International Journal of Biometeorology
https://doi.org/10.1007/s00484-021-02159-0

ORIGINAL PAPER

Can flowers affect land surface albedo and soil microclimates?

Amy M. Iler[1,2,3,4] · A. Sarah Walwema[3,4] · Heidi Steltzer[3,5] · Alfonso Blázquez-Castro[1,6]

Received: 18 July 2020 / Revised: 20 April 2021 / Accepted: 1 June 2021

Abstract
The phenology of vegetation, namely leaf-out and senescence, can influence the Earth's climate over regional spatial scales and long time periods (e.g., over 30 years or more), in addition to microclimates over local spatial scales and shorter time periods (weeks to months). However, the effects of flowers on climate and microclimate are unknown. We investigate whether flowers can influence light reflected by the land surface and soil microclimate in a subalpine meadow. We conducted a flower removal experiment with a common sunflower species, *Helianthella quinquenervis*, for 3 years (2015, 2017, and 2019). The flower removal treatment simulates the appearance of the meadow when *Helianthella* flowers earlier under climate change and loses its flowers to frost (other plant structures are not damaged by frost). We test the hypotheses that a reduction in cover of yellow flowers leads to a greener land surface, lower reflectance, warmer and drier soils, and increased plant water stress. Flower removal plots are greener, reflect less light, exhibit up to 1.2 °C warmer soil temperatures during the warmest daylight hours, and contain *ca.* 1% less soil moisture compared to controls. However, soils were warmer in only 2 of the 3 years, when flower abundance was high. *Helianthella* water use efficiency did not differ between removal and control plots. Our study provides evidence for a previously undocumented effect of flowers on soil microclimate, an effect that is likely mediated by climate change and flowering phenology. Many anthropogenic environmental changes alter landscape albedo, all of which could be mediated by flowers: climate change, plant invasions, and agriculture. This study highlights how further consideration of the effects of flowers on land surface albedo could improve our understanding of the effects of vegetation on microclimate.

Keywords Biosphere-atmosphere interactions · Climate change · Frost · Phenology · Reflectance · Soil moisture · Soil temperature

Introduction

Climate change is affecting the timing of life history events in a variety of organisms (Menzel et al. 2006; Parmesan 2007). These climate-induced phenological shifts affect various levels of biological organization, ranging from exposure of individuals to novel abiotic or biotic conditions that can affect survival and reproduction (Franks et al. 2007; Inouye 2008; Boggs and Inouye 2012; Stenson and Hammill 2014), to re-shuffling of ecological communities and changes in ecosystem-level processes (Sparks and Menzel 2002; Edwards and Richardson 2004; Linderholm 2006; Cleland et al. 2007; Richardson et al. 2010; CaraDonna et al. 2014). Just as climate affects phenology, the phenology of vegetation can also feedback to affect climate (Peñuelas et al. 2009). The timing of plant green-up and senescence affects carbon uptake, water exchange, and land surface albedo (the proportion of incident solar radiation reflected by a surface), all of which can affect local-scale microclimates (i.e., within a few meters up to 100 m, and over relatively short timescales like weeks to months) (Richardson et al. 2013; Bramer et al. 2018). Changes in microclimate in turn can feedback to affect the larger-scale climate system (i.e., hundreds of kilometers or more and weather conditions averaged over several years) (Richardson et al. 2013; IPCC 2014).

✉ Amy M. Iler
ailer@chicagobotanic.org

1 Aarhus Institute of Advanced Studies, Aarhus University, Aarhus, Denmark

2 Chicago Botanic Garden, The Negaunee Institute for Plant Science Conservation and Action, Glencoe, IL, USA

3 Rocky Mountain Biological Laboratory, Crested Butte, CO, USA

4 Northwestern University, Evanston, IL, USA

5 Department of Environment and Sustainability, Fort Lewis College, Durango, CO, USA

6 Centro Integrativo de Biología y Química Aplicada (CIBQA), Universidad Bernardo, O'Higgins, General Gana 1702, 8370854 Santiago, Chile

Published online: 12 June 2021

Our understanding of the effects of the phenology of vegetation on microclimate (and also climate) is limited to leaf and stem structures and therefore to leaf-out and senescence. For example, the timing of leaf emergence and senescence in temperate deciduous forests determines the amount of incoming solar radiation to the forest floor, and therefore sensible heat flux (Wilson et al. 2000). Vegetated land surfaces vary in their albedo as a result of plant cover (i.e., fractional photosynthetic cover of the ground surface), the characteristics of the vegetation present (stems vs. leaves, stem height, leaf orientation, and leaf color), and the type of vegetation present (e.g., grass vs. forest) (Hollinger et al. 2010), all of which can affect microclimate (e.g., De Frenne et al. 2019; Zellweger et al. 2019). Reproductive structures like flowers may also affect land surface albedo, especially because they appear during times of high solar irradiation (spring–summer) and are positioned above leaves. Yet reproductive structures have been ignored in this context. Flowers can almost completely cover other vegetative structures, depending on the species, and therefore intercept incoming solar radiation before many leaves. At a landscape scale, flowers can blanket the landscape in both natural and agricultural ecosystems, such as in flowering crops, super blooms in desert ecosystems, and invasive plant blooms (Fig. 1a, b). Such flowering events could affect land surface albedo, which in turn could affect microclimates. However, the role of flowers in affecting the albedo of vegetated land surfaces is unknown.

Here we investigate whether flowers can influence meadow albedo and soil microclimate (soil temperature and soil moisture, following Harte et al. 1995) in a subalpine ecosystem. Although flowers may influence albedo in a variety of contexts, we focus on phenology-mediated changes to the vegetated land surface. When plants flower earlier in response to climate change, flower abundance can be reduced through frost damage to developing flowers (other plant structures are unaffected by frost; Inouye 2000, 2008). In years with little-to-no frost damage, meadows with the aspen sunflower, *Helianthella quinquenervis*, appear mostly yellow because of the abundant flowers of this plant species (Fig. 1c). In contrast, in years with substantial frost damage to *H. quinquenervis* flower buds, the same meadows appear mostly green (Fig. 1d). Substantial frost damage occurs frequently, with > 80% of *H. quinquenervis* flower stalks frosted in 6 of 13 years at our study site (Iler et al. 2019). We specifically ask: (1) Do meadow plots without flowers reflect less light than meadow plots with flowers? (2) Is soil temperature warmer in plots without flowers compared to plots with flowers? (3) Is soil moisture lower and, therefore, plant water stress higher in plots without flowers compared to plots with flowers? We hypothesize that meadows without flowers will have a lower albedo, and therefore enhanced absorbance of incoming shortwave solar radiation and warmer and drier soils, compared to meadows with flowers. Additionally, if soils are drier, plant water stress might be higher in the absence of flowers.

