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Temperature-driven homogenization of an ant community over 60 years in a montane ecosystem

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Abstract

Identifying the mechanisms underlying the changes in the distribution of species is critical to accurately predict how species have responded and will respond to climate change. Here, we take advantage of a late-1950s study on ant assemblages in a canyon near Boulder, Colorado, USA, to understand how and why species distributions have changed over a 60-year period. Community composition changed over 60 years with increasing compositional similarity among ant assemblages. Community composition differed significantly between the periods, with aspect and tree cover influencing composition. Species that foraged in broader temperature ranges became more widespread over the 60-year period. Our work highlights that shifts in community composition and biotic homogenization can occur even in undisturbed areas without strong habitat degradation. We also show the power of pairing historical and contemporary data and encourage more mechanistic studies to predict species changes under climate change.

KEYWORDS

climate change, community resampling, foraging temperature, homogenization, Hymenoptera: Formicidae, occupancy dynamics, Rocky Mountains

INTRODUCTION

Understanding how communities respond to anthropogenic climate change is critical as global climate change is increasing mean temperatures (Easterling et al., 2000; IPCC, 2021; Jentsch & Beierkuhnlein, 2008; Vasseur et al., 2014). Species respond to changing environments in a variety of ways, including shifting their geographic ranges (e.g., along latitudinal or elevational gradients; Parmesan et al., 1999), acclimating (Somero, 2010), or adapting (Hoffmann & Sgrò, 2011) to new conditions, or becoming locally extirpated. As a result of climate change, some species have experienced range shifts (Chen et al., 2011; Diamond, 2018; Hickling et al., 2006), while others have incurred range losses (Davis & Shaw, 2001; Devictor et al., 2012; Kerr et al., 2015).

Changing temperature regimes in the Anthropocene have been linked to species declines (Halsch et al., 2021; IUCN, 2019), and many predict a continued loss of biodiversity in the future (Thomas et al., 2004; Turvey & Crees, 2019). There is increasing evidence that insect species are declining in abundance (Hallmann et al., 2017; Lister & Garcia, 2018; Seibold et al., 2019; Wagner, 2020; Wagner et al., 2021). Many of the changes in insect communities are likely the result of climate change (Halsch et al., 2021; Parr & Bishop, 2022).

Ants are a useful taxon for studying the impacts of climate change on biodiversity because they occur in almost all habitat types, are ectothermic, and vary in their environmental tolerances (Diamond et al., 2012; Kaspari et al., 2015; Nowrouzi et al., 2016; Roeder et al., 2021). Additionally, temperature dictates the

functioning of ant colonies by influencing metabolic rates and restricting activity periods for foraging (Roeder et al., 2022). Pairing historical studies on distributions with contemporary sampling and environmental data can provide a unique opportunity to examine how environmental change has affected communities over long time scales (Kerr et al., 2015; Lewthwaite & Mooers, 2022; Resasco et al., 2014; Sanders et al., 2023; Tingley et al., 2009). Historical data sets provide us baseline data to compare against and help us understand changes in species phenology, genotypes, distributions, and interactions (Davis et al., 2023; Pyke et al., 2012, 2016; Sanders et al., 2023). Examining long-term community trends provides the ability to identify how climate change is contributing to current biodiversity loss (Hooper et al., 2012). However, confounding factors often complicate our ability to understand the ecological effects of climate change (Parmesan, 2006). For example, tree cover has increased in the Colorado Front Range (Rodman et al., 2019), likely due to land-use and fire-suppression practices (Veblen et al., 2000), meaning that changes to contemporary communities could be driven by a combination of climate change and increased tree cover and that contemporary communities may be experiencing greater temperature buffering than they have historically (De Frenne et al., 2019; Kašpar et al., 2021).

We examined changes in an ant community over a 60-year period. We compared contemporary community composition and species occurrence data to a survey conducted in the 1950s by Browne and Gregg (1969) in Gregory Canyon near Boulder, Colorado, USA. Gregory Canyon provides an interesting opportunity to examine community change over time, because it is a protected natural area that has remained largely unaltered by land-use change and urbanization over the last 60 years allowing us to understand associations between climate and community change. We specifically posed the following questions:

- 1. Have ant species occurrences and distributions in Gregory Canyon changed since the sampling done by Browne and Gregg (1969) in 1957–1958?
- 2. Does temperature explain the changes in ant species occurrence?
- 3. Does change in tree cover relate to changes in ant species occurrence?

