme heat wave are mitigated by spatial heterogeneity in an annual monkeyflower, Ecol. Evol. 13 (2023) e10397, https://doi.org/10.1002/ece3.10397.
[107] X. Lu, X. Zheng, E. Liang, S. Piao, F. Babst, G.P. Elliott, S.R. Sigdel, T. Wang, Y. Wang, X. Li, S. Gao, L. Zhang, J. Sun, J. Li, H. Zhu, S. Rossi, J. Peñuelas, J. J. Camarero, Patterns, dynamics and drivers of alpine treelines and shrublines, Nat. Rev. Earth. Environ. 6 (2025) 489–502, https://doi.org/10.1038/s43017-025-00703-9.
[108] R.J. Harris, P.R. Alvarez, C. Bryant, V.F. Briceño, A.M. Cook, A. Leigh, A. B. Nicotra, Acclimation of thermal tolerance in juvenile plants from three biomes is suppressed when extremes co-occur, Conserv. Physiol. 12 (2024) coae027, https://doi.org/10.1093/conphys/coae027.
[109] V.F. Briceño, P.A. Arnold, A.M. Cook, S.K.C. Jones, R.V. Gallagher, K. French, L.A. Bravo, A.B. Nicotra, A. Leigh, Drivers of thermal tolerance breadth of plants across contrasting biomes: do mean or seasonality in climate indices matter more?, (2024) 2023.10.02.560437. https://doi.org/10.1101/2023.10.02.560437.
[110] L.M. Danzey, V.F. Briceño, A.M. Cook, A.B. Nicotra, G. Peyre, M. Rossetto, J.Y. S. Yap, A. Leigh, Environmental and biogeographic drivers behind Alpine plant thermal tolerance and genetic variation, Plants 13 (2024) 1271, https://doi.org/10.3390/plants13091271.
[111] P. Sklenář, R. Jaramillo, S.S. Wojtasiak, R.I. Meneses, P. Muriel, A. Klimeš, Thermal tolerance of tropical and temperate alpine plants suggests that 'mountain passes are not higher in the tropics, Glob. Ecol. Biogeograph. 32 (2023) 1073–1086, https://doi.org/10.1111/geb.13678.
[112] X. Li, E. Liang, J.J. Camarero, S. Rossi, J. Zhang, H. Zhu, Y.H. Fu, J. Sun, T. Wang, S. Piao, J. Peñuelas, Warming-induced phenological mismatch between trees and shrubs explains high-elevation forest expansion, Natl. Sci. Rev. 10 (2023) nwad182, https://doi.org/10.1093/nsr/nwad182.
[113] X. Lu, E. Liang, F. Babst, J.J. Camarero, U. Büntgen, Warming-induced tipping points of Arctic and alpine shrub recruitment, Proceed. Nat. Acad. Sci. 119 (2022) e2118120119, https://doi.org/10.1073/pnas.2118120119.
[114] C. Bässler, T. Hothorn, R. Brandl, J. Müller, Insects overshoot the expected upslope shift caused by climate warming, PLoS. One 8 (2013) e65842, https://doi.org/10.1371/journal.pone.0065842.
[115] J.M. Sunday, A.E. Bates, N.K. Dulvy, Thermal tolerance and the global redistribution of animals, Nat. Clim. Chang. 2 (2012) 686–690, https://doi.org/10.1038/nclimate1539.
[116] M.P. Thakur, W.H. van der Putten, F. Apon, E. Angelini, B. Vreš, S. Geisen, Resilience of rhizosphere microbial predators and their prey communities after an extreme heat event, Funct. Ecol. 35 (2021) 216–225, https://doi.org/10.1111/1365-2435.13696.
[117] H. Hillebrand, C. Kunze, Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems, Ecol. Lett. 23 (2020) 575–585, https://doi.org/10.1111/ele.13457.

[118] G. Steinacher, J. Wagner, Effect of temperature on the progamic phase in high-mountain plants, Plant Biol. 14 (2012) 295–305, https://doi.org/10.1111/j.1438-8677.2011.00498.x.