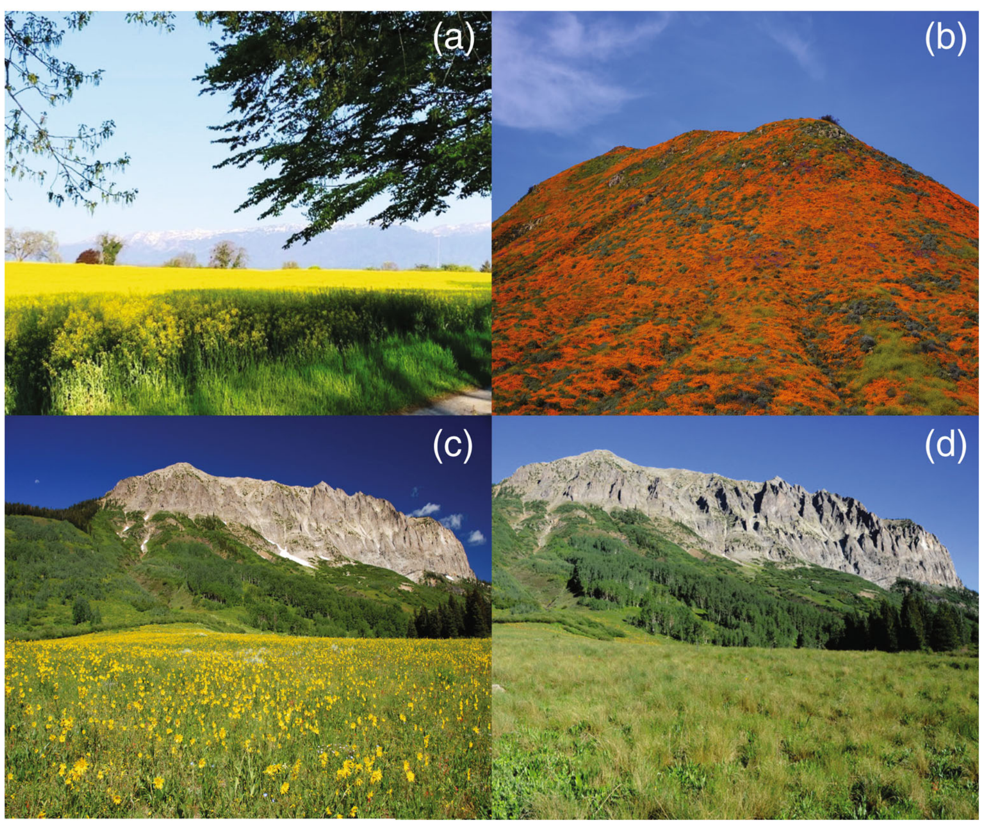

Fig. 1 Examples of flowers covering the landscape. **a** An agricultural field in the Jura Mountains of Switzerland. **b** A superbloom in Walker Canyon, Lake Elsinore, California, USA. **c** The study meadow in Gothic, Colorado, USA, in a year in which snowmelt was late; the yellow flowers are *Helianthella quinquenervis*. **d** A year in which snowmelt was early, and all of the *Helianthella* flower buds developed early and were damaged by frost due to cold nighttime air temperatures (photo credits **a** Steven Smith; **b** Jane Ogilvie; **c**, **d** David W. Inouye)

Materials and methods

Study site and species

This experiment was conducted at the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA (38°57.50 N, 106°59.30 W, 2,900 m above sea level), across 3 years: 2015, 2017, and 2019. *Helianthella quinquenervis* (aspen sunflower), hereafter *Helianthella*, is an abundant and common species in montane and subalpine meadows from ca. 2,700–3,500 m a.s.l across western North America (Weber, 1952). It is a long-lived plant that produces large, yellow flowerheads (capitulae), typically during the month of July (mean flowerhead diameter is 5.7 cm). *Helianthella* flowerheads are positioned above the leaves of all of the plants in our study plots, so that *Helianthella* flowers are the first plant object to intercept incoming shortwave radiation. Below the *Helianthella* flowers are multiple layers of leaves, and our study meadow contains little bare ground in mid-summer (Panel S1). Open flowers are present for 2 weeks to over 1 month at our study site, depending in part on the amount of frost damage (Table S1). In high-elevation ecosystems such as our study site, earlier flowering is associated with both warmer air temperatures and earlier spring snowmelt (Iler et al. 2017; Theobald et al. 2017). Earlier initiation of flowering in response to these changing abiotic conditions can result in exposure of plant reproductive structures to lower nighttime air temperatures—despite warmer air temperatures on average—which can result in frost damage to flower buds and total reproductive failure in the case of *Helianthella* (Inouye 2008; Iler et al. 2019). Although damage to small, developing flower buds can be severe, resulting in no flower production, other plant structures are usually not damaged by frost in this subalpine plant community (Inouye 2000; AMI, *personal observation*).

Experimental design

We conducted a *Helianthella* flower removal experiment to simulate the appearance of the meadow when flower buds experience frost damage in an early spring. Twenty 2 m × 2 m plots (10 control and 10 flower removal) were established in 2015, and each of our plots was located at the center of a larger, circular plot of the same treatment that was 14 m in diameter. These larger plots were part of a different study that also removed *Helianthella* flowers. In the flower removal plots, flowers were removed from the total area of the larger plots, which prevents any edge effects due to flower removal in our 2 m × 2 m plots. To avoid disturbing the soil and vegetated land surface within the focal 2 m × 2 m plots, flowers were removed while standing along the plot edges, so that no walking occurred within the plots. Plots were paired based on spatial proximity, and plots in each pair were randomly assigned to either control or *Helianthella* removal. All flowerheads were removed below the receptacle when the flowers were in the bud stage.

In 2015, 2017, and 2019, we measured flowering phenology, soil temperature, and soil moisture (detailed methods are below; 2016 was not included due to logistical constraints, and all flowers were frost damaged in 2018). All open flowerheads were counted in the control plots every week during the experiment in all years (Table S1), to monitor flowering phenology and to compare floral abundance across years.

Reflectance measurements

Measures of reflectance varied across years and became more targeted as we gathered evidence consistent with the hypothesis that flower albedo affects soil microclimate: NDVI in 2015, reflectance of flowers and leaves in the lab in 2017, and reflectance in the field in 2019. We conducted our measurements of reflectance during peak flowering, so that we would be able to document a difference between treatments if one existed, and because of limited access to shared field equipment used to measure reflectance.

On July 16, 2015, during peak *Helianthella* flowering (Table S1), Normalized Difference Vegetation Index (higher NDVI = greener) was measured with a SpectroSense2 light meter that measures red and infrared incoming and reflected light in the same bandwidths as MODIS satellite-sensing of NDVI (Skye Instruments, Great Britain). The light meter was positioned 2.4 m above the ground, which allowed for the measurement of four 1-m diameter circular subareas in each quadrant of each plot (total of 80 measurements). Measurements were conducted under full sun conditions. We used NDVI to quantify differences in canopy reflectance, because of how commonly this index has been used in land surface phenology studies.

In 2017, the reflectance of both ray florets and leaves was measured in the lab using a spectroradiometer (ASD HandHeld 2, Malvern Panalytical, UK), which measures the amount of light reflected from a sample across the visible and near-infrared spectra (325–1,075 nm). Ten leaf samples and ten flower samples were collected from ten different plants and immediately brought into the lab for measurements. One individual was haphazardly chosen near each control plot, to make sure we sampled individuals across the study site. Ray florets were clipped at the base, arranged side by side without overlap, and taped at the edges of the petals to a sheet of white paper. Ray florets are the flowers along the outer margin of a flowerhead that possess the large, visible flower petals. Taping the petals was necessary to fill the sample chamber, which contained only plant tissues. Flowers and leaves were handled with forceps to avoid contaminating the samples. Three measurements were taken for each sample, and mean reflectance was calculated for each wavelength for each sample. Reflectance values from leaves and flowers were combined with estimations of percent cover of *Helianthella* flowers to estimate plot-level reflectance in all 3 years (Fig. S1).

In 2019, we measured reflectance in the field with a hand-held spectrometer (Spectra Vista Corporation, model HR1024i, 338.0–2,516.6 nm) during the week of peak flowering (5–6 August). Peak flowering was later than average in 2019 because spring snowmelt date was later than average. Although reflectance is often measured repeatedly across a growing season for use in parameterization of land surface models, our goal was to determine whether reflectance differed between plots at peak flowering. This is a reasonable starting point for addressing the question of whether flowers can affect reflectance. The spectrometer was held *ca.* 1 m above the ground surface to take measurements, for which the field of view is a circle with an approximately 0.5-m diameter. Thus, we took 20 measurements per plot (4 along each side and 4 in the plot center) under full sun conditions. Reflectance is functionally equivalent to albedo when measured under full sun conditions near solar noon. Measurements were calibrated against a white reference (Spectralon, 99% reflectance) approximately every 30 min. Measurements were taken from 10 to 14:00 to minimize the effect of sun angle on reflectance. Due to limited access to the field spectrometer and clouds, we were unable to measure all plots within the ideal timeframe of 10–14:00, and we were additionally unable to measure all plots during peak flowering. This resulted in a reduced dataset of 13 plots measured during ideal conditions (5 controls, 8 flower removals).

Abiotic environment

Soil temperature was measured with data loggers set to record every 30 min (HOBO Pendant Temperature Loggers, HOBO, Onset, USA), starting a few days before *Helianthella* began to flower and ending after flowering had finished in each year. Loggers were buried at a depth of 8 cm because much of *Helianthella* root biomass is concentrated from the soil surface down to this depth. There was also a HOBO data logger in the study site measuring indirect sunlight every 15 min (HOBO Pendant Temperature/Light Logger), which was used to classify days as sunny or not sunny for analysis. This data logger was mounted *ca.* 15 cm above the soil surface on the underside of a north-facing, white piece of PVC plastic, at an angle of approximately 45% from the ground surface.