MATERIALS AND METHODS

Study site

Robert E. Gregg was an entomologist and expert on ants (especially the ants of Colorado) who was a professor

at the University of Colorado (CU) Boulder. John T. Browne was a Master's graduate student of Gregg's who assisted him in documenting the local ant community. Browne and Gregg (1969) examined the distributions of ants in Gregory Canyon near Boulder, Colorado, USA (39.999143, -105.302537) in 1957 and 1958 to determine the differences among ant assemblages due to the differing habitats created by slope aspect. This canyon spans an elevational range of 1645 to 2485 m. Due to the differences in temperature and moisture based on slope aspect, specifically the north-facing slopes, south-facing slopes, and canyon bottom (Figure 1), Browne and Gregg (1969) sought to determine how the differing environmental conditions within the canyon influenced species representation. The records of collection sites in Gregory Canyon, dates, and methods were documented in Browne and Gregg (1969). They found that based on aspect, the ant assemblages varied (Appendix S1: Table S1) due to differences in species-specific environmental tolerances. Browne and Gregg (1969) determined that the environment influenced local distributions of species in Gregory Canyon.

Gregory Canyon is currently maintained by the City of Boulder Open Space and Mountain Parks. We resampled the same 33 sites as in Browne and Gregg (1969). Sites ranged in size from 1.9 to 10.0 ha (mean = 4.62 ± 1.95). Gregory Canyon has variable topography and habitat types were defined by Browne and Gregg (1969) by slope aspect (13 south-facing slope sites, 14 north-facing slope sites, and six canyon bottom sites). North-facing slopes are characterized by a forested habitat with lower temperatures and higher soil moisture and are dominated by ponderosa pine (Pinus ponderosa) and lodgepole pine (Pinus contorta ssp. Latifolia) and Douglas fir (Pseudotsuga menziesii) at higher elevations. South-facing slopes are characterized by lower soil moisture content and higher temperatures. The vegetation on south-facing slopes is generally mixed shrubland and perennial graminoids with Kentucky bluegrass (Poa pratensis), Canadian brome (Bromopsis canadensis), yucca (Yucca glauca), and New Mexico prickly-pear cactus (Opuntia phaeacantha). Canyon bottoms are characterized by riparian vegetation, including narrowleaf cottonwood (Populus angustifolia), willow (Salix spp.), American plum (Prunus americana), and wild raspberry (Rubus idaeus).

Environmental conditions

Browne and Gregg (1969) collected data to characterize the abiotic environment across Gregory Canyon. To measure percentage soil moisture, Browne and Gregg (1969) also collected soil samples along two north–south transects. Each transect consisted of a collection point for each



FIGURE 1 Visualizations of study site located in Gregory Canyon near Boulder, CO, USA. (A) Map of sampling sites from Browne and Gregg (1969), with sampling sites in red. (B) Georeferenced sampling sites overlaid on 2015 satellite imagery (site outlines adapted from Browne and Gregg [1969]). (C) Photograph of entrance to Gregory Canyon included in Browne and Gregg (1969). (D) A 2020 photograph of entrance of Gregory Canyon from roughly the same location. (E) Conceptual figure of habitat created by aspect depicting savanna-type habitat on south-facing slopes due to higher sun exposure and denser forested habitat on north-facing slopes where sun exposure is more reduced. Publication map in panel (A) reproduced with permission from University of Colorado Boulder. Historical photo in panel (C) courtesy of University of Colorado Boulder. Photo credit for panel (D): Julian Resasco.

aspect, north-facing, south-facing, and canyon bottom. Soil samples were collected three times in 1958 (28 May, June, and July) at each transect and transect point. Three samples at a depth of 12.7 cm (5 in.) were taken from each point in both transects from underneath medium-sized rocks. Samples were dried in an oven at 105°C and the weight (in grams) was recorded. To compare changes in soil moisture between time periods, we collected soil samples on the same calendar dates recorded in Browne and Gregg (1969) following the same methods. Percentage soil moisture was calculated employing the same methods as Browne and Gregg (1969) using the gravimetric soil water content equation (Gravimetric soil water content (%) = [mass of moist soil (g) - mass of oven-dried soil(g)/mass of oven-dried soil $(g) \ge 100$. To determine whether percentage soil moisture differed among aspects and time periods, we ran a two-way ANOVA with percentage soil moisture as the response variable and time period and aspect as the predictor variables. We then used a post hoc Tukey test to determine which aspects differed. All analyses were run in R version 4.0.2 (R Core Team, 2022).

