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RESEARCH ARTICLE

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Elevational cline in herbivore abundance driven by a monotonic increase in trophic-level sensitivity to aridity

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Abstract

1. The abiotic environment drives species abundances and distributions both directly and indirectly through effects on multi-trophic species interactions. However, few studies have documented the individual and combined consequences of these direct and indirect effects.
2. We studied an ant-tended aphid along an elevational gradient, where lower elevations were more arid. Hypotheses of stronger species interactions at lower elevations and a greater sensitivity of higher trophic levels to climate led us to predict increased top-down control of aphids by natural enemies (third trophic level) but even stronger protection from mutualist ants (fourth trophic level) with increasing aridity. As a result, we predicted that mutualism strength and aphid abundance would increase with aridity.
3. We documented patterns of aphid abundance and tested for both the direct and multi-trophic indirect effects of aridity on aphid performance. To do so, we used both observational and manipulative methods across two years in replicate high- and low-elevation valleys, where summer temperatures decreased by 3.7°C and precipitation increased by 27 mm/mo from low to high elevations.
4. Aphid colonies were 75% larger in the most (vs. least) arid sites, and this was best explained by changes in interactions with predators and ants. Aphids were unaffected by the direct effects of the abiotic environment or its indirect effects via host plant quality. In contrast, natural enemy effects increased with aridity; under ant exclusion, natural enemies had no effect on aphids in the least arid sites but depressed colony growth by 252% in the most arid sites. Ant activity also increased with aridity, with ants discovering more aphid colonies and experimental baits and allocating more foragers per aphid, although there was no effect of aridity on ant abundance or community composition. Correspondingly, the mutualist services provided by ants increased with aridity; ants provided no benefits to aphids in the least arid sites but doubled colony growth in the most arid sites.
5. In summary, an elevational cline in herbivore abundance was driven by a monotonic increase in trophic-level sensitivity to aridity. These findings illustrate that predicting species responses to climate change will require a multi-trophic perspective.

KEYWORDS
ant–aphid mutualism, climate change, elevation, indirect effects, multi-trophic interactions, plant–herbivore interactions, *Populus tremuloides*

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1 | INTRODUCTION

The abiotic environment is a key driver of species abundances and distributions. Nevertheless, our understanding of the precise mechanisms underlying species responses to the abiotic environment is often limited (Abdala-Roberts & Mooney, 2013). While the abiotic environment can affect species abundances and distributions through direct physiological effects, it can also do so indirectly by altering interactions with other species at multiple trophic levels (Gilman et al., 2010; Mooney et al., 2016; Parmesan, 2006). Thus, understanding how climate affects species interactions is essential for predicting changes in community structure under future climate change (Gilman et al., 2010; Tylianakis et al., 2008). However, because experimental manipulations of multi-trophic interactions along climatic gradients are rare, the exact mechanisms driving variation in species abundances and distributions are not well understood (Mooney et al., 2016; Moreira et al., 2018; Walther, 2010).

Species interactions have classically been proposed to be stronger at lower latitudes and elevations where the climate is warmer and less seasonal (Coley & Barone, 1996; Moreira et al., 2018; Schemske et al., 2009), but recent studies have questioned the generality of this paradigm (Moles et al., 2011; Moles & Ollerton, 2016; Zhang et al., 2015). Such discrepancies may arise in part because most tests for gradients in species interactions fail to adequately incorporate the ecological complexity in which the interactions are embedded (Moreira et al., 2018). Climate may alter interactions between two focal species through direct physiological effects on one or both of the species involved in the interaction (Gilman et al., 2010). Additionally, biotic interactions may vary if climate affects how one or both focal species interact with other species in the community, either at lower (e.g., resources) or higher (e.g., natural enemies) trophic levels (Gilman et al., 2010; Mooney et al., 2016; Moreira et al., 2018).

Evidence suggests that higher trophic levels are more sensitive to abiotic change and thus may be particularly important drivers of variation in species interactions (Nelson, Pratt, et al., 2019). The increased sensitivity of higher trophic levels is likely due to their relatively smaller population sizes and greater metabolic demands (Petchey et al., 1999; Vasseur & McCann, 2005; Voigt et al., 2003). Such sensitivity of higher trophic levels may alter interactions with species at lower trophic levels, ultimately affecting their abundances and distributions (Barton, Beckerman, & Schmitz, 2009). For example, Barton et al. (2009) found that warming increased the top-down control of herbivores by predators, which indirectly affected plant biomass. Because higher trophic levels are often more sensitive to abiotic change and have strong fitness effects on species at lower trophic levels (Vidal & Murphy, 2018), a multi-trophic perspective is necessary for understanding the mechanisms by which climate alters species abundances and distributions.

