

ARTICLE

Flowers that cool themselves: Thermal ecology of summer-blooming thistles in hot Mediterranean environments

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Abstract

Flower exposure to high temperature reduces the production, viability, and performance of pollen, ovules, and seeds, which in turn impairs individual fecundity and risks the survival of populations. Autonomous floral cooling could alleviate the effects of flower exposure to harmful temperatures, yet investigations on thermal ecology of flowers in hot environments are needed to evaluate the reality, magnitude, and ecological significance of thermoregulatory cooling. This paper reports a study on the thermal ecology of the flower heads (=capitula) of 15 species of summer-blooming Asteraceae, tribe Cardueae, from hot-dry habitats in the southern Iberian Peninsula. Temperature inside (T_{in}) and outside (T_{out}) capitula were assessed under natural field conditions using two complementary sampling and measurement procedures, which provided information on the relationships between the two temperatures at the levels of individual capitula (“continuous recording”) and local plant populations (“instantaneous measurements”). Baselines for the T_{in} - T_{out} relationship in the absence of physiological activity were obtained by exposing dehydrated capitula to variable ambient temperatures in the field. To assess whether the co-flowering capitula of summer-blooming Asteraceae defined collectively a distinct thermal layer, the vertical distribution of capitula relative to the ground was quantified. Bees visiting capitula were watched and temperature of the air beside the visited capitulum was measured. Results were remarkably similar for all plant species. The capitula experienced high ambient temperatures during long periods, yet their interior was cooler than the air most of the time, with temperature differentials ($\Delta T = T_{in} - T_{out}$) often approaching, and sometimes exceeding -10°C . The relationship between T_{in} and T_{out} was best described by a composite of one steep and one shallow linear relationship separated by a breakpoint (Ψ , interspecific range = $25\text{--}35^{\circ}\text{C}$). Capitula were only weakly thermoregulated when $T_{out} < \Psi$, but switched to closely thermoregulated cooling when $T_{out} > \Psi$. Narrow vertical distributions of capitula above the ground and similar cooling responses by all species resulted in a “refrigerated floral layer” where most bees foraged at $T_{out} > \Psi$ and presumably visited cooled capitula. Thermoregulatory refrigeration of capitula (“thermal engineering”) can benefit not only plant reproduction by reducing pollen and

ovule exposure to high temperatures during the summer but also the populations of bee pollinators and other floricolous insects.

KEYWORDS

Asteraceae, Cardueae, diel rhythm, floral thermoregulation, flower cooling, hot environments, Megachilidae, Mediterranean habitats, segmented regression, thermal ecology, thermal gradient

INTRODUCTION

Plant exposure to high ambient temperature can have detrimental impacts on critical physiological, developmental, and ecological processes. The photosynthetic rate of leaves (Jones, 1992; Lambers et al., 2008) and the production, viability, and performance of pollen, ovules, and seeds (Arathi & Smith, 2023; Chaturvedi et al., 2021; Rosbakh et al., 2018; Rosenberger et al., 2024; Seymour et al., 2009; Tushabe & Rosbakh, 2024) all decline following exposure to ambient temperatures exceeding some species- or population-specific threshold. By combining through a variety of mechanisms, such detrimental effects of high temperature can eventually impair the fecundity of individuals and jeopardize the persistence of plant populations (Hemberger et al., 2023; Lohani et al., 2020; Posch et al., 2024; Rosbakh et al., 2018; Rosenberger et al., 2024). Since thermally induced harmful effects on plant fitness are expected to become more frequent in the current scenario of global warming, there has been a recent upsurge of interest in the possible means whereby plants could buffer, alleviate, and/or tolerate the effects of rising ambient temperatures and increasing frequency of heatwaves (Lorenzo et al., 2021; Perkins-Kirkpatrick & Lewis, 2020). Most of these studies have focused on the plants' vegetative parts and, more specifically, have addressed the possibility that the long-known ability of leaves to cool themselves to temperatures lower than the ambient (Drake et al., 1970; Ehrlert, 1973; Linacre, 1964, 1967; Pearcy et al., 1972; Smith, 1978; Upchurch & Mahan, 1988) could provide a community-wide thermoregulatory mechanism allowing a "thermal escape" to leaves in the face of rising temperatures (Cook et al., 2021; Guo, Still, et al., 2023; Manzi et al., 2024; Michaletz et al., 2016; Posch et al., 2024; Still et al., 2022; Tarvainen et al., 2022). Few ecological studies, however, have explicitly examined to date how wild plants can cope with exposure of reproductive structures to high temperatures, despite the fact that the reproductive phase seems more sensitive to elevated temperatures than the vegetative one (Chaturvedi et al., 2021; Lohani et al., 2020; Tushabe & Rosbakh, 2024).

Limited evidence has shown so far that autonomous flower cooling could represent an efficacious way of

reducing the exposure of pollen and ovules to high ambient temperatures (Galen, 2006; Herrera, 2024a; Karban et al., 2023; Patiño & Grace, 2002; Rejsková et al., 2010; Sherer et al., 2024). Nevertheless, investigations into the thermal ecology of flowers in hot environments are still needed to evaluate the reality, magnitude, and ecological significance of floral thermoregulatory cooling. For example, from a plant community viewpoint it remains to be investigated whether concurrent flower cooling by coexisting, simultaneously flowering species in hot environments could collectively produce a "refrigerated flower layer" sufficiently persistent as to be of ecological significance, for example, by providing thermally favorable microhabitats from the perspective of pollinators (Herrera, 2024a). This paper presents the results of a study on the thermal ecology of the flower heads of a group of species of Asteraceae which bloom simultaneously during the hot summer in open sunny habitats of the southern Iberian Peninsula. The climate of the region is of a Mediterranean type, with hot-dry summers where maximum daily temperature $>40^{\circ}\text{C}$ and air relative humidity $<15\%$ are not exceptional during July–August (Capel Molina, 1981; Herrera et al., 2023). Few plants bloom in southern Iberia during the climatically harsh summer (Herrera, 2024a). The species of Asteraceae included in this study represent outstanding exceptions to this phenological pattern. They thus are good candidate systems to investigate floral responses to high temperatures and, more specifically, to evaluate the extent of thermoregulatory cooling by species whose flowering seasons are predictably linked to hot environments. By combining population-level sampling and continuous monitoring of the internal and external thermal environments of individual flower heads, this study found considerable autonomous cooling of the interior of the flower heads in all species examined when ambient temperature exceeded a species-specific threshold. A refrigerated, multispecies floral layer arose in summer in open sunny habitats as a consequence of the narrow vertical distribution of flower heads above the ground and their similar cooling responses to high ambient temperatures. Most bee pollinators foraged at ambient temperatures which were higher than the cooling thresholds of the visited flower heads.

MATERIALS AND METHODS

Study plants and field sites

Patterns of variation of temperature in the interior of flower heads (“capitula,” singular “capitulum,” hereafter), in relation to external air temperature, were studied during June–September 2020–2024 in 15 species of summer-flowering Asteraceae, tribe Cardueae, belonging to subtribes Carduinae (genera *Carduus*, *Cirsium*, *Picnomon*, *Ptilostemon*; seven species), Centaureinae (*Carthamus*, *Centaurea*, *Mantiscalca*; four species) and Carlininae (*Carlina*; four species) (Figure 1; subtribal classification follows Herrando-Moraira et al., 2019). The capitula of the species included in the study exhibited a broad variety of size, flower color, and features of the bract envelope (Figure 1). Most taxa chosen for study are widely distributed over the southern third of the Iberian Peninsula. They are often locally abundant in suitable habitats, where up to seven different species can coexist and flower simultaneously (C. M. Herrera, unpublished data). All species typically occur in sunlit places, such as large forest clearings, roadsides, understory of sparse woodland, or extensive natural or anthropogenic disturbances, and the capitula were exposed to direct sunshine during most or all daytime. The local flowering period of each species generally encompasses 1.5–2.5 months over June–September (Blanca et al., 2011; C. M. Herrera, unpublished data). With the single exception of *Mantiscalca salmantica*, all species considered here are thistles with prickly edged leaves and densely spinescent stems and capitula (Figure 1). Most species were studied at sites in the Sierra de Cazorla area (Jaén province, 700–1600 m above sea level [asl]), a large mountain system in the Betic ranges that is characterized by well-preserved vegetation and high plant and habitat diversity (Gómez Mercado, 2011; Pugnaire et al., 2024). To broaden the taxonomic and microclimatic ranges represented in the study, additional data for four species were collected in central Sierra Morena (Córdoba province, 760 m asl.; three species) or the lowlands of the Guadalquivir River valley (Sevilla province, 25 m asl.; one species), 160 and 280 km away, respectively, from the Cazorla main study area (see caption to Figure 1 for sampling locations of each species).

Field methods: Natural capitula

Two complementary sampling and measurement procedures were used to assess variations of temperature inside and outside capitula under natural field conditions, which provided information on the relationships between

the two temperatures at the levels of the individual capitula and the local plant populations, respectively.