We used a local weather station (NOAA, 2019) to characterize climatic changes in the study area between the historical and contemporary sampling periods. The weather station (GHCND:USC00050848) is located ~1.7 km from the closest sampling site and 4 km from the farthest sampling site. Maximum daily temperature was acquired from the weather station for the sampling season (1 May-31 October). To determine how climatic variables differed among all sampling years (1957, 1958, 2021, 2022) throughout the sampling season and among aspects, we used a quadratic regression with maximum daily air temperature recorded from the local weather station as the response variable and year, day of year, and day of year squared as predictor variables. We used the R package emmeans (Lenth, 2022) to obtain estimated marginal means. Additionally, we used the weather station data from 1900 to present to examine temperature trends over time. We averaged maximum daily temperatures for each year and calculated the temperature departure from a baseline average for 1900–1930 using a linear regression.

Question 1: Have ant species occurrences and distributions in Gregory Canyon, Boulder, Colorado, USA, changed since sampling done by Browne and Gregg (1969) in 1957–1958?

Historical field collections

Sites were sampled from late May to late October in 1957 and 1958 by Browne and Gregg (1969). Ants were hand collected, a method of direct sampling (Bestelmeyer et al., 2000), by Browne and Gregg (1969) by opening soil or thatch nests, turning rocks or logs, and picking up foragers, which is an effective method of sampling ant diversity (Agosti et al., 2000). Browne and Gregg (1969) conducted collections between 8:30 a.m. and 3:00 p.m., but the length of time at sampling sites was not specified. Browne and Gregg (1969) identified ants to species using Creighton (1950) and stored them in 85% ethyl alcohol. To compare species between time periods, we updated Browne and Gregg's (1969) species determinations to contemporary names. Species identifications were compared to those of Gregg's using his collections housed at the Field Museum in Chicago, Illinois, as well as the synoptic collection at the CU Boulder Museum of Natural History to ensure that species-level identifications matched.

Georeferencing and occurrence records

Browne and Gregg (1969) included a map of Gregory Canyon and the surrounding area, with polygons of their sampling locations (Figure 1). To determine the locations of the sites and ant species collections based on a modern coordinate system, we used the Georeferencing Tool in ArcGIS (Figure 1; ESRI, 2011). We projected the historical maps to NAD 83, UTM 13N. Other layers used for georeferencing were a City of Boulder Open Space and Mountain Parks streams and ditches laver (City of Boulder, 2021), a Bureau of Land Management Public Land Survey System (PLSS) First division layer (BLM, 2018), and National Agriculture Imagery Program (NAIP) imagery from 2015 (United States Forest Service, National Agriculture Imagery Program 2015). Eight control points (locations that can be accurately identified on the historical map and in contemporary imagery and coordinates) were used with a second-order polynomial transformation. To verify and adjust images, the control points used included landmarks, road intersections, PLSS lines, and stream confluences. Polygons of the sampling sites and points of species collections were then able to be created and plotted onto a contemporary projected coordinate system to define sampling locations. After determining site locations via georeferencing, one record of Pogonomyrmex occidentalis was removed from the historical data set as it did not correspond to any site or collection date. Additionally, the record of Ponera pennsylvanica was removed from the historical data set as it was collected in 1956 as part of a different study (Borchert, 1956), so it was not associated with any of Browne and Gregg's (1969) sites, and its precise location could not be determined.

Contemporary field collections

We sampled each site on approximately the same date (SD = 1.22 days) on which it was sampled in the original study from late May to late October of 2021 for ~6 h between 8:00 a.m. and 5:00 p.m. We collected ants using the same methods as Browne and Gregg (1969) described earlier. Ants were taken back to the lab for curation and species-level identification using dichotomous keys (AntWiki, 2020; Gregg, 1963; Mackay & Mackay, 2002). Specimens from contemporary collections will be vouchered at CU Boulder Museum of Natural History.

To determine the extent to which changes in community composition between historical and contemporary time periods could be attributed to short-term interannual fluctuations in ant communities, we randomly selected and resampled a subset of eight sites stratified by aspect (two canyon bottom, three north-facing slope, three south-facing slope) in the summer of 2022 using the same methodology as previously. To determine the level of interannual variation in ant community composition between years we used a permutational multivariate analysis of variance (PERMANOVA) as described above for the subset sites to compare short-term and long-term species turnover.

To compare species richness between the time periods, we used a first-order jackknife estimator calculated using the "specpool" function from the vegan R package (Oksanen et al., 2019). To account for differences in the sampling effort between the two time periods, we used rarefaction using the R package iNEXT (Chao et al., 2014; Hsieh et al., 2022). This analysis was done with the historical collections data and the 2021 samples to directly compare between the two studies. We rarefied species richness by both the number of sites and sampling events. To test whether community composition differed between time periods and whether assemblages differed across aspects, we used species presence at sites. We next analyzed the effects of time period, aspect, and percentage tree cover on ant species composition by site. This analysis was only done with the historical collections data and the 2021 samples. We used a PERMANOVA (Anderson, 2001) using the "adonis" function in the vegan R package (Oksanen et al., 2019) with 999 permutations. We used nonmetric multidimensional scaling (NMDS) from the vegan R package (Oksanen et al., 2019) to visualize the differences. To test for changes in the homogeneity of assemblages between time periods we used the betadisper function in the vegan R package (Oksanen et al., 2019), which tests for multivariate homogeneity of group dispersions (variance).