Ant protection mutualisms are experimentally tractable multi-trophic interactions that are ideal for testing for trophic gradients in sensitivity to abiotic change and the resulting effects on species abundances and distributions. In these interactions, myrmecophilous plants and insects (e.g., aphids) provide ants with carbohydrate-rich resources in exchange for protection against herbivores (Chamberlain & Holland, 2009) or predators and parasitoids (Stadler & Dixon, 2005), respectively. By doing so, ants can alter the abundance, distribution and evolution of their mutualist partners (Abdala-Roberts et al., 2012; Olmstead & Wood, 1990; Pellissier et al., 2012). Some evidence suggests that ant protection mutualisms are stronger at lower elevations and latitudes (Chamberlain & Holland, 2009; Koptur, 1985; Olmstead & Wood, 1990), and this pattern may be driven by changes in plant quality (first trophic level) or the traits, abundances and community composition of herbivores (second trophic level), natural enemies (third trophic level) or mutualist ants (fourth trophic level) (Chamberlain et al., 2014; Mooney et al., 2016; Petry et al., 2012; Staab.et al., 2015). Thus, ant protection mutualisms provide opportunity to test for the multi-trophic mechanisms underlying gradients in species interactions and species abundances and distributions. Along these lines, one past study has tested for elevational variation in ant foraging behaviours and ant–aphid interactions. Nelson, Pratt, et al. (2019) found that colonies of a single ant species (*Formica podzolica*) in more arid sites were more active and provided stronger tending and protection to aphids (*Aphis varians*) on potted plants (*Chamerion angustifolium*) placed adjacent to ant mounds. However, the study did not assess whether aridity affected aphids directly or indirectly through effects on host plant quality or top-down control by natural enemies, nor did it conduct surveys of naturally occurring aphids to determine the net effects of these dynamics on wild aphid abundance.

In this study, we assessed the multi-trophic mechanisms by which changes in aridity affect the abundance of the ant-tended aphid *Pterocomma beulahense* (Hemiptera: Aphididae) feeding on *Populus tremuloides* (Salicaceae; quaking aspen). To do so, we conducted observational and manipulative studies in replicate high- and low-elevation valleys, with study sites spanning approximately 630 m in elevation. As elevation increased, mean summer temperature decreased by 3.7°C and summer precipitation increased by 27 mm/month, thus constituting a gradient in aridity. We investigated the extent to which aridity affects aphid abundance (a) directly and indirectly by mediating host plant quality, (b) by mediating top-down control by natural enemies, and (c) by mediating protection provided by ants due to changes in ant abundance, taxonomic composition, or activity. Based on hypotheses and past evidence for stronger species interactions at lower elevations and a greater sensitivity of higher trophic levels to abiotic change, we predicted stronger negative effects of natural enemies (third trophic level) but even stronger positive effects of mutualist ants (fourth trophic level) with increasing aridity. As a result, we predicted that aphid abundance would increase with aridity. Accordingly, this study documents the individual and combined direct and multi-trophic indirect effects of climatic variation on species abundance.

2 | MATERIALS AND METHODS

2.1 | Study sites

This research was conducted near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO (38.96°N, −106.99°W), in

June–August 2012 and 2015. We worked in plots separated by at least 100 m in three "high-elevation" valleys (East River, Slate River and Washington Gulch), ranging in elevation from 2,880 to 3,196 m (2,999 m ± 85 *SD*), and in three "low-elevation" valleys (Cement Creek, Spring Creek and Taylor River), ranging in elevation from 2,567 to 2,758 m (2,681 m ± 71 *SD*; Figure 1; site coordinates and climatic variables are in Appendix S1). We worked within separate valleys to provide relatively isolated populations and thus true replication of elevation and its abiotic correlates. Valleys within an elevational category (high vs. low) were 3 km or more apart, while high- versus low-elevation valleys were 17 km or more apart.