In one procedure (“continuous monitoring” hereafter), paired measurements of temperatures inside individual capitula (T_{in} hereafter) and in the air 2 cm away (T_{out}) were uninterruptedly recorded over periods of 2–6 days, which roughly matched in each case the functional duration of the capitulum. One fine type K thermocouple (exposed junction, 0.2 mm probe diameter, RS PRO Reference 110-4482) was inserted perpendicularly to the surface of the capitulum until it reached the receptacle. A second, similar thermocouple was attached to the capitulum and its tip remained in the air ~2 cm away from the surface of florets (see Appendix S1: Figure S1, for examples of measurement setup). Strips of masking tape were used to attach and hold the wires in place. Thermocouples were connected to a battery-powered Omega HH520 data logger thermometer. For each monitored capitulum, paired temperature measurements were continuously recorded at either 3-min (2021) or 1-min intervals (2022–2024). The potential bias introduced by heating of the exposed probe by solar irradiance was considered negligible, and no attempt was made at either shading the external probe or correcting T_{out} values (Herrera, 2024a). A total of 57 capitula from 12 species were monitored over 91 different dates, yielding a cumulative total of 209,273 paired T_{in} – T_{out} records and 178 capitulum-day of temperature data, all species combined. These data were used to assess the extent of cooling achieved by individual capitula and to examine whether regular diel rhythms existed in capitulum temperature at the individual and population levels.

The other procedure (“instantaneous measurements” hereafter) consisted of measuring T_{in} and T_{out} on a large number of randomly chosen capitula in one or more populations of each species. Measurements were taken between one hour past sunrise and noon, the period within which the daily shift in thermoregulatory regime ordinarily takes place (see *Results: Continuous monitoring*). One type K thermocouple (similar to the ones used for continuous measurements) was inserted into the capitulum, and the tip of another thermocouple was left 2 cm away in the air outside. The two probes were connected to a Fluke 54 IIB dual input digital thermometer logger. Measurements were recorded at 1-s intervals for 20–25 s, and the respective averages were used as instantaneous estimates of T_{in} and T_{out} for the individual capitulum. Instantaneous measurements for a given species were taken on separate dates and populations and over a broad range of ambient temperatures. A total of 2283 paired T_{in} – T_{out} measurements from 14 species were taken on 61 different dates, all species combined. These data were used to elucidate the shape of the functional response of T_{in} to changes in T_{out} and to evaluate the ability of capitula for autonomous thermoregulatory cooling.

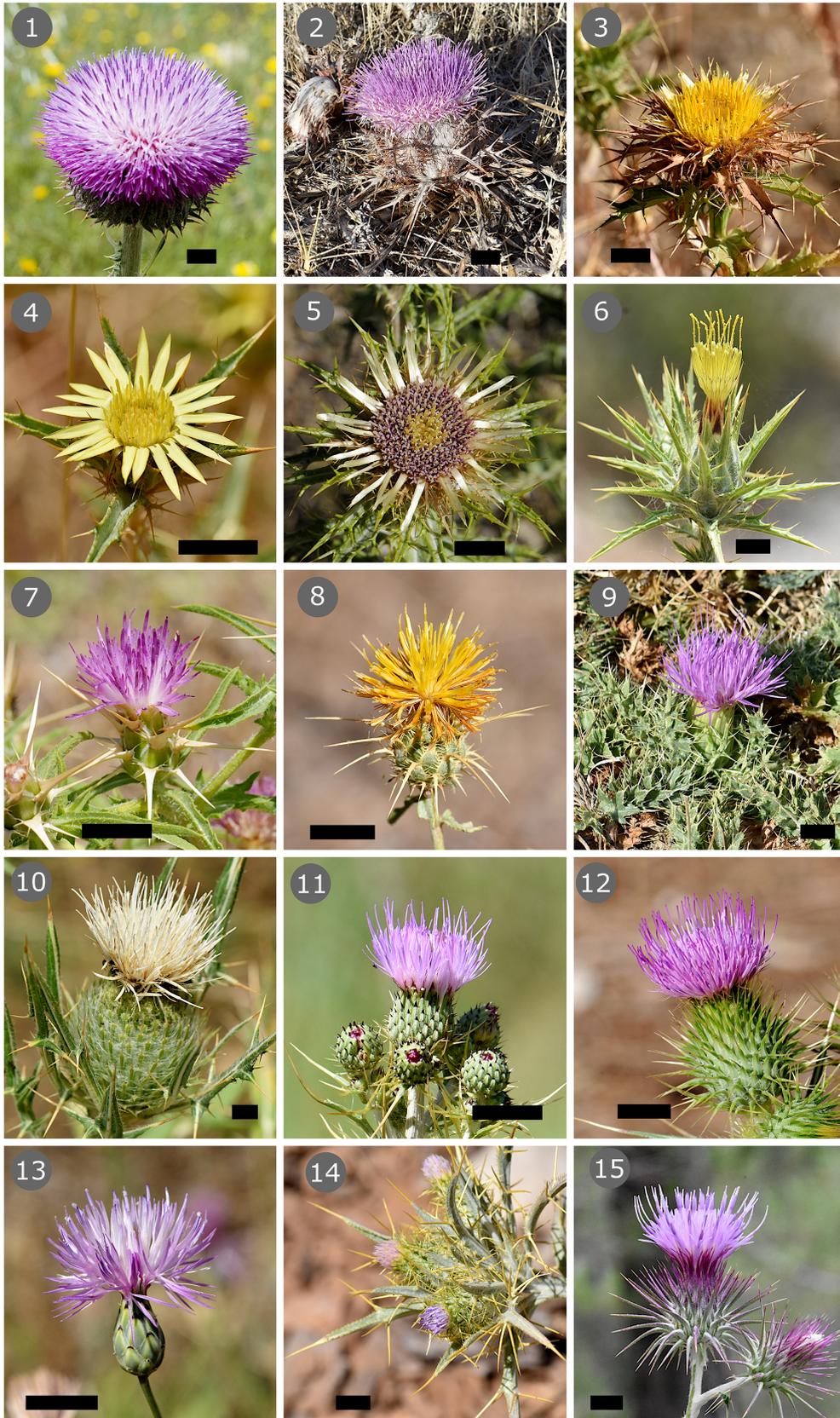


FIGURE 1 Legend on next page.

To assess the extent to which the capitula of summer-flowering Asteraceae actually define a thermally distinct multispecies layer in the habitats studied, I determined the vertical distribution of capitula in relation to the ground for nine species by measuring the height of individual capitula in a random subset of those that were sampled for instantaneous T_{in} and T_{out} measurements.

Field methods: Experimental capitula

Experiments were performed in the field to obtain species-specific baselines against which to compare the T_{in} - T_{out} relationships obtained from instantaneous measurements on unmanipulated, living capitula under natural conditions. Capitula were turned into inert objects without any possible participation in thermoregulation by whatever means. Individual capitula were severed from plants and immediately immersed in a large volume of silica gel at ambient temperature to induce a quick drying. Preliminary tests showed that in nine of the species studied, the shape, color, general structure, and external appearance of the capitula remained essentially unaltered after fast dehydration. In the rest of the species, the capitula experienced significant structural deformations and/or color changes during the drying process and were excluded from the experiments. For the capitula of the nine species chosen, baselines for the T_{in} - T_{out} relationship in the absence of physiological activity were obtained by pinning the dehydrated, inert capitula to styrofoam pieces and exposing them to the sun in the field at different times over the morning under a broad range of ambient temperatures (see Appendix S1: Figure S2, for examples of experimental setup). Instantaneous measurements of T_{in} and T_{out} ($N = 628$, all species combined) were taken on 12 different dates using the same procedure as for living capitula described in the preceding section.

Bee visitation to capitula

Over June–September of 2022 and 2024, between early morning and noon, I watched bees that were probing

capitula of six of the plant species considered here, which coexisted locally at several locations in the Sierra de Cazorla, where paired T_{in} - T_{out} instantaneous measurements on capitula were also being taken on approximately the same dates. For each watched bee, I identified the species and measured the temperature of the air 2–5 cm away from the capitulum where it was feeding using a digital thermometer and a fast-response 0.22 mm-diameter thermocouple. I measured air temperature at the foraging sites of 388 bees on 22 different dates.

Data analysis

Due to time, equipment, or access limitations, or because of methodological restrictions (dry capitula suitable to experiments could be produced only for some species), I was unable to obtain all types of data for each of the 15 plant species considered in this study. A summary of the kind of information available for each species is shown in Appendix S1: Table 1. All the raw data used in this paper are available in Herrera (2025).

All statistical analyses reported in this paper were carried out using the R environment (R Core Team, 2024). Preliminary examination of bivariate relationships between instantaneous measurements of T_{in} and T_{out} on living capitula of all species consistently revealed non-monotonic, nonlinear relationships between the two variables that could not be satisfactorily modeled using either parametric polynomial regressions or nonparametric smoothers (cubic splines). Since it was apparent that, within species, different linear relationships between T_{in} and T_{out} held for different ranges of T_{out} , the functional relationship between the two temperatures in each set of instantaneous measurements was addressed by applying segmented regression (also sometimes named “two-phase,” “piecewise,” or “broken-line” regression; Ryan & Porth, 2007; Toms & Lesperance, 2003). Segmented regression is a form of regression allowing multiple linear models to be fit to the data for different ranges of x . “Breakpoints” (Ψ) are the values of x at which the slope of the linear function

FIGURE 1 Capitula of the 15 species of summer-flowering Asteraceae, tribe Cardueae, from the southern Iberian Peninsula considered in this study. In parentheses following species names are average dry mass of individual capitula and abbreviations for the study site(s) where each species was investigated (SC, Sierra de Cazorla; SM, Sierra Morena; LG, lowlands of Guadalquivir River valley): 1, *Carduus granatensis* (2.68 g, SC); 2, *Carlina gummifera* (6.20 g, LG); 3, *Carlina hispanica* (0.52 g, SC, SM); 4, *Carlina racemosa* (0.26 g, SC, SM); 5, *Carlina vulgaris* (0.54 g, SC); 6, *Carthamus lanatus* (0.70 g, SC); 7, *Centaurea calcitrapa* (0.18 g, SC); 8, *Centaurea ornata* (0.45 g, SM); 9, *Cirsium acaule* (0.33 g, SC); 10, *Cirsium odontolepis* (5.98 g, SC); 11, *Cirsium pyrenaicum* (0.11 g, SC); 12, *Cirsium vulgare* (1.07 g, SC); 13, *Mantisalca salmantica* (0.10 g, SC); 14, *Picnomon acarna* (0.29 g, SC); 15, *Ptilostemon hispanicus* (1.23 g, SC). Species are depicted at different scales, black bar = 10 mm. Photo credit: Carlos M. Herrera.