Question 2: Does temperature explain changes in ant species occurrence in Gregory Canyon?

Air temperatures and surface temperatures were recorded at each ant collection during the surveys. Air temperatures were recorded ~15–20 cm (6–8 in.) above the collection location of the ant using a Kestrel Instruments 3500 weather meter. Surface temperatures were recorded at the location where the ant was collected using a Fluke 62 MAX+ Handheld Infrared Laser Thermometer. If an ant was found under a rock or log, the surface temperature was immediately measured on the spot where the ant was found and then the ant was collected. Ant collections were categorized as surface foragers, individuals who were on the surface and exposed to ambient conditions, or nonsurface foragers, individuals who were in a thermally buffered environment when they were collected (e.g., under a rock or inside a log).

To determine whether foraging temperature was related to changes in the community, we compared the ranges of temperatures at which ants were collected to their change in occurrence at sites between time periods. We used temperature data from both 2021 and 2022 collections to increase sample sizes of species foraging data but used occurrence data from the 2021 sampling to have equivalent sampling effort among sites. Species included in these analyses had 10 or more contemporary observations and were present in both time periods. To standardize the change in occurrence and account for variability between abundant and rare species, *z*-scores (*z*-score = [observed value – mean value]/SD of values) were used. *Z*-scoring centers the mean for each value of change in occurrence and converts the measurements into SDs from the mean.

To determine whether species with broader environmental tolerances increased in distribution, we regressed species change in occurrence at sites between contemporary (2021 sampling) and historical time periods against the range of surface and air temperatures for ants in thermally buffered, exposed environments and the combination of the two. We calculated range as the difference between the 95th and 5th percentiles of the data (95% range).

Question 3: Does change in tree cover in Gregory Canyon relate to changes in ant species occurrence?

Tree cover quantification

To determine whether tree cover was related to changes observed in community composition or richness, we used occurrence data from all collection years and aerial imagery of Gregory Canyon from 1938/1940 and 2015. The historical images used were acquired during flights commissioned by the U.S. Forest Service and Soil Conservation Service in 1938 and 1940. The contemporary images used were acquired by NAIP in the fall of 2015 (United States Forest Service, National Agriculture Imagery Program 2015). Images were classified by Rodman et al., 2019 (see *Acknowledgments*). To quantify percentage tree cover at each site, we calculated the sum of 1-m pixels on the classified image layers for 1938/1940 and 2015 (1 = forest presence, 0 = forest absence) falling within site boundaries using the zonal statistics tool in ArcGIS, then divided the sum by the total number of 1-m pixels within each site.

To determine whether percentage tree cover differed between time periods and across aspects, we performed a two-way ANOVA with percentage tree cover as the response variable and time period and aspect as the predictor variables. We then used a post hoc Tukey test to determine which aspects differed. Change in percentage tree cover (2015 percentage tree cover - 1938/1940 percentage tree cover) for each site was compared to species richness data from the 2021 collections. We used a linear regression with species richness as the response variable and percentage tree cover and time period as predictor variables. We used linear regressions to determine whether there was a significant relationship between the change in percentage tree cover by site and the change in species richness by site. To determine whether tree cover influenced community composition, we used the "vegdist" function from the vegan R package (Oksanen et al., 2019) to calculate Bray-Curtis dissimilarity values. We then used a linear regression to determine whether the dissimilarity value of each site was correlated with the change in percentage tree cover.

RESULTS

Question 1: Have ant species occurrences and distributions in Gregory Canyon, Boulder, Colorado, changed since sampling done by Browne and Gregg (1969) in 1957–1958?

There were differences in environmental variables that could have led to shifts in ant communities and species occurrences between sampling periods (Tables 1–3). Browne and Gregg (1969) made a total of 443 unique collections of ants in the field. In 2021, we made 3669 collections, 50 (1.4%) of which we were not able to identify to species due to damage to the specimens. For the **TABLE 1** Results of two-way ANOVA used to determine differences in percentage soil moisture between time periods (contemporary 2021 and historical 1958) and among aspects (north-facing slopes, south-facing slopes, and canyon bottoms).

Percentage soil moisture comparison	F-value	Degrees of freedom	<i>p</i> -value
Aspects	27.06	2	<i>p</i> = 3.45e-10
Time periods	87.22	1	<i>p</i> = 2.01e-15

TABLE 2 Differences in percentage soil moisture between periods (contemporary 2021 and historical 1958) and among aspects.