Volumetric water content of the soil was measured weekly using a soil moisture meter, except during the week of peak flowering when soil moisture was measured twice. These soil moisture measurements began before *Helianthella* began to flower in each year, and concluded during the last week of flowering (Table S1). In 2015, soil moisture was measured at a depth of 12 cm (HydroSense II Probe, Campbell Scientific, Logan, UT, USA) until 30 July when a sample prong was broken due to rocky soil conditions. Therefore, soil moisture measurements were completed at a shallower depth (7.62 cm) for the rest of the 2015 season and in 2017 and 2019 (FieldScout TDR 100 Meter, Spectrum Technologies, USA). The plots were divided into four subplots, and soil moisture was measured in the middle of each subplot on each sample date.

Plant water stress

In 2015 and 2017, we collected one leaf each from two non-flowering individuals and one leaf each from two flowering individuals per plot (four leaves per plot) for analysis of leaf carbon isotope ratios (Δ13C). Carbon isotope ratios are a measurement of water use efficiency (WUE), or carbon assimilated per unit of water transpired, and can therefore provide information on the level of water stress of an individual plant over the course of the growing season (Farquhar et al. 1989). Lower values of Δ13C indicate higher WUE, which is a common plant response to water stress (Lambers et al. 1998). Leaves were collected after flowering finished (leaves were still green and healthy-looking), and leaves that showed signs of herbivory or disease were avoided. Leaves were placed in small paper envelopes and dried under ambient air temperature in the lab. The leaves were ground (using an MP Fast Prep-24 homogenizer), weighed into 2-mg samples, and sent to the Isotope Ratio Mass Spectrometry Laboratory at Northwestern University for processing (Costech 4010 Elemental Analyzer; ThermoFisher Delta V plus Elemental Analyzer).

Because plants may only experience water stress during certain times of the season, we also took instantaneous measures of plant water stress during peak flowering in 2017 (19–27 July). Leaf water pressure was measured using a pressure chamber (PMS model I505D, USA). Four leaves were sampled from four different individuals per plot (two flowering, two non-flowering plants). Leaves were cut off at the base of the petiole and immediately inserted into the sample chamber of the PMS instrument. The chamber was pressurized with a portable N tank, and the amount of pressure needed to squeeze water from the leaf was recorded (higher pressure readings indicate higher levels of water stress at that moment in time).

Analysis

The years of the study were analyzed separately because of different levels of flowering among years (Table S1) and differences in abiotic conditions among years. The year 2015 was cooler and wetter on average compared to 2017 and 2019 [mean high air temperature during the month of flowering (July in 2015 and 2017, August in 2019) = 18.9 °C, 22.9 °C, 22.2 °C, respectively; total precipitation during the month of flowering = 11.91 cm, 6.20 cm, and 2.51 cm, respectively, from a weather station *ca.* 1 km and 40 m higher in elevation from the study site)]. We compared the number of flowers in control plots among the 3 years of the study ($n = 10$ plots per year) using a generalized linear mixed effects model (GLMM) with date as a random intercept term and a negative binomial error distribution to account for overdispersion. Weeks were only included that contained non-zero flower counts. We then compared flower abundance among each pair of years using the Tukey's HSD procedure.

Mean NDVI was calculated for each plot and compared between treatments using a t-test. Mean reflectance (across the three measures for each leaf or flower sample) was compared between flower petals and leaves using a t-test ($n = 10$ plants). We also examined the effect of wavelength on mean reflectance using a linear model with reflectance as a continuous response variable, plant tissue type (leaf vs. flower) as a categorical predictor, and wavelength as a continuous predictor, in addition to the interaction between wavelength and tissue type.

To analyze field reflectance values from 2019, we first calculated an average plot-level reflectance value for each wavelength (across the 20 measurements per plot). We limit the analysis to a maximum wavelength of 1,500 nm, because 90% of the energy in solar emission occurs between 300 and 1,500 nm (few photons arrive at wavelengths greater than 1,500 nm; Gueymard 2004). Based on the spectral data of *Helianthella* leaves and flowers in the lab from 2017, the effect of tissue type on reflectance seemed to depend on whether measurements were in the visible or near-infrared wavelengths. We therefore treated wavelength as a categorical predictor with two levels: visible (338–740 nm) and near-infrared (741–1,500 nm), and included an interaction between treatment and wavelength category in our model. We used a linear mixed effects model (LMM) with mean reflectance as a continuous response, treatment and wavelength as categorical predictors, the interaction between treatment and wavelength category, and plot as a random intercept.

To analyze effects of flower removal on soil temperature, we focused on sunny days during the *Helianthella* flowering period. In 2015 and 2019, we defined sunny days as days with mean lux > 20,000 between the hours of 10:00–14:00 (hours of most intense and direct sunlight). In 2015, the flowering period was defined as 5–31 July (Table S1), and there were 15 sunny days during the flowering period. In 2019, the flowering period was defined as 31 July–14 August (when most flowers were senescing), and there were 13 sunny days during the flowering period. In 2017, the datalogger was inadvertently more shielded from direct solar radiation, and we defined sunny days as days with lux > mean lux (7,500) from all the samples from 10:00–14:00. In 2017, the flowering period was 15–28 July (there were flowers in all plots in 15 July), and there were 7 sunny days during the flowering period. Soil temperature data were then summarized in two ways: (1) mean temperature across all hours of the day, for each plot on each of the sunny days and (2) mean temperature across the two warmest hours of the day (14:00–16:00), for each plot on each of the sunny days, presumably when treatment effects would be most pronounced. Soil temperature was a continuous response variable in a LMM with treatment as a fixed effect and date as a random intercept, to account for repeated samples across days.

We also determined whether soil temperatures differed between treatments before the treatments were applied. In 2015, soil temperature recordings started on 27 June, and we began removing flower buds on 30 June, so our pre-treatment soil temperature records span 27–29 June (mean lux was > 30,000 on all three of these days). In 2017, soil temperature recordings started on 30 June, and we began removing flower buds on 5 July, so pre-treatment soil temperature records span 30 June–4 July (mean lux was 10,029 across these days, with the lowest light day at 9,341 lux). In 2019, soil temperature recordings started on 12 July and buds were removed on 16–17 July, so pre-treatment soil temperature records span 12–15 July (mean lux was > 28,000 on all four of these days). Finally, we also analyze soil temperature across all days during flowering, with the expectation that treatment effects will be weaker when cloudy days are included.

To compare soil moisture between treatments, we first calculated average soil moisture (as volumetric water content: % water) for each plot in each week of the study (soil moisture was measured four times during flowering in 2015 and 2019 and five times during flowering in 2017). We used LMMs with plot-level mean percent water content as a continuous response, treatment as a categorical predictor, and week as a random intercept term. We also examined whether soil moisture differed between treatments in the week before flowers were removed using a t-test with mean percent water as the response and treatment as the predictor.

To analyze whether our measures of water stress, leaf water pressure and Δ13C, differed between treatments, we used LMMs. For each response, plot was a random intercept term to account for multiple leaf samples per plot. We took leaf water pressure measurements across several days, so for this response we first confirmed that measurement date did not affect leaf water pressure (results not shown).

All analyses were conducted in R v. 3.5.1 (R Core Team, 2018). We used the package 'lme4' (Bates *et al.,* 2015) to fit mixed effects models and estimated p-values using the package 'lmerTest' (Kuznetsova *et al.,* 2017). The 'tidyverse' package was used for data handling and figure making (Wickham et al. 2019).

Results

Helianthella flower abundance varied significantly across years, with an average of 95.7 ± 23.6 flowers per plot during peak flowering in 2015, 18.4 ± 7.9 flowers per plot in 2017, and 87.5 ± 5.9 flowers per plot in 2019 (mean ± 1 SE throughout). There were more flowers in 2015 and 2019 compared to 2017 (2015 vs. 2017: $z = -4.19$, $p < 0.001$; 2017 vs. 2019: $z = 1.52$, $p = < 0.001$; 2015 vs. 2019: $z = 1.28$, $p = 0.41$; TableS1). In 2015 and 2019, *Helianthella* flower abundance was five times higher, and flowers covered on average 5.7% and 5.2% of the area of the control plots during peak flowering, respectively, compared to 1.1% in 2017.