TABLE 1 Segmented linear regression analysis of the relationship between internal capitulum temperature (T_{in}) and temperature of the air outside (T_{out}) for summer-flowering Asteraceae with available paired T_{in} - T_{out} instantaneous measurements at the population level (N = number of paired measurements).

| Species | N | Score test ($H_1 = 2$ slopes vs. $H_0 = 1$ slopes) | | Estimated breakpoint | | T_{in} versus T_{out} slopes | |
|-------------------------------|-----|--|---------|------------------------|-----------|----------------------------------|------------------|
| | | Statistic | p-value | Ψ (T_{out} °C) | CI | $T_{out} < \Psi$ | $T_{out} > \Psi$ |
| <i>Carduus granatensis</i> | 162 | -5.9 | 2.0E-08 | 28.3 | 26.7-29.1 | 0.527 | -0.114 |
| <i>Carlina gummifera</i> | 143 | -8.4 | 3.5E-14 | 35.4 | 34.5-37.2 | 1.025 | 0.231 |
| <i>Carlina hispanica</i> | 234 | -13.3 | 2.2E-16 | 32.3 | 31.3-33.3 | 1.083 | 0.074 |
| <i>Carlina racemosa</i> | 161 | -9.6 | 2.2E-16 | 31.0 | 29.2-32.4 | 0.922 | 0.024 |
| <i>Carthamus lanatus</i> | 143 | -7.7 | 2.5E-12 | 27.3 | 26.6-28.3 | 0.906 | 0.080 |
| <i>Centaurea calcitrapa</i> | 209 | -9.2 | 2.2E-16 | 26.7 | 25.3-27.7 | 0.889 | 0.296 |
| <i>Centaurea ornata</i> | 139 | -6.2 | 6.5E-09 | 30.1 | 29.1-31.9 | 0.911 | 0.231 |
| <i>Cirsium acaule</i> | 199 | -6.8 | 1.4E-10 | 28.7 | 26.5-30.4 | 0.934 | 0.343 |
| <i>Cirsium odontolepis</i> | 107 | -4.0 | 0.00011 | 28.5 | 27.1-29.6 | 1.350 | 0.380 |
| <i>Cirsium pyrenaicum</i> | 151 | -8.2 | 1.0E-13 | 28.8 | 26.9-29.3 | 0.846 | 0.362 |
| <i>Cirsium vulgare</i> | 184 | -8.3 | 2.8E-14 | 27.8 | 25.9-29.4 | 0.719 | 0.183 |
| <i>Mantiscalca salmantica</i> | 143 | -8.1 | 2.1E-13 | 26.6 | 25.8-27.8 | 0.985 | 0.321 |
| <i>Picnomon acarna</i> | 168 | -9.9 | 2.2E-16 | 25.0 | 24.1-26.4 | 1.110 | 0.374 |
| <i>Ptilostemon hispanicus</i> | 140 | -9.1 | 7.7E-16 | 25.2 | 24.6-26.7 | 1.354 | 0.282 |

Note: See Figure 4 for plots of fitted segmented regressions.

changes, and typically they are unknown and must be estimated. Computations were performed using the segmented package, which implements a test for the existence of breakpoints ($H_1 = 2$ slopes vs. $H_0 = 1$ slope, over the whole x range sampled; function `pscore.test`) and provides breakpoint estimates and CIs (function `confint.segmented`) as well as predicted values from the fitted regression (function `segmented`) (Muggeo, 2008, 2016, 2017). The number of plant species was insufficient to perform a formal test of phylogenetic signal in the thermal parameters estimated from segmented regressions. Instead, interspecific variance in thermal parameters was partitioned into components due to subtribe, and genera nested within subtribe, using function `lme` in the `nlme` package (Pinheiro et al., 2024).

RESULTS

Instantaneous measurements: Inert capitula

In the nine species that could be tested experimentally, the internal temperature (T_{in}) of dehydrated, inert capitula exposed to natural sunny conditions in the field increased linearly with the temperature of the surrounding air (T_{out}), and variation in T_{out} accounted for nearly all variance in T_{in} (91%–98%, Figure 2). The linear slopes of the T_{in} - T_{out}

relationships were close to unity in all cases, and the capitulum-air thermal gradient ($\Delta T = T_{in} - T_{out}$) predicted from the regressions was always positive and tended to remain between +5 and +10°C over the whole range of ambient temperatures under which the tests were conducted (Figure 2). Under natural field conditions, therefore, inert capitula consistently built up a large thermal excess over their immediate environment that tended to remain fairly constant across the broad range of ambient temperatures sampled.

Instantaneous measurements: Living capitula

The temperature inside living, unmanipulated capitula under natural field conditions (T_{in}) increased with the temperature of the surrounding air (T_{out}) in all species, but the shape of the relationship departed in every case from a simple linear, monotonously increasing relationship of the sort exhibited by the dehydrated, inert capitula (Figure 3). Segmented regression analyses rejected for all species the null hypothesis of a single slope over the whole range of T_{out} in favor of the alternative hypothesis of two distinct slopes separated by a breakpoint (Table 1, Figure 3). Estimated breakpoints varied widely among species (range $\Psi = 25.0$ – 35.4 °C), with

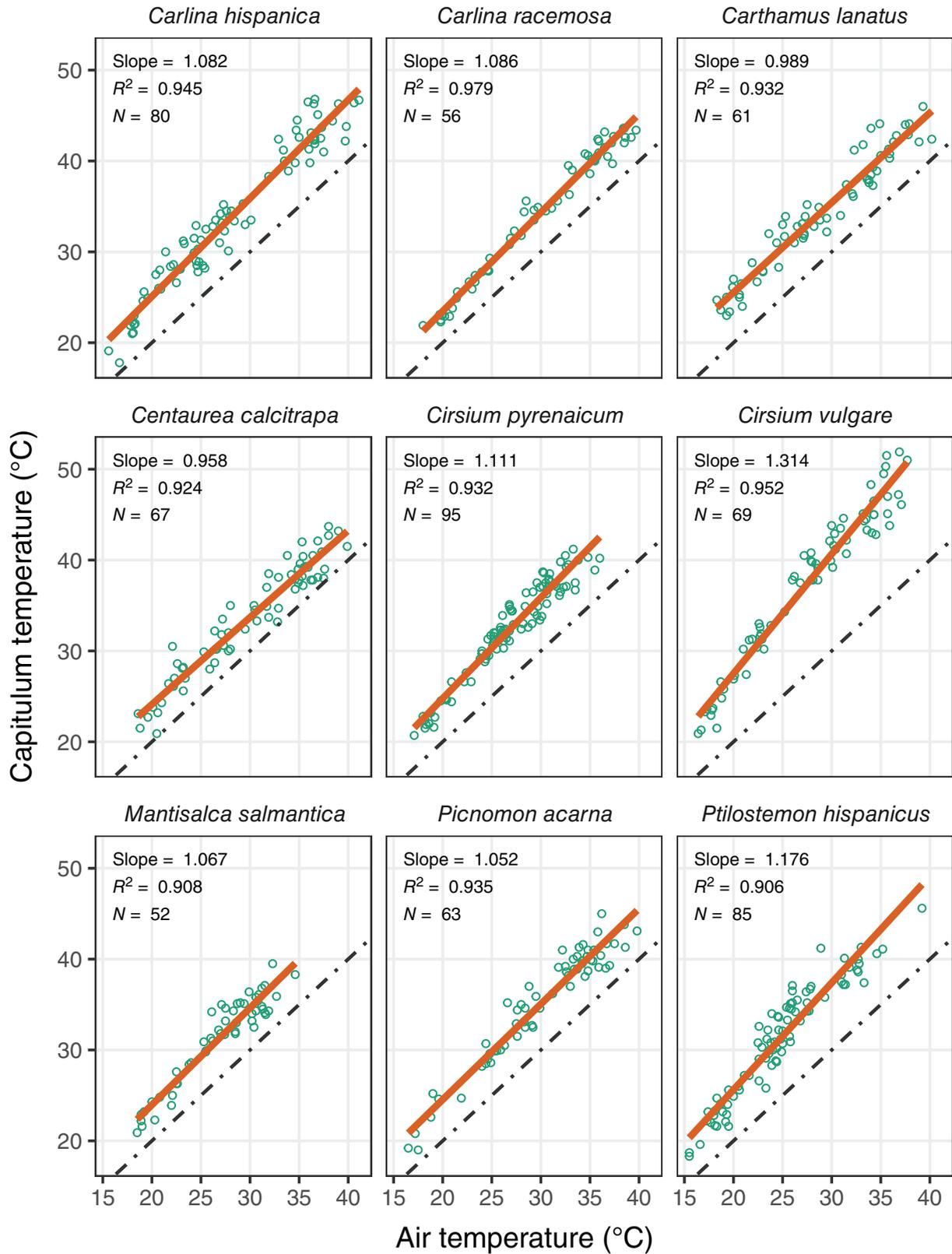


FIGURE 2 Relationship between the temperature inside the capitulum and the temperature of the surrounding air (gray dots) in samples of inert, experimentally dried capitula exposed in the field to natural variations in the thermal environment. Red lines are ordinary least-squares linear regressions fitted to the data (insets show summary statistics). Dot-dash lines represent the $y = x$ isothermal condition.