Period	North-facing slopes	South-facing slopes	Canyon bottoms
Historical percentage soil moisture	28.92%	15.52%	20.14%
Contemporary percentage soil moisture	14.21%	8.44%	12.05%

subset of sites sampled in 2022, we collected 999 specimens. Overall, we recorded 56 ant species in 2021 while Browne and Gregg (1969) collected 43 species in the historical study (Table 4). When we corrected for differences in sampling effort using jackknife estimations of species richness, we found that the estimated historical species richness was 52.70 ± 4.59 (SE) species and the contemporary estimated richness was 64.73 ± 3.78 (SE) species. Rarefaction based upon the number of collections indicated that species richness did not significantly differ between time periods (Figure 2); however, rarefaction based upon the number of sites species occurred in showed species richness was higher contemporarily than historically, specifically for north-facing slopes (Figure 2E). Finally, 31 species were found in both time periods, while 12 ant species decreased, 18 increased, and one showed no change in their occurrence at sites (Figure 3).

North-facing slopes showed the largest increase in species richness (27 historical and 46 contemporary; Table 4). South-facing slopes showed a modest increase in observed species richness (32 historical and 37 contemporary), but not estimated (45 historical and 44 contemporary). Canyon bottoms showed only a modest increase in both observed (28 historical and 33 contemporary) and estimated (37 historical and 44 contemporary) species richness. In the contemporary surveys, we documented only one invasive species, *Tetramorium immigrans*, which was found mainly in areas that had higher levels of human traffic

TABLE 3 Differences in mean contemporary (2021 and 2022) surface/air temperatures among aspects (north-facing slopes, south-facing slopes, and canyon bottoms).

Temperature measurement	<i>t</i> -value	Degrees of freedom	β	SE	<i>p</i> -value	North-facing slopes	South-facing slopes	Canyon bottoms
Surface temperature	8.93	4634	2.76	0.31	<i>p</i> = 2e-16	21.3°C	25.0°C	22.2°C
Air temperature	11.11	4634	2.16	0.19	<i>p</i> = 2e-16	24.1°C	26.1°C	24.1°C

TABLE 4 Differences in species richness in Gregory Canyon. Species richness observed (and jackknife estimation) for each aspect and period (contemporary: 2021 and historical: 1957–1958).

Comparison	Historical	Contemporary
All sites	43 (52.69)	56 (64.73)
North-facing slopes	27 (32.57)	46 (57.14)
South-facing slopes	32 (44.92)	37 (43.46)
Canyon bottoms	28 (37.17)	33 (43.83)

(along roadways, parking areas, or major trail junctions). None were documented in the historical surveys.

Communities differed significantly between time periods (Figure 4; Appendix S1: Figure S1; pseudo- $F_{1.54} = 42.42$, p = 0.001 PERMANOVA). Dissimilarity in composition between the historical and contemporary (2021) surveys was high (Bray–Curtis dissimilarity = 0.62). Assemblages differed significantly in composition among aspects (Figure 4; pseudo- $F_{2.54} = 22.42$, p = 0.001) and with percentage tree cover (pseudo- $F_{1.54} = 108.73$, p = 0.001). There was a significant interaction between time period and percentage tree cover (pseudo- $F_{1.54} = 26.09$, p = 0.001) such that the effect of tree cover varied by time period. Additionally, there was a significant interaction between aspect and percentage tree cover (pseudo- $F_{2,54} = 3.94$, p = 0.008) such that the effect of percentage tree cover depended on aspect. Dispersion between time periods differed significantly ($F_{1.64} = 8.03$, p = 0.006), with the contemporary survey showing greater homogenization (less variance) in species composition among sites than the historical survey (Appendix S1: Figure S1).

The subset of sites sampled in 2022 did not differ significantly from 2021 sites (Appendix S1: Figure S2). The dissimilarity for the 2021 and 2022 subset of sites was much lower (0.32) than the same sites compared between the historical and 2021 surveys (0.68).

Question 2: Does temperature explain the changes in ant species occurrence in Gregory Canyon?