On average across light wavelengths, ray petals reflect significantly more light than leaves (flowers: 0.61 ± 0.0047; leaves: 0.29 ± 0.0020; $t = 61.5$, $p < 0.001$). The effect of tissue type depends on wavelength (Table 1; Fig. 2). In 2015, NDVI was significantly higher (i.e., greener) in the removal plots compared to the control plots, although the effect size was small (control = 0.836 ± 0.005, removal = 0.859 ± 0.005; $t = -3.25$, $p = 0.0045$). Estimated plot-level albedo was significantly lower in removal plots than in control plots in all years of the study (2015: $t = 12.84$, $p < 0.0001$; 2017: $t = 2.32$, $p = 0.045$; 2019: $t = 14.84$, $p < 0.0001$; Fig. S1). Finally, there was a significant interaction between wavelength and treatment for reflectance measured in the field in 2019 (Table 1; Fig. 2). Mean reflectance was higher in controls compared to removals, but only in the near IR spectrum (Table 1; Fig. 2). On average, plots with flowers (controls) were only 0.14% more reflective than plots without flowers (removals) in the visible spectrum, whereas plots with flowers were 1.3% more reflective in the near IR spectrum. Across all wavelengths, plots with flowers were on average 0.7% more reflective than plots without flowers (22.1% in removals vs. 22.8% in controls).

There was no difference in pre-treatment soil temperatures between control and removal plots in any years of the experiment (Table S2). On sunny days, soils were significantly warmer in removal plots compared to controls during the flowering period of *Helianthella* in both 2015 and 2019 (Table 1; Fig. 3). Soil temperature in the removal vs. the control plots was on average 0.24 °C warmer in 2015 and 0.72 °C warmer in 2019, across all hours of the day (Fig. 3). During the warmest 2 h of the day, soil temperature was on average 0.48 °C warmer in 2015 and 1.2 °C warmer in 2019 (Fig. 3). Soils were significantly warmer in removal plots across *all* days of the flowering period, but the effect size was slightly smaller compared to sunny days (Table S2). In 2017, when flower abundance was low, there was no effect of flower removal on soil temperatures (Table 1, Fig. 3, Table S2).

Before *Helianthella* began to flower, there was no difference in soil moisture between control and removal plots in any year of the experiment (2015: $t = 0.49$, $p = 0.63$, control: 10.36%; removal: 10.08%; 2017: $t = -0.11$, $p = 0.92$, control:

Table 1 Reflectance of *H. quinquenervis* flower petals vs. leaves in the lab (tissue type), reflectance of meadow surface in flower removal vs. control plots (treatment), and soil temperature in flower removal vs. control plots across all hours of the day (0:00–24:00) and across the warmest 2 h of the day (14:00–16:00). Coefficients are from linear mixed effects models, with wavelength as a categorical predictor (visible vs. near IR) for reflectance. Sample ID is a random intercept term for lab reflectance, plot is a random intercept term for field reflectance, and date is a random intercept term for soil temperature

Response	Year	Coefficients	Estimate ± 1 SE	df	t	p-value
Reflectance in lab	2017	Intercept	0.46 ± 0.0040	26.68	115.78	< 0.0001
		Tissue type	−0.35 ± 0.057	26.68	−62.64	< 0.0001
		Wavelength	0.32 ± 0.0038	15,000	85.66	< 0.0001
		Tissue type × wavelength	0.088 ± 0.0054	15,000	16.36	< 0.0001
Reflectance in field	2019	Intercept	36.58 ± 0.87	11.35	42.05	< 0.0001
		Treatment	−1.23 ± 1.11	11.35	−1.11	0.29
		Wavelength	−30.14 ± 0.24	8136.00	−126.89	< 0.0001
		Treatment × wavelength	1.09 ± 0.30	8136.00	3.60	0.0003
Soil temperature (0:00–24:00)	2015	Intercept	12.52 ± 0.13	16.93	95.18	< 0.0001
		Treatment	0.24 ± 0.061	270.00	3.96	< 0.0001
	2017	Intercept	15.84 ± 0.16	9.09	100.15	< 0.0001
		Treatment	−0.20 ± 0.12	119.00	−1.64	0.11
	2019	Intercept	15.24 ± 0.16	15.76	96.79	< 0.0001
		Treatment	0.72 ± 0.095	247.00	7.51	< 0.0001
Soil temperature (14:00–16:00)	2015	Intercept	16.10 ± 0.20	20.37	79.46	< 0.0001
		Treatment	0.48 ± 0.15	270.00	3.30	0.0011
	2017	Intercept	21.51 ± 0.39	9.56	55.64	< 0.0001
		Treatment	−0.40 ± 0.33	119.00	−1.22	0.23
	2019	Intercept	20.39 ± 0.45	15.13	45.34	< 0.0001
		Treatment	1.20 ± 0.24	247.00	4.94	< 0.0001

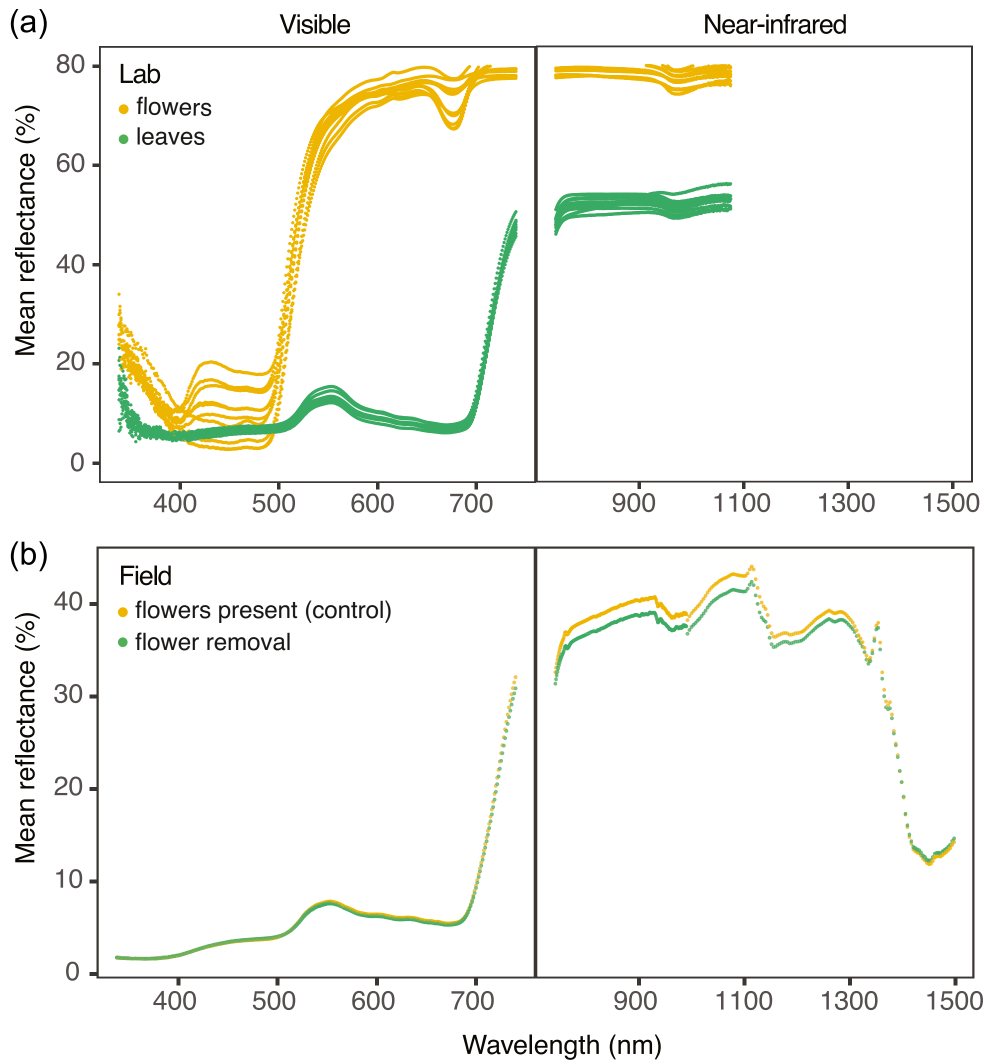

Fig. 2 Reflectance of *Helianthella quinquenervis* (aspen sunflower) (a) leaf and flower tissue (ray petals) in the lab and (b) plots at the meadow scale in the field. (a) Each line is one of ten flower or leaf samples. (b) Each line is the average for each treatment across all plots

4.79%, removal: 4.85%; 2019: t = 0.43, p = 0.68, control: 8.01%, removal: 7.88%). During the *Helianthella* flowering period, soil moisture was lower in removal plots compared to controls in all years of the study (on average 0.96% lower in 2015, 1.09% lower in 2017, and 0.77% lower in 2019; Table 2; Fig. 4).