Our sites spanned a regional aridity gradient (Petry et al., 2016) such as those often observed in mountain ecosystems (McCain, 2007). From low to high elevations in 2012–2015, mean summer (May–September) temperature decreased by 3.7°C (12.6°C–8.9°C) and monthly precipitation increased by 27 mm/month (49–76 mm/month) (PRISM Climate Group 2015). Thus, while multiple covarying factors along this elevational gradient prevent us from disentangling the effects of individual abiotic factors (Körner, 2007), collectively these differences constitute a gradient in aridity (Petry et al., 2016; Appendix S2).

2.2 | Natural history

Pterocomma beulahense (Aphididae) is an ant-tended aphid that, like all aphids, is viviparous and reproduces clonally during the summer, resulting in short generation times and rapid population growth (Dixon, 1985). *Pterocomma beulahense* colonizes stems of quaking aspen (Salicaceae: *Populus tremuloides*), which typically occurs between elevations of 2,200 m and 3,300 m in Colorado (Bretfeld, Franklin, & Peet, 2016). Our sites thus spanned approximately 60% of aspen's elevational range in the region, reaching elevations close to the upper limit. In the region surrounding RMBL, *Pt. beulahense* is tended by multiple ant taxa including *Camponotus* spp., *Formica fusca* and *Formica rufa* species groups (subfamily Formicinae); *Myrmica* spp. (subfamily Myrmicinae); and *Tapinoma sessile* (subfamily Dolichoderinae; Mooney et al., 2016). To confirm the identity of the aphids, we collected voucher specimens from each valley in July 2018 and compared them to specimens at the C. P. Gillette Museum of Arthropod Diversity at Colorado State University using the "Aphids on the World's Plants" online identification guide (Blackman & Eastop, 2018). Specimens were slide-mounted in PVA Mounting Medium (BioQuip Products, Inc.) and deposited in the RMBL collection. Ants were identified to taxonomic group with reference to the RMBL collection.

2.3 | Aspen canopy surveys

To evaluate whether aphid abundance and multi-trophic interactions varied with aridity, we surveyed for ants and aphids in three plots within each valley in 2012. Plots were located on the periphery of mature aspen stands to include only small saplings with accessible canopies. To consist of similar canopy areas, plots ranged in size from 27 to 81 m^2 based on ramet density. We searched