Maximum daily temperatures throughout the sampling season differed significantly only for 1957 ($t_{725} = -3.55$,

 $\beta = -1.71$, p = 0.004; Appendix S1: Figure S3A), with temperatures being ~1.5°C lower on average. Annual average maximum temperatures have been increasing from the baseline average for 1900–1930 ($F_{1,121} = 32.73$, p = 7.82e-08, $R^2 = 0.21$; Appendix S1: Figure S3B). There was a positive relationship between change in the number of sites a species occurred in and both the range of surface temperatures ($F_{1,9} = 7.10$, p = 0.026, $R^2 = 0.38$; Figure 5A) and the range of air temperatures ($F_{1,9} = 9.42$, p = 0.013, $R^2 = 0.46$; Figure 5B) at which foragers were collected at in the contemporary surveys. We did not detect a relationship between change in the number of sites at which a species occurred and the range of surface $(F_{1,9} = 0.0009, p = 0.98, R^2 = -0.11)$ and air temperatures $(F_{1,9} = 1.64, p = 0.23, R^2 = 0.06)$ experienced by nonsurface forager ants. The number of sites a species occurred in was not related to the range of surface temperatures for buffered ants ($F_{1,9} = 4.19$, p = 0.071, $R^2 = 0.24$; Figure 5C); however, it was positively related to the range of air temperatures for buffered ants $(F_{1,9} = 11.9, p = 0.007, R^2 = 0.52;$ Figure 5D).

Question 3: Does change in tree cover in Gregory Canyon relate to changes in ant species occurrence?

Contemporary tree cover in 2015 was 20% greater than in 1940 ($F_{1,60} = 19.50$, p = 4.28e-05; Appendix S1: Figure S4). Additionally, percentage tree cover differed significantly between aspects ($F_{2.60} = 10.87$, p = 9.36e-05; Appendix S1: Figure S4) with roughly 20% more tree cover on north-facing slopes than south-facing slopes. There was not a significant relationship between change in species richness and change in percentage tree cover $(F_{1,31} = 0.95, p = 0.34, R^2 = 0.002)$. There was a significant positive relationship between species richness and percentage tree cover (overall model: $F_{3.62} = 20.04$, $p = 3.383e-09, R^2 = 0.47$; tree cover: $t = 3.99, \beta = 0.119, \beta$ p = 0.0002; Figure 6), but no relationship with time period ($t = 0.66, \beta = 1.75, p = 0.51$). There was no relationship between site species composition and change in percentage tree cover ($F_{1,31} = 1.88$, p = 0.18, $R^2 = 0.03$; Appendix S1: Figure S5).



FIGURE 2 Rarefaction and extrapolation curves of species richness for the number of sampling sites (species site occurrence) and the number of collection events separated for each aspect (south-facing slopes, north-facing slopes, and canyon bottoms) and time period (contemporary: 2021 and historical: 1957–1958). Color envelopes represent 95% confidence intervals for rarefied and extrapolated data. (A) Rarefied and extrapolated species richness based on number of sampling sites for all Gregory Canyon sites. (B) Rarefied and extrapolated species richness based on number of sampling sites for all of Gregory Canyon. (C) Rarefied and extrapolated species richness based on number of sampling sites for south-facing slope sites. (D) Rarefied and extrapolated species richness based on number of collection events for south-facing slope sites. (E) Rarefied and extrapolated species richness based on number of collection events for north-facing slope sites. (F) Rarefied and extrapolated species richness based on number of collection events for anyon bottom sites. (H) Rarefied and extrapolated species richness based on number of collection events for canyon bottom sites. (H) Rarefied and extrapolated species richness based on number of collection events for canyon bottom sites.

DISCUSSION

We found that ant species richness increased in Gregory Canyon, Boulder, Colorado, from the late 1950s and that there were large differences in composition based on aspect and time period. While assemblages still differed between aspects, they were more homogeneous than they had been historically. We found that temperature was related to changes in the number of sites at which species occurred. Specifically, we found that species that foraged across a wider range of temperatures became more widespread across sites between time periods. While tree



FIGURE 3 Observed changes in ant species site occurrence between two time periods (contemporary: 2021 and historical: 1957/1958) for 33 sites in Gregory Canyon. Bar plots of (A) observed increases in number of sites in which species occurred, (B) observed decreases in number of sites that species occurred in, and (C) number of sites in which unique species (species that were only found in one time period) occurred.

cover increased, the change in percentage tree cover for each site was not related to the change in species composition.