Flower removal had no significant effect on Δ13C in either year of the experiment (Table 2; Fig. 5), and there was no significant effect of flower removal on leaf water pressure (Table 2).

Discussion

Here we show that the floral displays of a subalpine sunflower species, *H. quinquenervis*, can cover sufficient land surface area to affect reflectance. Although not previously considered in relationships between vegetation and microclimate, flowers may affect surface reflectance, so that meadows without flowers reflect less light and increase absorbance of incoming shortwave solar radiation, thereby warming soils, compared to meadows with flowers. Consistent with this hypothesis, we find warmer soils in the flower removal treatment in the 2 years with high floral abundance (2015 and 2019). In these 2 years, soils were up to 1.2 °C warmer during the warmest part of the day at a soil depth of 8 cm, in plots in which flowers were removed compared to controls. These results provide evidence for a newly documented effect of vegetation on soil microclimates, via flowers. *Helianthella* flower abundance varies across years, and flowers can be absent in some years due to earlier snowmelt and flower bud formation prior to the last spring frost (Inouye, 2008). Thus, the effect of flowers on local microclimate that we present here could be mediated by phenological responses to climate change. Our results suggest that when developing *Helianthella* flowers are frosted as a result of climate change-induced earlier flowering, the albedo

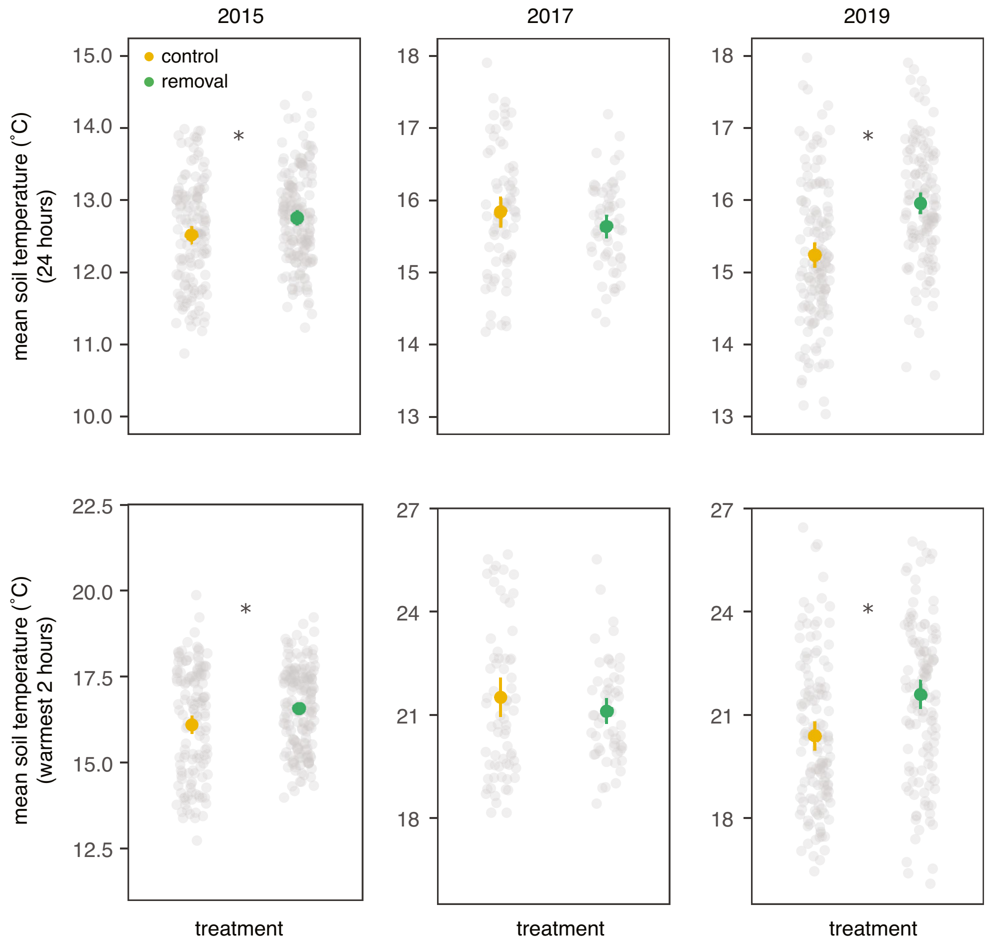

Fig. 3 Each data point represents mean daily soil temperature across all hours of the day (top panels) or across the warmest 2 h of the day (bottom panels) in each study plot. Data points for mean soil temperatures are jittered across the x-axis for visualization. Large dots are means across all plots, and error bars are 95% confidence intervals. Only sunny days during the flowering period of *Helianthella* are included here, but results are consistent when temperatures across all days during the flowering period are included (Table S2). Asterisks indicate significant differences ($p <$ 0.005) between treatments (Table 1). The range of soil temperatures across the y-axis are consistent for each response variable (5 °C range on top panels; 10.5 °C range on bottom panels), but the values differ because 2017 and 2019 were warmer than 2015

of the meadow is reduced, leading to warmer soils, and also perhaps to drier soils, but the cause of soil drying in our study is less clear.

Large differences in the reflectance of plant structures measured in the laboratory translate to fairly small but significant differences in the field, and only in the near-IR spectrum. We expected smaller differences in the field because flowers only

Table 2 Effects of *H. quinquenervis* flower removal on soil moisture (measured as volumetric water content) and plant water stress, measured as an integrated measure across the flowering season: Δ13C (water use efficiency) and as an instantaneous measure: leaf water pressure (lwp). Results for soil moisture are from linear mixed models with week as a random intercept term. Results for water stress are from linear mixed models with plot as a random intercept term

Response	Year	Coefficient	Estimate ± 1 se	df	t	p-value (estimated)
Soil moisture	2015	Intercept	18.57 ± 2.40	3.07	7.74	0.0041
		Treatment	−0.96 ± 0.52	75.00	−1.86	0.066
	2017	Intercept	12.60 ± 0.91	5.39	13.77	< 0.0001
		Treatment	−1.09 ± 0.35	95.00	−3.07	0.0028
	2019	Intercept	13.04 ± 2.09	3.04	6.25	0.0079
		Treatment	−0.77 ± 0.35	75.00	−2.21	0.030
Δ13C	2015	Intercept	−28.58 ± 0.12	20.00	−230.81	< 0.0001
		Treatment	0.06 ± 0.18	20.00	0.33	0.75
Δ13C	2017	Intercept	−27.93 ± 0.13	20.00	−219.10	< 0.0001
		Treatment	−0.11 ± 0.18	20.00	−0.60	0.55
lwp	2017	Intercept	14.99 ± 1.07	20.00	13.98	< 0.0001
		Treatment	2.13 ± 1.52	20.00	1.40	0.18