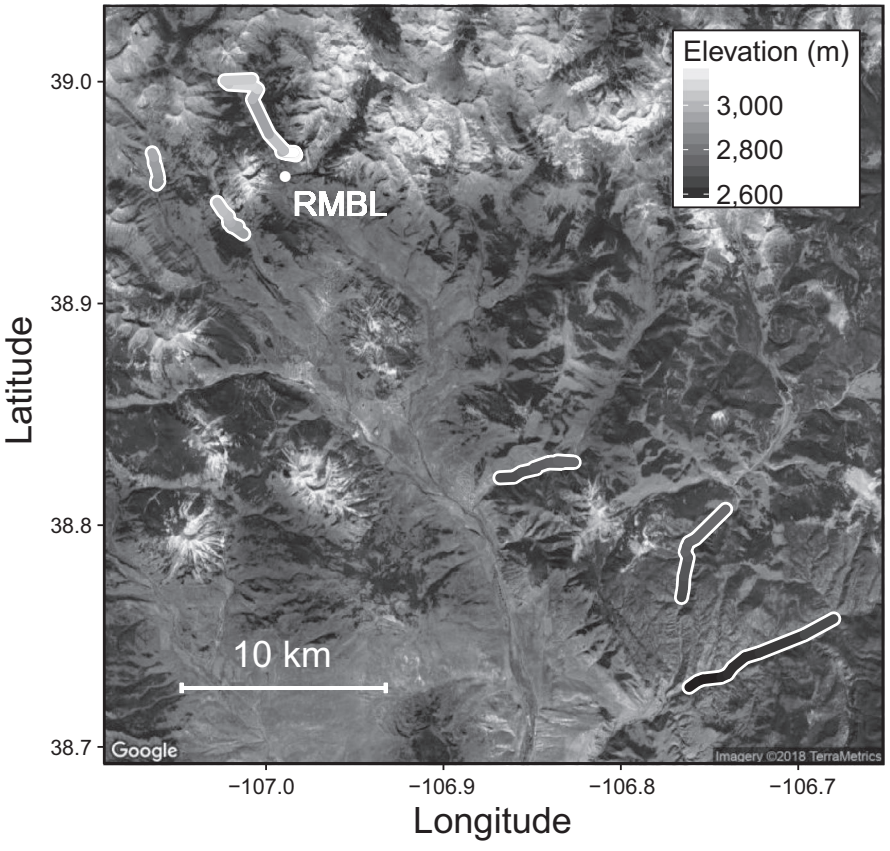

FIGURE 1 The distribution of plots in the three high- (top left) and low-elevation valleys (bottom right), with elevation (m) indicated by colour. Because multiple climate variables covary along this gradient, we used principal component analysis to create a linear combination of climatic variables. The first principal component (PC1), serving as an effective proxy for aridity, decreases with elevation. With decreases in PC1, mean summer temperature decreases by 3.7°C (12.6°C to 8.9°C; R^2 = 0.98), and mean monthly summer precipitation increases by 27 mm/month (49–76 mm/month; R^2 = 0.90)

canopies at a consistent rate, yielding comparable total sampling efforts (29 min ± 8 *SD* per plot). Individual ramets within plots were searched at different rates due to differences in canopy areas. For each ramet, we recorded the number and size of aphid colonies as well as the number and taxonomic identity of ants tending each colony and roaming elsewhere within the canopy. Sampling alternated between high- and low-elevation valleys so that sampling order and aridity were not confounded.

2.4 | Trophic-level manipulations

To determine how aridity altered interactions between *Pt. beulahense* and their resources, natural enemies and mutualist ants, we experimentally manipulated aphid multi-trophic interactions in 2015. In 10–13 plots per valley (overall $n = 63$), we established three experimental *Pt. beulahense* colonies on branch terminuses (branch length = 59.4 ± 1.3 cm) on separate ramets (diameter at breast height = 2.4 ± 0.1 cm) spaced approximately 3 m apart. Colonies were initiated with 10 unwinged aphids that were locally collected (within each valley) and protected in mesh bags. When the experiment started (July 14–22; 3–8 days after colony establishment), we added additional aphids to colonies with fewer than eight aphids, resulting in initial sizes of 8–83 aphids (16.7 ± 9.7 *SD*).

Colonies were randomly assigned, with one replicate per plot, to one of three treatments: (a) "two trophic levels" (plants and aphids; ants and natural enemies excluded), (b) "three trophic levels" (plants, aphids and natural enemies; ants excluded) or (c) "four trophic levels" (plants, aphids, natural enemies and ants). We placed electrical tape coated with Tanglefoot insect barrier (ScottsMiracle-Gro Corporation) around the branch below each aphid colony. For the three and four trophic-level treatments (colonies with natural enemies), we cut a slit in the mesh bag. For the four trophic-level treatment (colonies with ants), we secured a wire to the branch as a "bridge" for the ants to cross over the barrier (thus controlling for the presence of tape and Tanglefoot).

We visually surveyed each aphid colony for 20 s on at least four occasions before the experiment ended between August 11 and 13 (23–30 days after treatment establishment), recording the number and identity of aphids, natural enemies and ants. Colonies where ants breached exclusions were removed from all analyses, resulting in the following sample sizes: 54, 40 and 63 colonies of two, three and four trophic levels, respectively. Natural enemies present included parasitoid wasps (Hymenoptera: Braconidae), hover fly larvae (Diptera: Syrphidae), *Lygus* bugs (Hemiptera: Miridae), spiders (Araneae) and mites (Acari). Although many studies use insect barriers to experimentally manipulate multi-trophic interactions (e.g., Mooney et al., 2016), these methods may unintentionally exclude some ground-foraging predators such as spiders and mites. However, such bias presumably did not depend on aridity, and the most common natural enemies were either winged (e.g., parasitoid wasps) or oviposited by winged adults on or near aphid colonies (e.g., hover fly larvae). Furthermore, it is possible but unlikely that the ants preyed on aphids, since ants were never observed preying on aphids during the experiment or the 40 collective months of fieldwork performed by the authors on these interactions at these sites.

2.5 | Ant forager abundance and resource consumption

We sampled the ant community in all plots in both 2012 (18 plots) and 2015 (63 plots) using pitfall traps consisting of 50-ml plastic centrifuge tubes filled with soapy water and placed flush with the ground surface. Replicate traps in plots were separated by 3 m and placed at least 1 m away from ant mounds. We retrieved traps after 24–120 hr (depending on ant accumulation rates) and counted the number of ants in each taxonomic group (*Camponotus* spp., *F. fusca* species group, *F. rufa* species group, *Myrmica* spp. and *T. sessile*). Although we did not identify all ants to the species level, we identified ants to the level of taxonomic variation (genus or species group) likely to be most relevant to aphid performance, as has been done in other studies (Mooney et al., 2016). In 2012, we sampled ants once between July 2 and August 14, with 8–16 traps per plot on a grid (depending on plot size). In 2015, we sampled ants once between June 24 and 27 and once between July 21 and 30, both times with two traps per plot. Any differences in ant abundance detected using this method could be the result of differences in ant colony number, size or activity. All three of these factors may affect ant tending of aphids, and distinguishing between them was beyond the scope of this study.