Species richness and occurrences

We found that ant species richness on north-facing slopes within Gregory Canyon has increased since the time of the historical study. Other studies examining changes in ant communities over time have found modest increases in ant species richness and abundance (Kaspari et al., 2019; Resasco et al., 2014) concurrent with increases in local temperatures. This does not follow the pattern of global declines in insect diversity and abundance (Hallmann et al., 2017; Lister & Garcia, 2018; Seibold et al., 2019; Wagner, 2020; Wagner et al., 2021), likely due to landscape-level differences creating variation in how species respond to environmental change. Additionally, species richness may increase in some areas as insects expand their distributions with climate change. One caveat concerns the differences in sampling effort between the two studies. It is possible that Browne and Gregg (1969) did not record every single collection of species that they had already encountered within a site, especially for more common species. However, the scope of Browne and Gregg's study was to document



FIGURE 4 Change in ant community composition between slope aspects over time. Dissimilarity of ant species composition between historical (1957–1958) and contemporary sites (2021) using nonmetric multidimensional scaling (NMDS) ordination plot. Each polygon represents ant assemblages between aspects (north-facing slopes, south-facing slopes, and canyon bottoms) for historical and contemporary samples. Within each polygon, dots represent individual sites.

species distributions and aspect representation, so they likely recorded all species encountered at each site. Consequently, species site occurrence between the two studies is likely more comparable than abundance (Figure 2).

Homogenization

Local ant assemblages differed between aspects, and overall communities differed between time periods. However, the contemporary ant community was more similar or homogenized in its composition across sites and aspects than the historical community. Biotic homogenization is the process by which ecologically distinct communities become more similar over time (McKinney & Lockwood, 1999; Olden & Rooney, 2006). Homogenization of insect communities has been observed as a result of climate change, land-use change, and invasions (Gossner et al., 2023). This reduction in beta diversity among communities on differing aspects is consistent with studies looking at changes in communities regionally (Finderup Nielsen et al., 2019; Lewthwaite & Mooers, 2022; Li et al., 2020) and globally (Newbold et al., 2018) over time (but see Dornelas et al., 2019).

Homogenization has been linked to climate-driven range shifts (Diamond, 2018) as species that are able to persist or expand their ranges are deemed "winners," and species that are unable to cope with the changing conditions and experience range losses or extirpation are deemed "losers" (McKinney & Lockwood, 1999). Ultimately, winning species increase their occurrence, replacing the losing species, resulting in decreasing beta diversity across sites (Olden & Rooney, 2006). This is consistent with the distributional changes that we see in Gregory Canyon, with some species largely increasing their site occurrence, others decreasing, and a high level of species turnover between time periods. Species range size has been used as a predictor for whether species will persist



FIGURE 5 Linear regressions of microsite temperatures experienced by ant species compared to aspects of site occurrence. (A) Change in species site occurrence by 95% range of surface temperatures for foraging ants. (B) Change in species site occurrence by 95% range of air temperatures for foraging ants. (C) Number of sites in which a species occurred in contemporary period by 95% range of surface temperatures for ants found in thermally buffered environments. (D) Number of sites in which a species occurred in contemporary period compared to 95% range of air temperatures for ants collected from thermally buffered environments.

under anthropogenic change, with wide-ranging species being more likely to expand and species with a small range size being likely to experience contractions (Lewthwaite et al., 2018; Newbold et al., 2018; Schwartz et al., 2006). Species with a smaller range size may be "losers" in local communities facing disturbance (Borregaard & Rahbek, 2010; Staude et al., 2020). However, our results indicated that some species that were more spatially rare in the area historically had the largest increases in site occurrence. Consequently, the increases observed in species richness on north-facing slopes may be contributing to community homogenization.

Aspects of species' natural history may inform which species changed in their distribution within Gregory Canyon. For example, some wide-ranging generalist species such as *Tapinoma sessile* (Menke et al., 2010) and competitive species such as *Liometopum luctuosum* saw large increases in their occurrence (Figure 3A). Increases in generalist species have been documented over decades (Roeder et al., 2021). Reductions in more specialized species, such as the seed dispersers *Aphaenogaster occidentalis* and *Pheidole pilifera*, could have implications for ecosystem functioning as reductions in seed-dispersing species mean that plant distribution and abundance may be limited (Ness et al., 2009; Rodriguez-Cabal et al., 2012; Wittman et al., 2010). Species that are heat-intolerant are typically negatively affected by interactions with more dominant heat-tolerant species



FIGURE 6 Comparison of species richness and percentage tree cover in Gregory Canyon. Linear regressions of percentage tree cover and observed species richness in each site for both contemporary (2021–2022) and historical (1957–1958) periods.

(Diamond, Chick, Penick, et al., 2017; Retana & Cerdá, 2000). Additionally, under altered temperature regimes, more cold-adapted species are outcompeted by the increasing warm-adapted species (Urban et al., 2012; Warren II & Chick, 2013). However, this is not necessarily the pattern we consistently see in this study as many cold-adapted species increased in their site occurrence as well (e.g., *Stenamma diecki*), which could be tied to increasing tree cover providing additional suitable microhabitats for species to colonize.