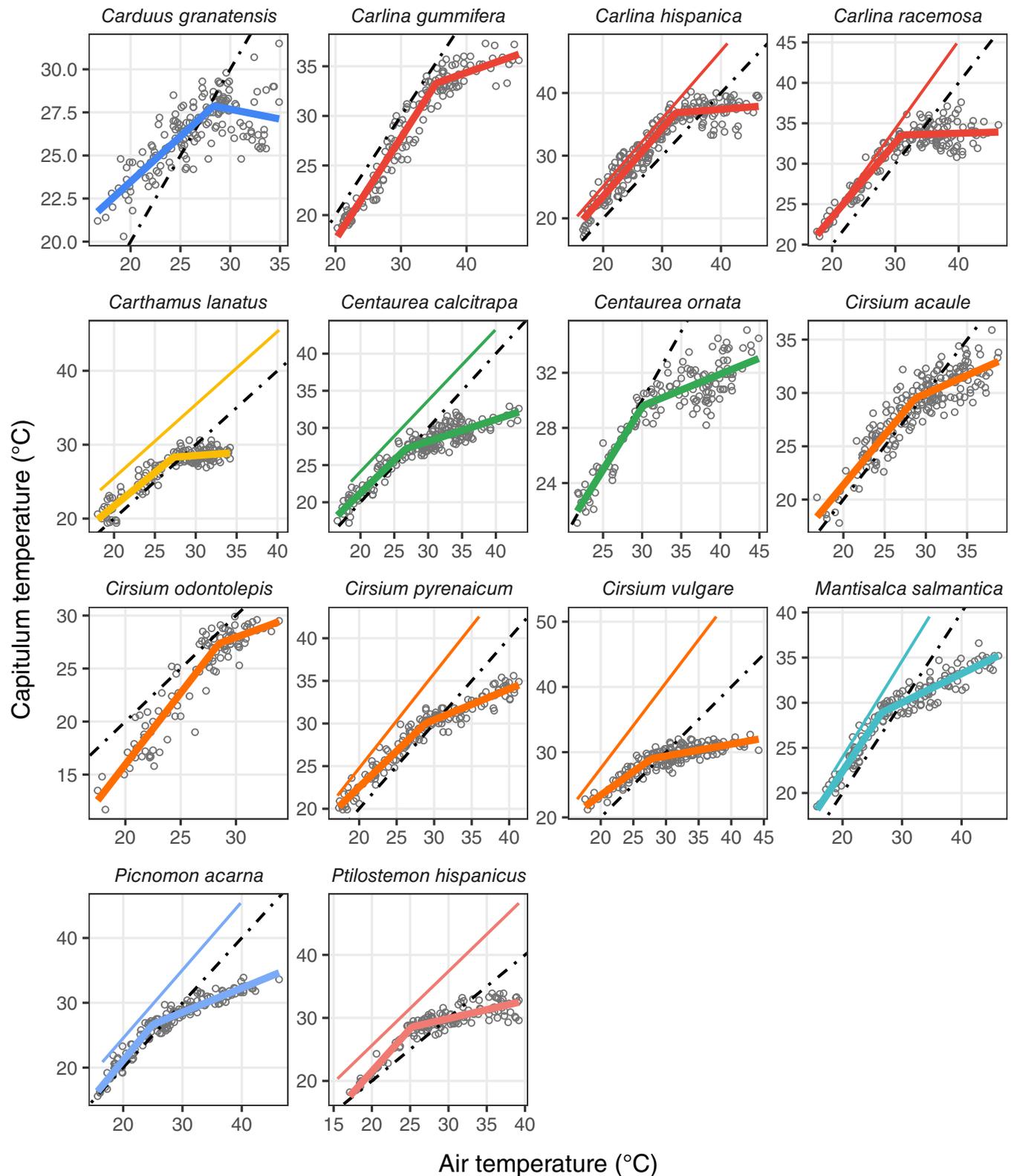


FIGURE 3 Bivariate relationships between the temperature inside capitula and the temperature of the surrounding air. Thick and thin colored lines are regressions fitted to field measurements on living (gray dots, segmented regressions, see Table 2 for details) and inert dried capitula (ordinary linear regressions shown in Figure 2), respectively, which are color-coded according to plant genus. For each species, paired temperature measurements were taken throughout the morning (06:00–12:00 h UTC) on capitula from different dates and populations. Dot-dash lines represent the $y = x$ isothermal condition.

the highest values consistently occurring in species of *Carlina* ($\Psi = 31.0\text{--}35.4^\circ$), followed by species of *Cirsium* ($\Psi = 27.8\text{--}28.8^\circ\text{C}$) (Table 1).

At ambient temperatures lower than breaking points, the internal temperature of living capitula in the field tended to fall somewhere between the two baselines represented by the $T_{\text{in}}\text{--}T_{\text{out}}$ relationship for dehydrated capitula, on the upper side, and the isothermic line $y = x$, on the lower one, while it fell well below these two reference lines when T_{out} exceeded Ψ (Figure 3). At the highest air temperatures sampled ($35\text{--}48^\circ\text{C}$), temperatures within the living capitula mostly were $5\text{--}14^\circ\text{C}$ lower than air temperature and up to $15\text{--}20^\circ\text{C}$ lower than those reached by the dehydrated, inert capitula (Figure 3).

Irrespective of interspecific differences in Ψ values, the overall shape of the segmented functional relationships linking T_{in} and T_{out} was remarkably similar for all species: steep slopes close to unity for $T_{\text{out}} < \Psi$ and a shift to distinctly shallower slopes for $T_{\text{out}} > \Psi$ (Table 1, Figure 3). Consequently, at ambient temperatures under Ψ the internal temperature of capitula generally tended to run parallel and remain fairly close to an isothermal relationship with the ambient, while an internal thermal deficit arose at T_{out} beyond Ψ whose magnitude increased steadily as ambient temperature increased. This shift in the $T_{\text{in}}\text{--}T_{\text{out}}$ relationship denoted a significant decoupling of T_{in} in relation to T_{out} when Ψ was exceeded, which was shared by all species to a greater or lesser extent. Such decoupling was remarkable in species of *Carlina* and *Carthamus*, in which the temperature inside the capitulum became virtually independent of ambient temperature when the latter exceeded Ψ (slopes close to zero for $T_{\text{out}} > \Psi$; Table 1 and Figure 3).

Interspecific variance in Ψ was largely accounted for by the variation among subtribes (71.3% of total), while the contribution of differences among genera within tribes was comparatively negligible (6.7%) (Appendix S2: Table S1).

Continuous monitoring

Continuous temperature measurements over most or all the functional life of individual capitula revealed that the capitulum-air thermal gradient (ΔT) was predominantly negative in every species except *Cirsium acaule* (Table 2). The proportion of measurements with $\Delta T < 0$ ranged between 72% and 95% among species, which denotes that the interior of individual capitula was consistently cooler than the surrounding air for most of their lives. Considering only those data with $\Delta T < 0$, the capitulum-air thermal gradients averaged between -4.2°C (*Carlina racemosa*) and -0.8°C (*Cirsium pyrenaicum*) (Table 2).

Both T_{in} and ΔT followed regular diel rhythms in the individual capitula of all species, as illustrated by the thermal time series for representative capitula shown in Figure 4. With only minor variations among species, the prevailing pattern involved T_{in} being roughly similar to T_{out} ($\Delta T \approx 0$) from early morning to shortly before noon, as both temperatures tended to increase in unison over that period. Subsequently, T_{in} and T_{out} followed increasingly divergent courses, leading to negative capitulum-air gradients that persisted for the rest of daytime (*Centaurea*, *Cirsium*, *Picnoman*), until around midnight (*Carduus*, *Ptilostemon*) or, in the most extreme cases (*Carlina*), up to the following day's sunrise. In some taxa, the negative ΔT started to build up immediately after a brief spike of $\Delta T > 0$ (see, e.g., the thermal series for *Carduus granatensis*, *C. racemosa*, *Carlina vulgaris*, and *Cirsium vulgare* in Figure 4). In species whose capitula lasted for several days, the absolute value of the daily peaks in negative ΔT tended to decline as the capitulum aged (e.g., *Carduus granatensis*, *C. racemosa*, *Centaurea calcitrapa*; Figure 4).