In 2015, we also tested for the effects of aridity on ant consumption of artificial baits, consisting of 10 ml of a 20% solution by mass of forest honey (produced by bees foraging on hemipteran honeydew [Langnese Forest Honey]) in 15-ml plastic centrifuge tubes fitted with cotton wicks. We paired baits with water controls and deployed them on the ground for 48–72 hr on the same dates as the pitfall traps, separated from the traps by 3 m. To determine bait consumption rates (mg/hr), we weighed baits before and after they were deployed and corrected for evaporative water loss (ants were never observed collecting water).

2.6 | Statistical analysis

2.6.1 | General approach

We tested for the effects of elevational changes in aridity on aphid abundance and multi-trophic interactions. To do so, we used principal component analysis (PCA) to create a linear combination of temperature and precipitation variables estimated for each site (Appendix S2). The first principal component (PC1) accounted for 86.8% of the multivariate covariation in the climate data and was positively correlated with all temperature variables but negatively correlated with precipitation. PC1 thus serves as an effective proxy for aridity (with aridity increasing along PC1) and was used as a continuous predictor variable (hereafter termed "aridity") in all statistical analyses.

All analyses were based on testing for the fixed effect of aridity while accounting for the random effect of valley. Some analyses

included the additional fixed effects of trophic-level manipulations and covariates (Appendix S3). We included the random effect of plot nested within valley for responses where plots were repeatedly sampled (over time or from multiple trees within a plot) and the random effect of tree nested within plot for responses measured at the level of the individual aphid colony. For univariate responses measured with count data (aphids, ants and natural enemies), we used hurdle models, which consist of a generalized linear mixed model (GLMM) with a binomial distribution evaluating the probability of observing a zero value (i.e. presence vs. absence) and a GLMM with a truncated-at-zero distribution for all non-zero count data (i.e., abundance when present) (Zuur et al., 2009). For univariate responses measured with binary data (ant discovery of baits), we used GLMMs with binomial distributions. For univariate responses measured with continuous data (aphid colony growth rates and ant consumption of experimental baits), we used linear mixed models (LMMs). Finally, to test whether dissimilarity in ant taxonomic composition in pitfall traps increased with differences in aridity, we used Mantel tests. Analyses were conducted in R 3.3.2 (R Core and Team, 2016) (further described in Appendix S3).

2.6.2 | Aspen canopy surveys

We tested for the effects of aridity on aphid abundance in terms of whether aphids were present ("aphid presence") and, where present, the number of colonies per tree ("aphid colony number") and the number of aphids per colony ("aphid colony size"; Appendix S3). Since one tree contained an unusually high number of colonies (37 vs. 3.1 ± 0.28 colonies), and three colonies on other trees were unusually large (>170 vs. 13.8 ± 0.77 aphids), we removed these outliers from the analyses (although with their inclusion, results were qualitatively similar). We assessed ant mutualistic services by testing for the effects of aridity and aphid colony size on whether ants were present ("tending ant presence") and, where present, for the effects of aridity, colony size and their interaction on the number of ants ("tending ant number"; Appendix S3). The test for a main effect of aridity assessed whether there was an overall difference in ant tending while controlling for aphid abundance, whereas the aridity x colony size interaction tested whether aridity altered the tending rate (i.e., number of ants per aphid). To assess ant foraging activity in the absence of aphid rewards, we assessed whether ants were present ("roaming ant presence") and the number of ants per tree where present ("roaming ant number") in the subset of trees lacking aphids (Appendix S3). For all tests of aphid and roaming ant abundance, the time spent searching each tree ("search time") was included as a covariate.