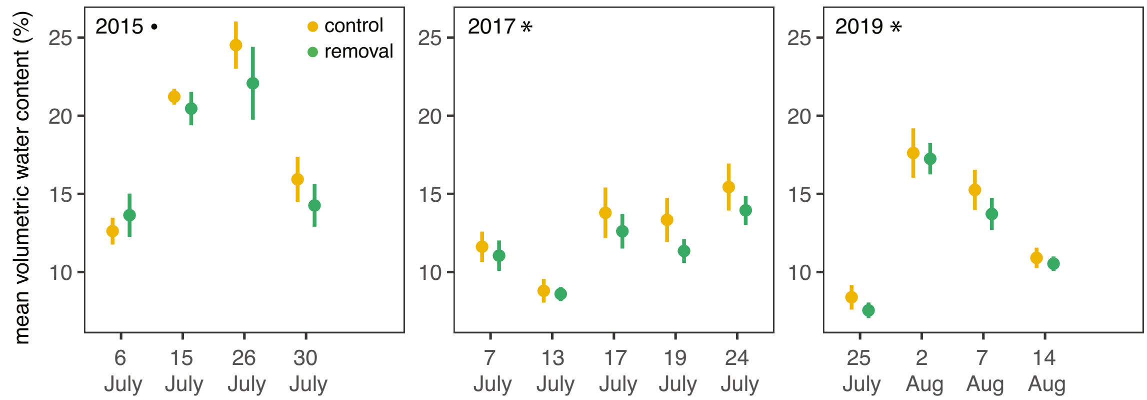

Fig. 4 Soil moisture, measured as volumetric water content, in control and flower removal plots for each sample date during the flowering period of *Helianthella*. Colored dots are plot-level means for each week, and error bars are 95% confidence intervals. Asterisks denote significant treatment effects at $p < 0.05$, and black dot at $p < 0.075$ (see Table 2 for statistical results). Soil moisture measurements are not directly comparable between years because the probe length of the soil moisture meter differed between years (12 cm in 2015 vs. 7.62 cm in 2017 and 2019; see Methods)

cover an estimated 5–6% of the area of our plots (in years with little to no frost damage). The larger difference in meadow-scale reflectance in the near-IR wavelengths could be explained by differences in reflectance between *Helianthella* flower vs. leaf tissue (Fig. 2). In the lab, flowers exhibit consistently higher reflectance values than leaves in the near-IR spectrum. In contrast, in the 400–500-nm range of the visible spectrum, some flower samples are even less reflective than leaves. However, the difference in reflectance between flowers and leaves is most pronounced between 550 and 700 nm, and it is unclear why this does not translate to meadow-scale reflectance over the same wavelengths. It could be that much of the light in those wavelengths is absorbed or transmitted in the field. Many other aspects of vegetation affect albedo besides color, such as scattering of incoming shortwave solar radiation by the leaf canopy, leaf and stem area index, solar elevation, and mass per unit area of plant tissue (Sellers 1985; Dorman and Sellers 1989; Bonan 1997; Hollinger et al. 2010). These other properties of vegetation also likely explain why the estimated difference in reflectance between plots with flowers vs. plots without flowers is higher than the measured value (estimated 1.7% vs. measured 0.7% more reflective with flowers; Fig. 2, S1). For example, *Helianthella* flowers face roughly east throughout the day, as opposed to being heliotropic like other sunflower species (AMI, personal observation), and we did not account for this in our simple, isotropic estimation of reflectance. The average reflectance measurements from our study are consistent with values reported for grasslands in Hollinger et al. (2010).

Although seemingly small in magnitude, the difference in measured reflectance between treatments at peak flowering is associated with warmer soils, as predicted. We expect to see the largest effects of flower removal on soil microclimates when flower abundance is high, because there are more sunflowers present to reflect sunlight. Indeed, mean daily soil temperatures were only warmer in removal plots in 2015 and 2019, when flower abundance was approximately five times higher than that in 2017. The effect of flower removal on soil temperatures is detectable across days with various levels of sunlight and across all hours of the day, and the warming effect is slightly larger when (i) only sunny days are considered and (ii) the warmest 2 h of the day are

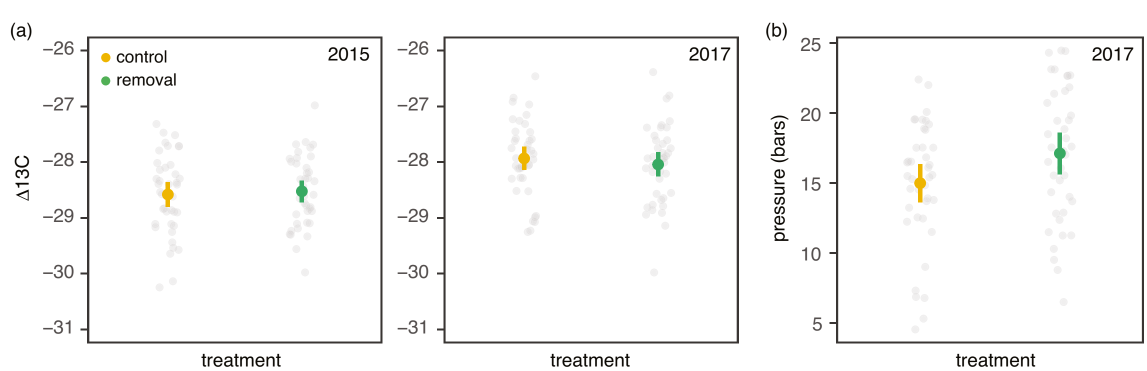

Fig. 5 Two measures of plant water stress, **a** Δ13C and **b** leaf water pressure, in control and flower removal plots. Small dots are for single plants in each treatment ($n = 4$ plants per plot; $n = 10$ plots per treatment). Large dots are plot-level means, and error bars are 95% confidence intervals. Points are jittered across the x-axis for ease of visualization. Flower removal did not significantly affect plant water stress

considered compared to all hours of the day (Table S2, Fig. 3). These results provide support for the interpretation that a reduction in surface albedo causes the increase in soil temperatures. That being said, we also emphasize that warming effects are smaller when all days are included in analyses, whether sunny or not. Soil warming is nonetheless still detectable across the flowering season. Furthermore, soil warming occurs at a depth of 8 cm below the soil surface, and we expect that the effect would be larger near the soil surface. Finally, it is also possible that longwave radiation (3–100 μm) could have affected soil temperature, via flowers, depending on whether flowers affect the amount of longwave radiation coming in during the day relative to the amount of longwave radiation going out at night. This is an important aspect for future studies to consider.

Soil warming is more pronounced in 2019 than in 2015, despite similar flower abundance between these 2 years. It is unclear why the warming effect was more pronounced in 2019, but there was a higher proportion of sunny days during *Helianthella* flowering in 2019 than in 2015 (2015: 15/25 = 60% days; 2019: 13/16 = 81.3% days). It could be that the shorter flowering duration with a higher proportion of sunny days allowed heat to accumulate in the soils more so in 2019 than in 2015. Additionally, 2015 was 4.7 times wetter than 2019 (11.91 cm vs. 2.51 cm of rainfall, respectively), and in moist soils a lower albedo is expected to first dry the soil before soil temperature starts to warm, due to the Bowen ratio (the ratio of sensible to latent energy flux) (Harte et al. 1995). Thus, the wetter soils of 2015 could have moderated the rise in soil temperature.

Soil moisture was drier by *ca.* 1% in flower removal plots across all years of the study, even though soil temperature only differed between treatments in 2 of the 3 years. This result suggests that soil moisture is responding to flower removal independently from changes in soil temperature. It is possible that either changes in evapotranspiration or reallocation of resources to growth may have caused the decrease in soil moisture, but these hypotheses require further study. Evapotranspiration could have increased in the flower removal plots in response to reduced albedo, which could reduce soil moisture in the absence of a change in soil temperature (i.e., latent heat). We did not measure evapotranspiration in this study, but 2017 was the warmest year of the study; mean max air temperature was 4 °C warmer than 2015 and 0.7 °C warmer than 2019, on average, thereby creating a higher evaporative demand, which could potentially explain why we detect drier soils in removal plots even with fewer flowers in 2017. It is also expected that *Helianthella* plants will allocate more resources to growth in flower removal plots in the absence of the opportunity to reproduce (Obeso 2002; Iler et al. 2019). At the same time, our experimental flower removal probably induced a response to herbivory, which typically reduces photosynthesis and plant growth via the release of secondary compounds (*reviewed in* Nabity et al. 2008). Therefore, it seems unlikely that plants would transpire more in the flower removal plots due to increased photosynthesis and vegetative growth. Instead, reproductive structures are likely a source of water loss for these plants (Galen et al. 1999), because of respiration by floral structures, which is especially pronounced during seed filling (Conor and Hall 1997). Water loss through flowers should bias our study against finding lower soil moisture in flower removal plots.