Diel and spatial patterns at the community level

The combination of the regular diel rhythms in ΔT which took place at the level of individual capitula led to well-defined diel rhythms in ΔT at the plant population level in the majority of the species studied (Figure 5). With minor departures (e.g., *Cirsium odontolepis*) ΔT was, on average, large and consistently negative in the flower populations from around midmorning until at least the late afternoon (Figure 5). Since the capitula of most species were spatially concentrated within 50 cm of the ground (Figure 6), the combined diel rhythms in ΔT created a multispecific layer of refrigerated capitula near the ground that lasted for most of the daytime and, for some species, also extended well into nighttime.

Bee visitation

A total of 33 bee species were recorded visiting the capitula of the six locally coexisting species chosen for field observations. The family Megachilidae was the most important numerically, contributing 57.2% of individuals and 48.5% of species, followed by Apidae (33.2% and 33.0% of individuals and species, respectively). Observations were very unevenly distributed among plant and bee species, and most bee species were recorded only a few times (Appendix S2: Table S2), hence the data for all bees and plants have been combined into a single sample for the analysis.

TABLE 2 Species for which temperatures inside (T_{in}) and outside (T_{out}) individual capitula were continuously monitored over one or more days, sampling effort, and summary statistics of the distributions of capitulum-air thermal gradient ($\Delta T = T_{in} - T_{out}$) for data points with $\Delta T < 0$.

| Species | Sampling effort | | Capitulum-air thermal gradient (ΔT) | | | |
|-------------------------------|-----------------|--------------|---|--|---|---|
| | No. dates | No. capitula | Paired $T_{in}-T_{out}$ measurements | $T_{in}-T_{out}$ pairs with $\Delta T < 0$ (%) | Mean \pm SE for data with $\Delta T < 0$ ($^{\circ}\text{C}$) | Interquartile range for data with $\Delta T < 0$ ($^{\circ}\text{C}$) |
| <i>Carduus granatensis</i> | 18 | 8 | 31,382 | 71.7 | -1.99 ± 0.01 | -2.7, -1.0 |
| <i>Carlina hispanica</i> | 21 | 7 | 24,519 | 88.2 | -3.68 ± 0.01 | -5.1, -1.9 |
| <i>Carlina racemosa</i> | 6 | 4 | 26,278 | 91.4 | -4.21 ± 0.02 | -5.8, -2.1 |
| <i>Carlina vulgaris</i> | 6 | 2 | 14,302 | 87.7 | -1.38 ± 0.01 | -1.7, -0.8 |
| <i>Centaurea calcitrapa</i> | 8 | 4 | 6252 | 88.1 | -1.37 ± 0.01 | -1.7, -0.7 |
| <i>Cirsium acaule</i> | 10 | 4 | 22,886 | 45.3 | -3.07 ± 0.02 | -4.6, -1.4 |
| <i>Cirsium odontolepis</i> | 4 | 2 | 8648 | 73.5 | -1.82 ± 0.01 | -2.4, -1.1 |
| <i>Cirsium pyrenaicum</i> | 9 | 4 | 20,138 | 83.4 | -0.76 ± 0.01 | -0.9, -0.4 |
| <i>Cirsium vulgare</i> | 5 | 10 | 21,396 | 86.6 | -1.75 ± 0.01 | -2.6, -0.7 |
| <i>Mantisalca salmantica</i> | 4 | 4 | 8324 | 82.8 | -1.54 ± 0.03 | -2.3, -0.6 |
| <i>Picnomon acarna</i> | 7 | 4 | 5024 | 94.8 | -2.53 ± 0.01 | -3.6, -0.9 |
| <i>Ptilostemon hispanicus</i> | 9 | 4 | 20,124 | 93.3 | -1.93 ± 0.01 | -3.0, -0.5 |

Bees were observed foraging under a broad range of air temperatures (range = 16–37 $^{\circ}\text{C}$, median = 29 $^{\circ}\text{C}$, interquartile range = 27–32 $^{\circ}\text{C}$) (Figure 7). Except for one plant species, air temperature beside the visited capitula was in most instances higher than the thermal breakpoint (Ψ) for the plant species involved (Figure 7). In other words, a large proportion of the capitula visited by bees was already in the actively cooled stage ($T_{out} > \Psi$): 79.0% (*M. salmantica*), 77% (*C. calcitrapa*), 68.0% (*Cirsium vulgare*), 59.0% (*C. odontolepis*), 55% (*C. pyrenaicum*), and 16% (*Carlina hispanica*).

DISCUSSION

Cooling

Instantaneous measurements and continuous monitoring revealed that the capitula of all species of summer-blooming Asteraceae studied here were regularly exposed in the field to long periods of high ambient temperatures (quite often >30 $^{\circ}\text{C}$, sometimes >40 $^{\circ}\text{C}$), yet the interior of the capitula was cooler than the surrounding air for most of their lives. The capitulum-air thermal gradient exhibited diel rhythms whose shapes varied relatively little among species and were remarkably constant over consecutive days for a given capitulum. As a general rule, the magnitude of negative capitulum-air gradients peaked around the hottest period of daytime, when they often

approached or even exceeded -10 $^{\circ}\text{C}$. As far as I know, these are the largest negative temperature differentials ever reported for flowers, as well as one of the first documented examples of diel rhythms in floral temperature differentials (see also, e.g., Patiño & Grace, 2002). Comparable results were advanced by Herrera (2024a) for *Carlina corymbosa* (a junior synonym of *C. hispanica*, the name used here following Blanca et al., 2011). The few studies that have so far documented an ability of flowers to cool themselves either failed to document negative flower-air gradients (Galen, 2006; Patiño & Grace, 2002) or, when such negative gradients were found, the magnitude was much smaller than that found here for the capitula of summer-flowering Asteraceae (e.g., -2.7 $^{\circ}\text{C}$ in *Galanthus nivalis*, Rejsková et al., 2010; -1.9 $^{\circ}\text{C}$ in *Hexastylis arifolia*, Sherer et al., 2024). Taken together, however, these results illustrate that floral cooling can be more frequent in nature than its usual neglect in the literature on floral thermal ecology would suggest, something that was already anticipated by van der Kooi et al. (2019). These authors emphasized that the prevalence of studies on floral warming in the literature mostly reflects geographical biases in the field of floral thermal ecology rather than a biological reality because most work on floral thermal ecology has been conducted in alpine, arctic, and midlatitude plants. Results of the present study support their view and also motivate the prediction that future investigations on the floral thermal ecology of plants inhabiting hot-dry environments akin to those prevailing

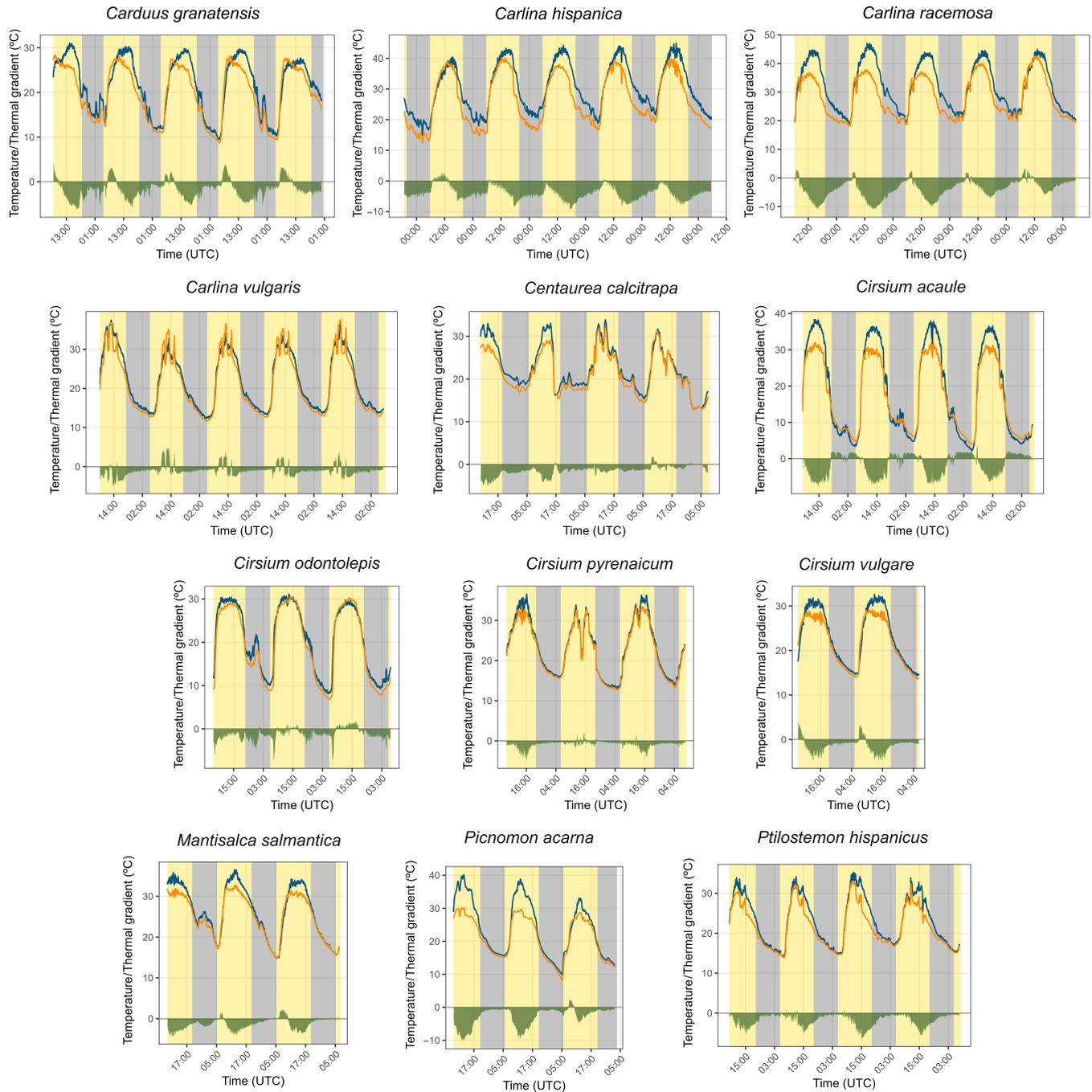


FIGURE 4 Variation of temperature inside representative capitula (one capitulum per species; T_{in} , orange lines), the air outside (T_{out} , blue lines), and capitulum-air thermal gradient ($\Delta T = T_{in} - T_{out}$, green area at the bottom of each plot, with bottom- and top-facing areas around $y = 0$ reflecting negative and positive gradients, respectively). Original measurements were smoothed for the graphs using a moving average procedure with a 10-min sliding window. Differences between species in the length of the measurement period mostly reflect interspecific differences in the duration of capitula. Daytime and nighttime periods are denoted by yellow and gray vertical bands, respectively.

during Mediterranean summers should reveal more examples of significant autonomous cooling.