2.6.3 | Trophic-level manipulations

We assessed the direct effects of aridity as well as its effects on host plant, natural enemy and ant effects on aphid colony per capita growth rate ("aphid colony growth") (Appendix S3). Aphid colony growth was calculated as $r = \ln(N_t/N_0)/t$, where N_0 is the initial population size at time $t = 0$, and N_t is the population size at the end of the experiment at time t, ranging from 20 to 25 days. We added one to all aphid counts to include aphid colonies that went extinct (so that $N_t = 1$). We tested for the effects of aridity, trophic-level treatment and their interaction. Because we found a significant interaction, we additionally tested for the effects of aridity directly and through changes in host plant quality by assessing aridity effects on aphid colony growth in the two trophic-level treatments only. We also tested whether aridity mediated natural enemy and ant effects in separate models comparing the two versus three trophic-level treatments and the three versus four trophic-level treatments, respectively.

We further tested for aridity effects on whether natural enemies were ever present at an aphid colony ("natural enemy presence") and, where present, the total number per colony ("natural enemy number"; Appendix S3). We also tested the effects of aridity on ant mutualistic services, assessing whether a colony was ever ant-tended ("tending ant presence") and, where present, the number of ants ("tending ant number"; Appendix S3). Analyses of natural enemy and tending ant presence included aphid colony size and aridity as fixed effects, and analyses of natural enemy and tending ant numbers also included the colony size x aridity interaction. The test for a main effect of aridity assessed overall differences in natural enemy and tending ant numbers while controlling for colony size, whereas the colony size x aridity interaction tested whether aridity altered recruitment rates (i.e., natural enemies or ants per aphid). Analyses of natural enemy presence and number also included trophic-level treatment (three vs. four trophic levels) to account for the effects of ants as well as the number of times a colony was observed to account for variation in sampling effort.

2.6.4 | Ant forager abundance and resource use

We tested for the effects of aridity on ant forager abundance and taxonomic composition in pitfall traps (in 2012 and 2015 separately), calculating ant abundance as the number of ants collected per trap per day ("per trap-day", ln-transformed for analyses of total abundance) (Appendix S3). We also tested for the effects of aridity on ant discovery ("bait discovery") and consumption ("bait consumption") of experimental baits (Appendix S3). We did not directly observe bait discovery, but bait consumption rates were bimodal, with one distribution centred at 0 mg/hr and the other at a positive value. The former distribution presumably represents baits that were not discovered by ants. Since the data were continuous, rather than using a hurdle model, we categorized each bait as discovered versus not discovered by fitting a Gaussian mixture model using the "normalmixEM()" function in the "mixtools" package (Benaglia et al., 2009), assigning each observation to one of the two distributions based on posterior probabilities (>50%). We then tested for the effects of aridity on bait discovery and consumption, calculated as the mass lost from baits averaged across both sampling dates.

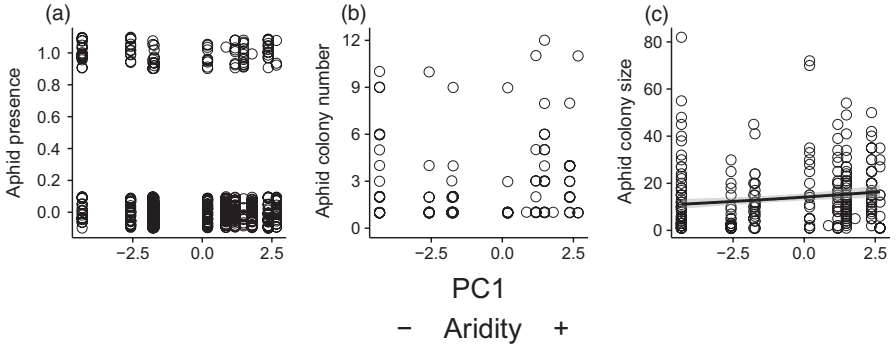

FIGURE 2 The relationship between PC1 (positively correlated with aridity; Figure 1 and Appendix S2) and the abundance of naturally occurring aphids, measured as (a) the presence (vs. absence) of aphids in a tree ("aphid presence") and, where present, (b) the number of aphid colonies per tree ("aphid colony number") and (c) the number of aphids per colony ("aphid colony size"). Points in panel (a) are vertically jittered to minimize overplotting