Overall, we do not find evidence that drier soils translate into increased water stress in *Helianthella*. Water stress in our focal species is only one of several ecological consequences of warmer and drier soils (Field et al. 1992). Warmer soils are associated with reduced plant and insect diversity and changes in community composition (Robinson et al. 2018). Warmer soils can also lead to increased soil respiration, faster rates of soil carbon decomposition, and lower storage capacity of carbon in soils (Teramoto et al. 2016; Romero-Olivares et al. 2017; Noh et al. 2017). Warmer soils tend to result in increases in primary production, although decreases are also observed (Rustad et al. 2001). Reductions in soil moisture have the opposite effect of soil warming, leading to decreases in soil respiration; soil drying may therefore constrain responses of soil respiration to warmer soil temperatures in some ecosystems (Liu et al. 2009; Falloon et al. 2011; Suseela et al. 2011). Soil warming of a comparable magnitude to our study (0.7–1.1 °C) in the Arctic has been shown to lead to earlier senescence (Livensperger et al. 2019). Therefore, warmer soils could potentially lead to earlier senescence for *Helianthella* and other plant species in our study, especially because soil warming occurs during the second community-level peak in flower abundance (CaraDonna et al. 2014), after which plants transition to senescence. Whether the magnitude of soil warming and drying that we find here (*ca.* 0.5–1.2 °C warmer and 1% drier) affects these other ecological relationships and processes requires much further study, but the warming we observe falls within the low range of warming effects from soil warming experiments (Romero-Olivares et al. 2017). That being said, vegetation has been shown to have larger effects on soil microclimate than what we show here. For example, the presence of herbaceous plants can decrease soil moisture by 7–10% compared to soils without vegetation or to soils with dormant plants (Eviner 2004; Liancort et al. 2012). Plant cover can also reduce soil temperature by up to 4 °C (Gornall et al. 2011). Any flower-mediated effects on microclimate should be more ephemeral than effects from leaves, because flowers tend to be present for fewer days and cover less surface area than leaves.

This study was motivated by previous research and observations showing that earlier snowmelt can lead to earlier flowering, increased frost damage to developing flower buds, reduced flower abundance, and altered appearance of the meadow (Inouye, 2008; Iler *et al.*, 2019; Fig. 1). There are many additional scenarios in which flowers are likely to affect land surface albedo. Flowers could alter land surface albedo as plant species naturally come into and out of bloom across a growing season. The effects of flower albedo should be greatest for species that are widespread and have flowers that cover a large amount of surface area, for example by producing many, small flowers or large flowers. Therefore, the flowers of many invasive plant species and crops are good candidates for further research on the question of whether flowers affect land surface albedo (e.g., rapeseed, or *Brassica napus*, and cultivated sunflowers, or *Helianthus annuus*). Additionally, *Helianthella* is not the only species at our study site with frost-sensitive flower buds or flowers (Inouye 2008; CaraDonna and Bain 2016), and spring-blooming fruit trees are especially prone to widespread frost damage, a risk that is predicted to increase as the climate changes (Labe et al. 2017). Frost damage in these other species could potentially affect land surface albedo, especially in cultivated fruit trees that produce abundant, white flowers often in large, continuous patches (e.g., apple, cherry, and almond orchards). Ultimately, whether alterations in flower albedo affect microclimate in other study systems should depend on the length of flowering time, the density and spatial extent of the bloom, and the color and other optical properties of flowers relative to the surrounding land surface before, during, and after flowering.

Conclusions

It is perhaps unsurprising that the effects of flowers on land surface albedo have been previously unstudied. The most obvious effect of vegetation on the land surface is green-up and senescence; it makes sense to focus on this aspect of vegetation when modeling the Earth's land surface because of trade-offs between computational efficiency and ecological complexity. Yet, a future research direction motivated by our results is to quantify the effect of flowers on remotely sensed land surface albedo (e.g., through satellite-generated images), and to quantify potential feedbacks of these changes in microclimate on climate. Recent developments in remote-sensing technology should allow for the flowers of many plant species to be correctly identified with machine-learning algorithms (Davis et al. 2020; Vanbrabant et al. 2020). Data should already be available to examine the effects of flowers on surface albedo at larger spatial scales than those considered in our study. Although it is possible that something else related to flower removal could cause the change in soil microclimates in this local-scale study, the results support the interpretation that reduced albedo in the absence of *Helianthella* flowers leads to warmer, and perhaps drier, soils. Humans have the potential to alter the albedo of the landscape and therefore the Earth's microclimate and climate via multiple environmental changes, all of which could be mediated by flowers: climate change, the spread of invasive plants, and agriculture.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00484-021-02159-0.

Acknowledgements Thanks to B. Blonder, R. Kapas, and K. Williams for the use of and assistance with their spectroradiometers, to D. Inouye for sharing light data, and to B. Barr for sharing weather data from his weather station in Gothic, CO. Special thanks to A. Henderson for training on use of a field spectroradiometer and assistance with data collection. We are additionally thankful to M. Holmstrup, T. Høye, J. Harte, and the Iler-CaraDonna lab group for helpful discussions.

Author contribution AMI and ABC conceptualized and designed the research; AMI, ABC, ASW, and HS collected data, AMI analyzed the data, AMI wrote the manuscript, and all authors edited the manuscript.

Funding This work was supported by the COFUND-Marie Curie Fellowships (AIAS-COFUND program, Grant 609033) awarded to AMI and ABC, and a Rocky Mountain Biological Laboratory Fellowship in memory of Dr. Navjot Sodhi and his contribution to Conservation Biology, awarded to AMI.

Data availability Iler, Amy (2020), Effects of flowers on land surface albedo and soil microclimate, Dryad, Dataset, https://doi.org/10.5061/dryad.zcrjdfn8m.

Code availability Iler, Amy (2020), Effects of flowers on land surface albedo and soil microclimate, Dryad, Dataset, https://doi.org/10.5061/dryad.zcrjdfn8m.

Declarations

Conflict of interest The authors declare no competing interests.

References

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Boggs CL, Inouye DW (2012) A single climate driver has direct and indirect effects on insect population dynamics. Ecol Lett 15:502–508. https://doi.org/10.1111/j.1461-0248.2012.01766.x

Bonan GB (1997) Effects of land use on the climate of the United States. Clim Chang 37:449–486. https://doi.org/10.1023/A:1005305708775

Bramer I, Anderson BJ, Bennie J, Bladon AJ, De Frenne P, Hemming D (2018) Advances in monitoring and modelling climate at ecologically relevant scales. Adv Ecol Res 58:101–161. https://doi.org/10.1016/bs.aecr.2017.12.005

CaraDonna PJ, Bain JA (2016) Frost sensitivity of leaves and flowers of subalpine plants is related to tissue type and phenology. J Ecol 104:55–64. https://doi.org/10.1111/1365-2745.12482

CaraDonna PJ, Iler AM, Inouye DW (2014) Shifts in flowering phenology reshape a subalpine plant community. Proc Natl Acad Sci 111:4916–4921. https://doi.org/10.1073/pnas.1323073111

Cleland EE, Chuine I, Menzel A et al (2007) Shifting plant phenology in response to global change. Trends Ecol Evol 22:357–365. https://doi.org/10.1016/j.tree.2007.04.003

ConnorDJ, Hall AJ (1997) Sunflower Physiology. In: Schneiter AA (ed) Sunflower Technology and Production, Volume 35, Academic Press, Inc., New York, pp 113–182

Davis CC, Champ J, Park DS, Plant IB et al (2020) A new method for counting reproductive structures in digitized herbarium specimens using Mask R-CNN. Front Plant Sci 11:1–13. https://doi.org/10.3389/fpls.2020.01129/full

De Frenne P, Zellweger F, Rodríguez-Sánchez F, Scheffers BR, Hylander K, Luoto M et al (2019) Global buffering of temperatures under forest canopies. Nat Ecol Evol 3:744–749. https://doi.org/10.1038/s41559-019-0842-1

Dorman JL, Sellers PJ (1989) A global climatology of albedo, roughness length and stomatal resistance for atmospheric general circulation models as represented by the Simple Biosphere Model. J Appl Meteorol 28:833–855

Edwards MM, Richardson AJA (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884. https://doi.org/10.1038/nature02808

Eviner VT (2004) Plant traits that influence ecosystem processes vary independently among species. Ecology 85:2215–2229. https://doi.org/10.1890/03-0405

Falloon P, Jones CD, Ades M, Paul K (2011) Direct soil moisture controls of future global soil carbon changes: an important source of uncertainty. Glob Biogeochem Cycles 25:GB3010. https://doi.org/10.1029/2010GB003938