[119] G. Distefano, A. Gentile, A. Hedhly, S.La Malfa, Temperatures during flower bud development affect pollen germination, self-incompatibility reaction and early fruit development of clementine (Citrus clementina Hort. ex Tan.), Plant Biol. 20 (2018) 191–198, https://doi.org/10.1111/plb.12656.
[120] Q.-Q. Hou, B.-M. Chen, S.-L. Peng, L.-Y. Chen, Effects of extreme temperature on seedling establishment of nonnative invasive plants, Biol. Invasions. 16 (2014) 2049–2061, https://doi.org/10.1007/s10530-014-0647-8.
[121] R.J. Dial, T. Scott Smeltz, P.F. Sullivan, C.L. Rinas, K. Timm, J.E. Geck, S. Carl Tobin, T.S. Golden, E.C. Berg, Shrubline but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska, Glob. Chang. Biol. 22 (2016) 1841–1856, https://doi.org/10.1111/gcb.13207.
[122] I.H. Myers-Smith, D.S. Hik, Climate warming as a driver of tundra shrubline advance, J. Ecol. 106 (2018) 547–560, https://doi.org/10.1111/1365-2745.12817.
[123] S.A. Duchicela, F. Cuesta, C. Tovar, P. Muriel, R. Jaramillo, E. Salazar, E. Pinto, Microclimatic warming leads to a decrease in species and growth form diversity: insights from a tropical alpine grassland, Front. Ecol. Evol. 9 (2021), https://doi.org/10.3389/fevo.2021.673655.
[124] G. Neuner, O. Buchner, The dose makes the poison: the longer the heat lasts, the lower the temperature for functional impairment and damage, Environ. Exp. Bot. 212 (2023) 105395, https://doi.org/10.1016/j.envexpbot.2023.105395.
[125] S.E. Perkins-Kirkpatrick, C.J. White, L.V. Alexander, D. Argüeso, G. Boschat, T. Cowan, J.P. Evans, M. Ekström, E.C.J. Oliver, A. Phatak, A. Purich, Natural hazards in Australia: heatwaves, Clim. Change 139 (2016) 101–114, https://doi.org/10.1007/s10584-016-1650-0.
[126] H.M. Alexander, R.D. Wulff, Experimental ecological genetics in Plantago: X. The effects of maternal temperature on seed and seedling characters in P. Lanceolata, J. Ecol. 73 (1985) 271–282, https://doi.org/10.2307/2259783.
[127] T.A. Mousseau, C.W. Fox, The adaptive significance of maternal effects, Trends Ecol. Evol. (Amst.) 13 (1998) 403–407, https://doi.org/10.1016/S0169-5347(98)01472-4.
[128] D.A. Roach, R.D. Wulff, Maternal effects in plants, Annu Rev. Ecol. Syst. 18 (1987) 209–235.
[129] S. Wang, K.M. Gowland, L.E.B. Kruuk, A.B. Nicotra, P.A. Arnold, Decoupling the effects of parental and offspring warming on seed and seedling traits, Alp. Botany 131 (2021) 105–115, https://doi.org/10.1007/s00035-021-00251-0.
[130] G. Bernareggi, M. Carbognani, A. Mondoni, A. Petraglia, Seed dormancy and germination changes of snowbed species under climate warming: the role of pre- and post-dispersal temperatures, Ann. Bot. 118 (2016) 529–539, https://doi.org/10.1093/aob/mcw125.
[131] G. Wang, C.C. Baskin, J.M. Baskin, X. Yang, G. Liu, X. Ye, X. Zhang, Z. Huang, Effects of climate warming and prolonged snow cover on phenology of the early life history stages of four alpine herbs on the southeastern Tibetan Plateau, Am. J. Bot. 105 (2018) 967–976, https://doi.org/10.1002/ajb2.1104.
[132] R. Zhang, R.S. Gallagher, K. Shea, Maternal warming affects early life stages of an invasive thistle, Plant Biol. 14 (2012) 783–788, https://doi.org/10.1111/j.1438-8677.2011.00561.x.