One important result of this study was the finding that the functional relationship linking internal temperature of the capitulum with ambient temperature was not a simple, monotonously linear or quasi-linear one, as frequently

assumed in research on the thermal ecology of leaves and flowers (Michaletz et al., 2015, 2016, Sherer et al., 2024; see also *Thermoregulation* below). In all species studied here, the functional response was best described by a composite of one steep and one shallow linear response separated by a (statistically estimated) breakpoint (Ψ), or

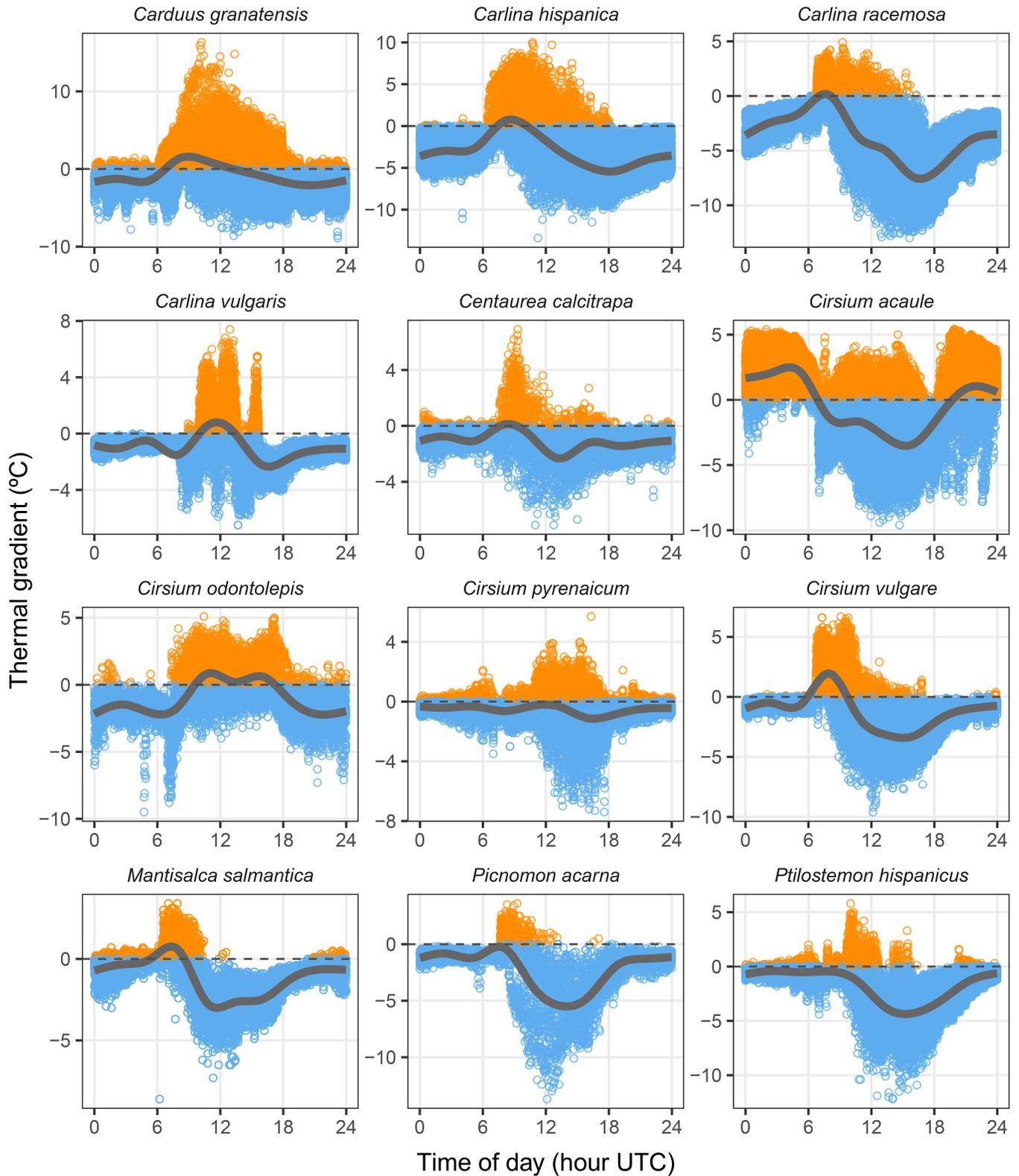


FIGURE 5 Daily variation in capitulum-air thermal gradient ($\Delta T = T_{in} - T_{out}$; positive and negative gradients are shown as orange and blue symbols, respectively) for the whole set of individual capitula that were continuously monitored over most or all their lifetimes. Each symbol corresponds to a pair of T_{in} and T_{out} measurements ($N = 209,273$, all species combined). Data from all dates and capitula are combined in the plot for a given species (see Table 2 for sample sizes). The gray curves are cubic splines fitted to the data.

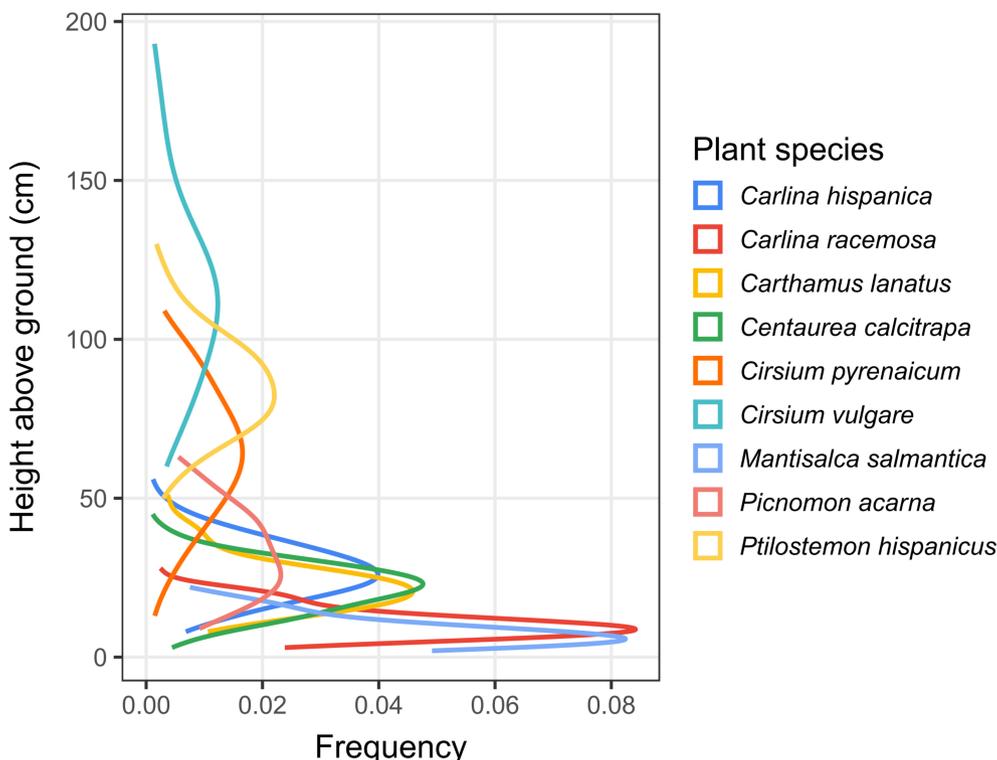


FIGURE 6 Frequency distributions of capitula height above the ground for nine of the species studied. In *Carlina gummifera* and *Cirsium acaule*, all the capitula occurred within 5 cm from the ground (Figure 1), and the very narrow height distributions for these two species have been omitted from the graph for clarity. Curves depict the fitted kernel estimates of data point density for each species.

“thermal threshold” In practical terms, this finding suggests that floral cooling (i.e., that occurring when $T_{out} > \Psi$) can remain unnoticed for a given plant species if the range of ambient temperatures sampled either is not broad enough to include the species-specific thermal threshold Ψ , and/or the statistical power to reject the null hypothesis of a single slope by means of segmented regression is too small because of insufficient sample size (Muggeo, 2016). Furthermore, since the species-specific Ψ values above which cooling occurred spanned over a range of $\sim 10^{\circ}\text{C}$, interspecific differences in cooling ability could sometimes be a spurious consequence of sampling thermal ranges that include the thresholds for some species but not for others.