Temperature

While temperatures did not differ significantly among all sampling years, average maximum temperature was almost 2°C higher than the 1900–1930 baseline average. Soil moisture was significantly lower in 2021 than it was in 1958. At the microsite level, species that foraged in a wider range of surface and air temperatures exhibited larger changes in the number of sites they occurred in. This finding aligns with Guo et al. (2020), who found ant foraging temperatures to be predictors of species distributions. However, the surface temperatures at which species were present in thermally buffered environments did not relate to the number of sites species occurred in. This suggests that species are able to behaviorally thermoregulate by retreating to nests and reducing the temperature variation they experience (Jones & Oldroyd, 2006). Since the range of temperature variation underground is largely dampened, buffered nest temperatures may not be the best predictor of species persistence. Species present in a wider range of air temperatures exhibited increases in occurrence and were present in a greater number of sites throughout Gregory Canyon. These findings suggest that temperature impacts on ant species importantly operate by increasing conditions favorable for foraging for some species while limiting the windows of available foraging time for others.

Temperatures are increasing in the Boulder area; however, tree cover in Gregory Canyon may complicate the interpretation of temperature influence on the ant community. Increasing tree cover throughout the canyon may be buffering the impact of increased temperatures (De Frenne et al., 2019; Kašpar et al., 2021). Another consideration is that the thermal space (the range of air and surface temperatures recorded for species collections) we documented species in may not be the same as it was in the historical study. Indeed, some ant species have exhibited plastic (Bujan et al., 2020) or adaptive responses (Diamond, Chick, Perez, et al., 2017) to temperature, indicating that the species documented in this study might be utilizing different thermal space than they had been using historically.

The thermal physiology of a species may dictate whether a species increased or decreased in occurrence between the two surveys. Warming temperatures also impact the windows of time for favorable foraging temperatures (Jayatilaka et al., 2011; Roeder et al., 2022), which may have important consequences for colony fitness. Changes in community composition over time have been linked to increasing temperatures (Lewthwaite et al., 2017). Species distributions can be limited by their physiological tolerances, as species decreasing in their ranges tend to have lower thermal tolerances (Roeder et al., 2021). Additionally, thermal tolerance can influence daily foraging patterns, with species with lower thermal tolerances showing preferences for more thermally buffered areas (Wittman et al., 2010). The range of temperatures that a species can forage in increases the likelihood of a species occupying a site (Braschler et al., 2020), which is evident in our results.

Tree cover

Contemporary tree cover was positively related to contemporary species richness, but there was no relationship between the change in community composition and change in percentage tree cover. Species richness (both observed and estimated) on north-facing slopes increased over time, while species richness on south-facing slopes and canyon bottom sites exhibited marginal increases over time. Change in species richness was not related to change in tree cover. Species richness increased in the study area even though the habitat structure was more homogenized than it had been historically, with more sites exhibiting higher percentages of tree cover and less variation in the percentage of tree cover between sites. One complication of interpretation is that the aerial imagery used to analyze tree cover in Gregory Canyon was taken in 1938/1940, and historical sampling was conducted in 1957/1958, meaning that the calculated tree cover percentage may not be an accurate representation of the historical habitat in which Browne and Gregg (1969) collected data.

Ant species composition was influenced by percentage tree cover (Andersen, 2019). Forested and open habitats tend to have strongly differing ant communities (Andersen, 1997, 2019; Lassau & Hochuli, 2004; Resasco & Fletcher, 2021), which we see represented in the differences between the north- and south-facing slope assemblages. Horizontal vegetation cover has been shown to have a negative relationship with ant species richness (Lubertazzi & Tschinkel, 2003; Muluvhahothe et al., 2021; Paraskevopoulos et al., 2023). However, vegetation cover may explain the increased site occurrence of common generalist species (Retana & Cerdá, 2000).

Conclusions

Browne and Gregg (1969) stated that "there are no physical barriers in Gregory Canyon to prevent the spread of colonizing individuals." The increasing presence of generalist species indicates that the colonization of individuals among sites is not being limited to this area. Temperature and habitat structure changes within Gregory Canyon have acted as an environmental filter for ant species, many of which are likely limited by their thermal environment, resulting in the different ant community that we see today compared to the community sampled by Browne and Gregg (1969). Increases in the species richness and occurrence of thermally generalist species have resulted in the homogenization of the community. Local biotic homogenization may have consequences for ecosystem functioning by reducing spatial asynchrony (Wang et al., 2021). Our findings highlight the power of detailed surveys and resampling to understand the drivers of biodiversity change.

AUTHOR CONTRIBUTIONS

All authors conceived and designed the research. AWP performed the research and analyzed the data with guidance from JR. All authors wrote and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Paraskevopoulos et al., 2024) are available in Dryad at https://doi.org/10.5061/dryad.2fqz612x4.

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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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