Farquhar GD, Ehleringer J, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol 40:503–537. https://doi.org/10.1146/annurev.pp.40.060189.002443

Field CB, Chapin FS III, Matson PA, Mooney HA (1992) Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. Annu Rev Ecol Syst 23:201–236

Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. Proc Natl Acad Sci 104:1278–1282

Galen C, Sherry RA, Carroll AB (1999) Are flowers physiological sinks or faucets? Costs and correlates of water use by flowers of *Polemonium viscosum*. Oecologia 118:461–470

Gornall JL, Woodin S, Jónsdóttir IS, van der Wal R (2011) Balancing positive and negative plant interactions: how mosses structure vascular plant communities. Oecologia 166:769–782. https://doi.org/10.1007/s00442-011-1911-6

Gueymard CA (2004) The sun's total and spectral irradiance for solar energy applications and solar radiation models. Sol Energy 76:423–453

Harte J, Torn MS, Chang F-R, Feifarek B, Kinzig AP, Shaw R, Shen K (1995) Global warming and soil microclimate: results from a meadow-warming experiment. Ecol Appl 5:132–150. https://doi.org/10.2307/1942058

Hollinger DY, Ollinger SV, Richardson AD et al (2010) Albedo estimates for land surface models and support for a new paradigm based on foliage nitrogen concentration. Glob Chang Biol 16:696–710. https://doi.org/10.1111/j.1365-2486.2009.02028.x

Iler AM, Compagnoni A, Inouye DW, Williams JL, CaraDonna PJ, Anderson A, Miller TEX (2019) Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. J Ecol 279:3843–3813. https://doi.org/10.1111/1365-2745.13146

Iler AM, Inouye DW, Schmidt NM, Høye TT (2017) Detrending phenological time series improves climate-phenology analyses and reveals evidence of plasticity. Ecology 98:647–655. https://doi.org/10.1002/ecy.1690

Inouye DW (2000) The ecological and evolutionary significance of frost in the context of climate change. Ecol Lett 3:457–463

Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362

IPCC (Intergovernmental Panel on Climate Change] 2014: Climate Change 2014: AR5 Synthesis Report

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest Package: tests in linear mixed effects models. J Stat Softw 82:1–26

Labe Z, Ault T, Zurita-Milla R (2017) Identifying anomalously early spring onsets in the CESM large ensemble project. Clim Dyn 48:3949–3966. https://doi.org/10.1007/s00382-016-3313-2

Lambers H, Chapin FS, Pons TL (1998) Plant physiological ecology. Springer-Verlag Inc., New York

Liancourt P, Sharkhuu A, Ariuntsetseg L, Boldgiv B, Helliker BR, Plante AF, Petraitis PS, Casper BB (2012) Temporal and spatial variation in how vegetation alters the soil moisture response to climate manipulation. Plant Soil 351:249–261. https://doi.org/10.1007/s11104-011-0956-y

Linderholm HW (2006) Growing season changes in the last century. Agric For Meteorol 137:1–14. https://doi.org/10.1016/j.agrformet.2006.03.006

Liu W, Zhang Z, Wan S (2009) Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. Glob Chang Biol 15:184–195. https://doi.org/10.1111/j.1365-2486.2008.01728.x

Livensperger C, Steltzer H, Darrouzet Nardi A, Sullivan PF, Wallenstein M, Weintraub MN (2019) Experimentally warmer and drier conditions in an Arctic plant community reveal microclimatic controls on senescence. Ecosphere 10:e02677–e02616. https://doi.org/10.1002/ecs2.2677

Menzel A, Sparks TH, Estrella N et al (2006) European phenological response to climate change matches the warming pattern. Glob Chang Biol 12:1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Nabity PD, Zavala JA, DeLucia EH (2008) Indirect suppression of photosynthesis on individual leaves by arthropod herbivory. Ann Bot 103:655–663. https://doi.org/10.1093/aob/mcn127

Noh NJ, Kuribayashi M, Saitoh TM, Muraoka H (2017) Different responses of soil, heterotrophic and autotrophic respirations to a 4-year soil warming experiment in a cool-temperate deciduous broadleaved forest in central Japan. Agric For Meteorol 247:560–570. https://doi.org/10.1016/j.agrformet.2017.09.002

Obeso JR (2002) The costs of reproduction in plants. New Phytol 155:321–348. https://doi.org/10.1046/j.1469-8137.2002.00477.x

Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Glob Chang Biol 13:1860–1872

Peñuelas J, Rutishauser T, Filella I (2009) Phenology feedbacks on climate change. Science 324:887–888. https://doi.org/10.1126/science.1171542

R Core Team (2018) R: a language and environment for statistical computing. In: R Foundation for Statistical Computing. Austria. URL, Vienna https://www.R-project.org/

Richardson AD, Andy Black T, Ciais P, Delbart N, Friedl MA, Gobron N, Hollinger DY, Kutsch WL, Longdoz B, Luyssaert S, Migliavacca M, Montagnani L, William Munger J, Moors E, Piao S, Rebmann C, Reichstein M, Saigusa N, Tomelleri E, Vargas R, Varlagin A (2010) Influence of spring and autumn phenological transitions on forest ecosystem productivity. Philos Trans R Soc Lond B 365:3227–3246. https://doi.org/10.1098/rstb.2010.0102

Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. Agric For Meteorol 169:156–173. https://doi.org/10.1016/j.agrformet.2012.09.012

Robinson SI, McLaughlin ÓB, Marteinsdóttir B, O'Gorman EJ (2018) Soil temperature effects on the structure and diversity of plant and invertebrate communities in a natural warming experiment. J Anim Ecol 87:634–646. https://doi.org/10.1111/1365-2656.12798

Romero-Olivares AL, Allison SD, Treseder KK (2017) Soil microbes and their response to experimental warming over time: a meta-analysis of field studies. Soil Biol Biochem 107:32–40. https://doi.org/10.1016/j.soilbio.2016.12.026

Rustad L, Campbell J, Marion G et al (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562. https://doi.org/10.1007/s004420000544

Sellers PJ (1985) Canopy reflectance, photosynthesis and transpiration. Int J Remote Sens 6:1335–1372. https://doi.org/10.1080/01431168508948283

Sparks TH, Menzel A (2002) Observed changes in seasons: an overview. Int J Climatol 22:1715–1725. https://doi.org/10.1002/joc.821

Stenson GB, Hammill MO (2014) Can ice breeding seals adapt to habitat loss in a time of climate change? ICES J Mar Sci 71:1977–1986. https://doi.org/10.1093/icesjms/fsu074

Suseela V, Conant RT, Wallenstein MD, Dukes JS (2011) Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. Glob Chang Biol 18:336–348. https://doi.org/10.1111/j.1365-2486.2011.02516.x

Teramoto M, Liang N, Takagi M, Zeng J, Grace J (2016) Sustained acceleration of soil carbon decomposition observed in a 6-year warming experiment in a warm-temperate forest in southern Japan. Sci Rep 6:1–14. https://doi.org/10.1038/srep35563

Theobald EJ, Breckheimer I, HilleRisLambers J (2017) Climate drives phenological reassembly of a mountain wildflower meadow community. Ecology 98:2799–2812. https://doi.org/10.1002/ecy.1996

Vanbrabant Y, Delalieux S, Tits L, Pauly K, Vandermaesen J, Somers B (2020) Pear flower cluster quantification using RGB drone imagery. Agronomy 10:407–426. https://doi.org/10.3390/agronomy10030407

Weber WA (1952) The genus *Helianthella* (Compositae). Am Midl Nat 48:1–35. https://doi.org/10.2307/2422128

Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the tidyverse. J Open Source Softw 4:1686. https://doi.org/10.21105/joss.01686

Wilson KB, Hanson PJ, Baldocchi D (2000) Factors controlling evaporation and energy partitioning beneath a deciduous forest over an annual cycle. Agric For Meteorol 102:83–103. https://doi.org/10.1016/S0168-1923(00)00124-6

Zellweger F, Coomes D, Lenoir J, Depauw L, Maes SL, Wulf M, Kirby KJ, Brunet J, Kopecký M, Máliš F, Schmidt W, Heinrichs S, den Ouden J, Jaroszewicz B, Buyse G, Spicher F, Verheyen K, de Frenne P (2019) Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. Glob Ecol Biogeogr 28:1774–1786. https://doi.org/10.1111/geb.12991