Two-slopes functional relationships between plant and ambient temperatures of the sort documented here for capitula of Asteraceae are often discernible in, or can be inferred from, $T_{in}-T_{out}$ plots from early studies on leaf thermal ecology (e.g., fig. 1 in Linacre, 1964; fig. 5 in Linacre, 1967; fig. 1 in Palmer, 1967; fig. 42 in Percy et al., 1972; fig. 3 in Upchurch & Mahan, 1988). Furthermore, the existence of underlying thermal “switching points” beyond which leaf cooling occurs, roughly equivalent to the Ψ thresholds analytically estimated here for capitula, was already documented nearly 40 years ago (Althawadi & Grace, 1986;

Upchurch & Mahan, 1988). These parallelisms suggest that the underlying mechanism(s) of plant response to high temperature are probably similar in leaves and flowers. In the case of leaves, it seems well established that high temperatures activate stomatal opening through a photosynthesis-uncoupled signaling pathway, which enhances transpiration and leads to evaporative cooling (Althawadi & Grace, 1986; Drake et al., 1970; Pankasem et al., 2024; Sadok et al., 2021). Evaporative cooling has also been tentatively proposed as the mechanism responsible for autonomous cooling in wild flowers (Herrera, 2024a; Sherer et al., 2024), mainly based on observations that flowers often bear functional stomata; similar geometric rules govern the distribution of stomata in leaves and flower parts; and transpiration through floral stomata can be greater than transpiration through leaf stomata when flowers are exposed to high temperatures (Azad et al., 2007; Blanke & Lovatt, 1993; Huang et al., 2018; Sinha et al., 2022; Zhang et al., 2018), sometimes playing a role in pollinator attraction and orientation (Dahake et al., 2022; Von Arx et al., 2012). In flowers with few or nonfunctional stomata, cuticular transpiration could be another pathway for evaporation (Cheng et al., 2021; Kitamura & Ueno, 2015) and could also contribute to floral cooling in hot environments, since

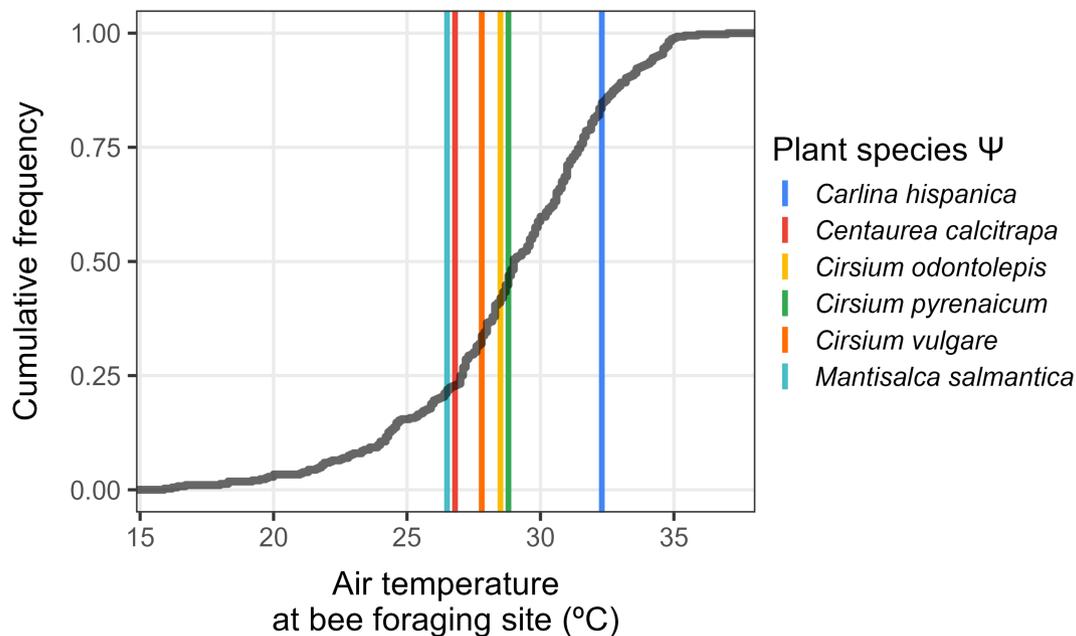


FIGURE 7 Cumulative frequency distribution of air temperature at the foraging sites of the bees watched probing capitula of six of the plant species considered in this study (gray line, $N = 388$ observations, all plant and bee species combined, see Appendix S2: Table S2 for details). Colored vertical lines mark the air temperature breakpoints (Ψ) for each plant species, as obtained from the segmented regressions of capitulum temperature (T_{in}) against ambient temperature (T_{out}) (Table 1).

water permeability of plant cuticles increases with ambient temperature (Riederer & Schreiber, 2001; Schönherr et al., 1979; Schönherr & Mérida, 1981). Irrespective of the relative importance of the stomatal and cuticular pathways for evaporation in flowers, the experimental results of this study showing that inert, dried capitula lacked any cooling capacity and built up considerable thermal excesses relative to the environment provide an indication that evaporative heat exchange with the environment was central to flower cooling, just as it is in leaf cooling (Jones, 1992; Lambers et al., 2008). The fact that the beginning of cooling by a capitulum often followed a short spike of positive ΔT suggests that biologically defined temperature thresholds did actually underlie the statistically defined, empirical breakpoints Ψ .

Thermoregulation

The extent to which plants are able to regulate their temperatures has manifold implications in relation to environmental changes, yet “thermoregulation remains a controversial topic in plant biological research” (Drake, 2023). Part of the controversy and contrasting published results could perhaps be associated with insufficiencies of the thermoregulatory model generally accepted. Studies on plant thermoregulation have most often adopted the classical definition of the

concept established by Huey and Slatkin (1976) for ectothermic vertebrates, namely that thermoregulation is a process whereby a plant keeps its temperature (somewhat) independent of the temperature of the surrounding environment. Under this general premise, a plant’s thermoregulatory capacity could be inversely quantified by the slope of the simple linear regression relating plant temperature to ambient temperature so that slopes close to zero denote better thermoregulatory ability than slopes closer to unity (Huey & Slatkin, 1976). This classical linear approach has been generally deemed acceptable to depict the relationships between leaf and air temperature, and alternative shapes of the functional relationship between plant and ambient temperatures have been rarely explored (Campbell & Norman, 1998; Drake, 2023; Michaletz et al., 2015, 2016; Miller et al., 2021; Still et al., 2022; Guo, Zhang, et al., 2023; but see Blonder & Michaletz, 2018). Results found here for the capitula of Asteraceae strongly suggest that the key assumption of a single linear relationship linking plant and air temperature may not universally apply, since the relationship was best described by two linear relationships with noticeably different slopes. A formal extension of the single-slope, canonical linear model of Huey and Slatkin (1976) is introduced in Figure 8 that accommodates the two-slopes thermal models which seem to follow some flowers (present study), and possibly some leaves too (examples mentioned in the preceding section). Under this extended thermal regulation framework,

different thermoregulatory possibilities are available to plants which differ in one or more of the following aspects: (1) the position of regression lines relative to null-model and isothermal $T_{in}-T_{out}$ relationships, both of whose slopes equal unity; (2) the comparative values of the two slopes involved; and (3) the position of break points along the gradient of environmental temperature. The different species of Asteraceae studied here exemplify some of these possibilities (Figure 8).

Interpreting separately the two slopes obtained for each species in light of Huey and Slatkin's (1976) linear model brings a similar conclusion for all species: capitula were only weakly thermoregulated (slopes close to unity) at low temperatures ($T_{out} < \Psi$) and switched to intense thermoregulation (slopes approaching zero) when ambient temperature exceeded Ψ . In some extreme cases (e.g., *Carlina*, *Carthamus*), T_{in} became truly independent of T_{out} when T_{out} was greater than Ψ , which denoted virtually perfect thermoregulation. In short, active floral thermoregulation was environmentally triggered when ambient temperature surpassed a species-specific thermal threshold Ψ . Declining slopes of the relationships between flower and ambient temperature as the latter increased were also reported by Rejsková et al. (2010) for *Anemone nemorosa* and *Galanthus nivalis*, two vernal flowers of temperate forest understory. This observation suggests that threshold-triggered thermoregulatory cooling would not be restricted to flowers from hot environments. Threshold-dependent thermoregulatory responses raise the issue of how plants sense temperature and, particularly, how they feel the heat (Franklin, 2010; Mittler et al., 2012; Ruelland & Zachowski, 2010), but these aspects will not be discussed here.

Ecological and evolutionary implications

Unless plants are able to decouple intrafloral temperature from that of the surrounding air, exposure of flowers to thermal environments that are harmful or suboptimal for aspects of their reproductive function (production and viability of pollen and ovules, pollen tube growth, ovule fertilization) will eventually have a negative impact on individual fecundity (see references in [Introduction](#)). Mechanisms favoring either floral warming or floral cooling should therefore have been selected for in environments where flowers are frequently exposed, respectively, to temperatures that are either too cold or too hot for optimal performance. The former possibility has been documented in detail for many plants from cold and temperate regions (Heiling & Koski, 2024; Kevan & Coates, 2024; van der Kooij et al., 2019). The possibility that plants can evolve means for controlled cooling of

their flowers, in contrast, has only begun to be investigated in some detail quite recently (Herrera, 2024a; Karban et al., 2023; Koski et al., 2024; Sherer et al., 2024). Although this recent evidence refers to few species and environments, it does support the expectation that plants can lower floral temperature so that damage to ovules and pollen from heat stress is avoided or alleviated. Results of the present investigation represent a significant addition to this literature, for they seem to be the first ones from a truly hot environment where flowers face high temperatures for long periods on a daily basis. Without ruling out the likely possibility of high thermal tolerance in these plants, their ability for thermoregulatory cooling found here was of a sufficient magnitude to have the potential to enhance reproductive performance under high ambient temperature, since estimated Ψ values were remarkably close to the average optimal temperature for pollen performance (Tushabe & Rosbakh, 2024).

The frequency and duration of summer heat waves are currently increasing in the southern Iberian Peninsula (Agencia Estatal de Meteorología, 2023; Díaz-Poso et al., 2023; Lorenzo et al., 2021), which highlights the value of floral cooling by the summer-flowering plants studied here. It must be stressed, however, that cooling by transpiration in these species comes at the price of increasing water loss precisely during the harshest period of the Mediterranean dry season. Plants could therefore face a delicate balance between the opposing forces of undertaking sufficient short-term cooling to avoid damage to pollen and ovules on one side and saving sufficient water to maintain vital physiological functions during the summer on the other (Sadok et al., 2021). The increasingly warming summer climate in the study area will lead to plants spending more time at $T_{out} > \Psi$ and thus increasing water expenses for capitula cooling, which could eventually reduce survival or fecundity even though their capitula had been successfully kept within safe temperature limits most of the time. The unexplored possibility remains, however, that summer-flowering Cardueae can afford such intensive water drains because of some still unrecognized anatomical or physiological capacity to improve water acquisition, storage, or retention.

Cooling of flowers can have indirect beneficial effects on both plant reproduction and pollinator populations, via enhancement of pollinator visitation arising from the appearance of a distinct, "thermally improved" habitat layer (Herrera, 2024a; Karban et al., 2023, 2024), functionally equivalent to the cooled canopy layer found in tropical and urban forests (Posch et al., 2024; Wang et al., 2023). The main pollinators of the plants studied here were medium- and large-sized endothermic bees in the families Megachilidae and Apidae, which could risk overheating and/or dehydration while foraging in the

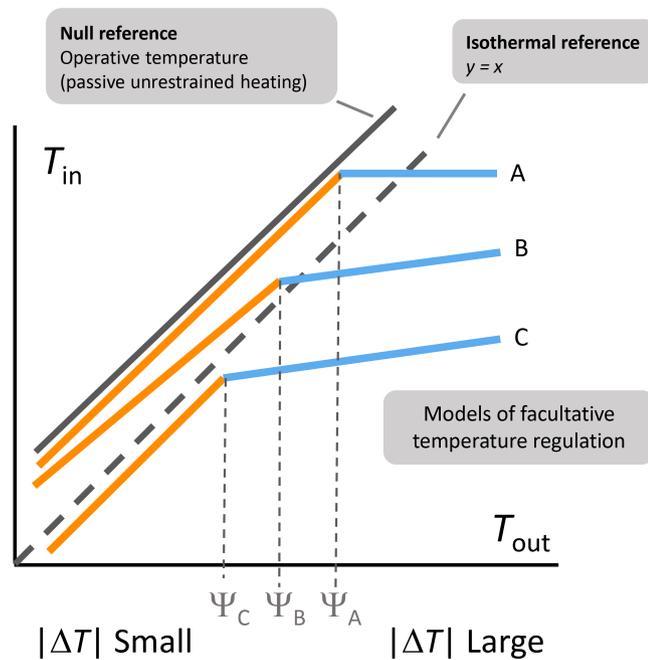


FIGURE 8 An expanded formulation of the single-slope, classical reference model of Huey and Slatkin (1976) linking organismal and ambient temperature, aimed at accommodating the two-slopes, facultative thermoregulation patterns exhibited by the capitula of Asteraceae investigated here (Figure 3). Under this expanded conceptual framework, interspecific differences in thermoregulatory capacity will simultaneously depend on the position of regression lines relative to the null-model and isothermal $T_{in} - T_{out}$ reference lines, the comparative values of the two regression slopes involved, and the position of break points (Ψ) along the gradient of environmental temperature. ΔT is the capitulum-air thermal gradient, $T_{in} - T_{out}$. See Figure 3 for the actual relationships exhibited by the species considered in this study. The three hypothesized patterns of facultative cooling patterns are exemplified by A, *Carlina hispanica*, *C. racemosa*; B, *Cirsium pyrenaicum*, *C. vulgare*; and C, *Carlina gummifera*, *Cirsium odontolepis* (see Figure 3).

hot-dry air of the Mediterranean summer (Corbet & Huang, 2016; Herrera, 2024b; Johnson et al., 2023; Kazenel et al., 2024; Rose-Person et al., 2024). Bees are able to discriminate among flowers on the basis of floral temperature, preferring to probe warmer flowers at low ambient temperatures and cooler ones at ambient temperatures above $\sim 30^{\circ}\text{C}$ (Descamps et al., 2021; Dyer et al., 2006; Harrap et al., 2017; Herrera, 1995; Norgate et al., 2010; Rands & Whitney, 2008; Shrestha et al., 2018; Whitney et al., 2008). Results of the present investigation, although limited to the bee pollinators of only six plant species, are consistent with this expectation. Most bee individuals were probing capitula at ambient temperatures higher than the corresponding cooling thresholds, and the visited capitula most likely were cooler than the air. The present data, however, do not allow for

rigorously proving a role of capitula temperature in itself in attracting bees, since these latter could be using floral temperature as a cue for other correlated factors such as, for example, nectar sugar concentration (Dyer et al., 2006; Whitney et al., 2008). This caveat notwithstanding, the finding that the capitula of most locally coexisting, summer-flowering Asteraceae in my study area tended to be concentrated within a narrow layer close to the ground, where air temperatures are ordinarily the highest (Geiger et al., 1995; Parry, 1951), highlights the potential significance at the plant community level of cooled capitula as a thermally favorable microhabitat for foraging bees during most of the daytime. The possible survival and reproductive advantages gained by summer bees from foraging within that refrigerated flower layer remain to be investigated.

All species studied here shared the ability to internally cool their capitula, but differed in the descriptive thermal parameters obtained from segmented regressions, particularly the breakpoint values. The number of species examined was too small to perform a full-fledged analysis of phylogenetic signal in thermal ecology parameters, but the results of variance partitions among nested taxonomic levels (Appendix S2: Table S1) provided an acceptable shortcut given the monophyletic nature of all the genera and tribes involved (Herrando-Moraira et al., 2019). Interspecific variance in breakpoints was taxonomically structured, with differences among subtribes being the main source of interspecific variance. This points to an early adaptive diversification of Ψ values within the Cardueae, which could perhaps have endowed this very species-rich lineage with the capacity to exploit a broad range of thermal environments. Large floral capitula are inherently prone to accumulate big heat loads under high ambient temperature and solar irradiance, and consequently will easily reach high, potentially harmful temperatures (see, e.g., Jones, 1992 for theoretical foundations, and results of experiments with inert capitula reported here for empirical proof). Floral thermoregulatory ability in species of Cardueae with large capitula possibly represented an adaptive breakthrough allowing the colonization of sunlit, hot-dry environments at times of year when few other plants were in bloom and competition for pollinators was probably at a yearly minimum. This speculative interpretation is supported by the fact that the earliest-diverging subtribe Carlininae (Herrando-Moraira et al., 2019) is characterized by high Ψ values and living in hotter, drier, and sunnier environments than the rest of the subtribes considered here. It remains to be tested whether other plant lineages displaying large flowers in hot-dry, sunny environments (e.g., Cactaceae) have also evolved facultative thermoregulatory cooling similar to that described here for the Asteraceae.

CONCLUDING REMARKS

Plants have been long acknowledged as transformers of abiotic features of the environment in a direction that benefits other organisms (Wright & Francia, 2024), or “ecosystem engineers” according to the original definition of the concept by Jones et al. (1994). As emphasized by these authors, however, separating engineering from other ecological processes may be difficult because these non-trophic interactions ordinarily co-occur with trophic interactions, a circumstance which has contributed to stirring controversy (Wright & Jones, 2006). Despite discrepancies about the appropriate use of the term “ecosystem engineering,” it is currently a well-recognized type of ecological interaction (Romero et al., 2015) that can apply to the case of the self-cooling, summer flower heads examined in this study. Mutualistic bees visited the cooled capitula of Asteraceae for food, as also did the egg-laying females of antagonistic seed-eating wasps, Tephritid flies, and Curculionid beetles (C. M. Herrera, unpublished data). Even though microhabitat enhancement brought about by floral cooling will be linked in all these instances to trophic relationships between plants and insects, the set of flower-dwelling bees, flies, wasps, and beetles could most likely benefit from the patches of benign microclimates “engineered” by thistles in such a hot-dry environment. This would represent a plausible mechanism whereby plant microclimatic engineering could contribute to maintaining local insect diversity in the context of the currently warming summer climate.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data, metadata, and R script (Herrera, 2025) are available in Figshare at <https://doi.org/10.6084/m9.figshare.27899763.v1>.

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SUPPORTING INFORMATION

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

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