3 | RESULTS

3.1 | Aspen canopy surveys

Aphid colony size significantly increased with aridity (GLMM; aridity, $Z = 2.72$, $p = 0.007$; search time $Z = -1.59$, $p = 0.111$), but there were no significant effects of aridity on aphid presence (GLMM; aridity, $Z = -0.39$, $p = 0.696$; search time, $Z = 2.07$, $p = 0.038$) or colony number per tree (GLMM; aridity, $Z = 0.31$, $p = 0.760$; search time, $Z = 1.58$, $p = 0.115$; Figure 2). There was no effect of aridity on roaming ant presence (GLMM; aridity, $Z = 0.26$, $p = 0.792$; search time, $Z = 3.47$, $p < 0.001$; Figure 3a) or roaming ant number (GLMM; aridity, $Z = 0.06$, $p = 0.949$; search time, $Z = 2.61$, $p = 0.009$). Tending ant presence was marginally significantly more frequent with increasing aridity ($Z = 1.83$, $p = 0.067$; Figure 3d) and significantly more frequent at larger aphid colonies (GLMM; $Z = 3.15$, $p = 0.002$). However, although tending ant number significantly increased with aphid colony size (GLMM; $Z = 6.56$, $p < 0.001$), there was no significant aridity x aphid number interaction ($Z = 0.90$, $p = 0.368$) or main effect of aridity ($Z = 0.35$, $p = 0.725$).

3.2 | Trophic-level manipulations

Aphid colony growth depended on the aridity × trophic-level treatment interaction (LMM; $F = 6.15$, $p = 0.003$) and the main effect of trophic-level treatment ($F = 26.64$, $p < 0.001$), but the main effect of aridity was not significant ($F = 0.29$, $p = 0.615$; Figure 4). For the two trophic-level treatment only (testing for the direct effects of aridity and host plant effects), aphid colony growth did not differ with aridity ($F = 2.03$, $p = 0.208$). For the two versus three trophic levels only (testing for natural enemy effects), there was a significant aridity × trophic-level treatment interaction (LMM; $F = 13.25$, $p = 0.001$), with predators having stronger effects with increasing aridity. The main effect of trophic-level treatment was significant ($F = 61.15$, $p < 0.001$), but the main effect of aridity was not ($F = 1.72$, $p = 0.246$). Similarly, for the three versus four trophic levels only (testing for ant effects), there was a significant aridity × trophic-level treatment interaction (LMM; $F = 6.22$, $p = 0.016$), with ants providing stronger benefits with increasing aridity. The main effect of trophic-level treatment was significant ($F = 8.04$, $p = 0.006$), but the main effect of aridity was not ($F = 1.92$, $p = 0.231$).

Natural enemy presence did not depend on aridity (GLMM; $Z = 0.87$, $p = 0.386$), aphid colony size ($Z = -1.69$, $p = 0.091$) or trophic-level treatment ($Z = 0.35$, $p = 0.723$) after accounting for sampling effort ($Z = 2.06$, $p = 0.040$). Similarly, natural enemy number where present did not depend on the aridity x colony size interaction (GLMM; $Z = -0.33$, $p = 0.744$) or the main effects of aridity (GLMM; $Z = 0.70$, $p = 0.485$), aphid colony size ($Z = -1.43$, $p = 0.153$), trophic-level treatment ($Z = 0.46$, $p = 0.646$) or sampling effort ($Z = -0.34$, $p = 0.732$). In contrast, tending ant presence was significantly more frequent with increasing aridity (GLMM; $Z = 2.79$, $p = 0.005$) (Figure 3c) and at larger aphid colonies ($Z = 3.12$, $p = 0.002$). Tending ant number where present depended on the aridity × aphid colony size interaction (GLMM; $Z = 2.02$, $p = 0.043$), where per capita tending rates increased with aridity. There were also significant main effects of aridity ($Z = -2.72$, $p = 0.006$) and colony size ($Z = 3.60$, $p < 0.001$).

3.3 | Ant forager abundance and resource use

Ant frequency in pitfall traps did not vary with aridity, since all traps contained at least one ant. Ant abundance also did not depend on aridity in 2012 or 2015 (LMMs; $F = 0.15$, $p = 0.704$ and $F = 0.66$, $p = 0.431$, respectively), and neither did ant taxonomic composition (Mantel tests; $r = 0.08$, $p = 0.221$ and $r = -0.04$, $p = 0.738$, respectively) (Figure 5). Ant bait discovery significantly increased with aridity (GLMM; $Z = 2.66$, $p = 0.008$) (Figure 3b), although, for those discovered, bait consumption did not depend on aridity (LMM; $F = 0.43$, $p = 0.524$).

4 | DISCUSSION

We have demonstrated that aphid abundance increases with aridity along an elevational gradient, and evidence suggests that this is

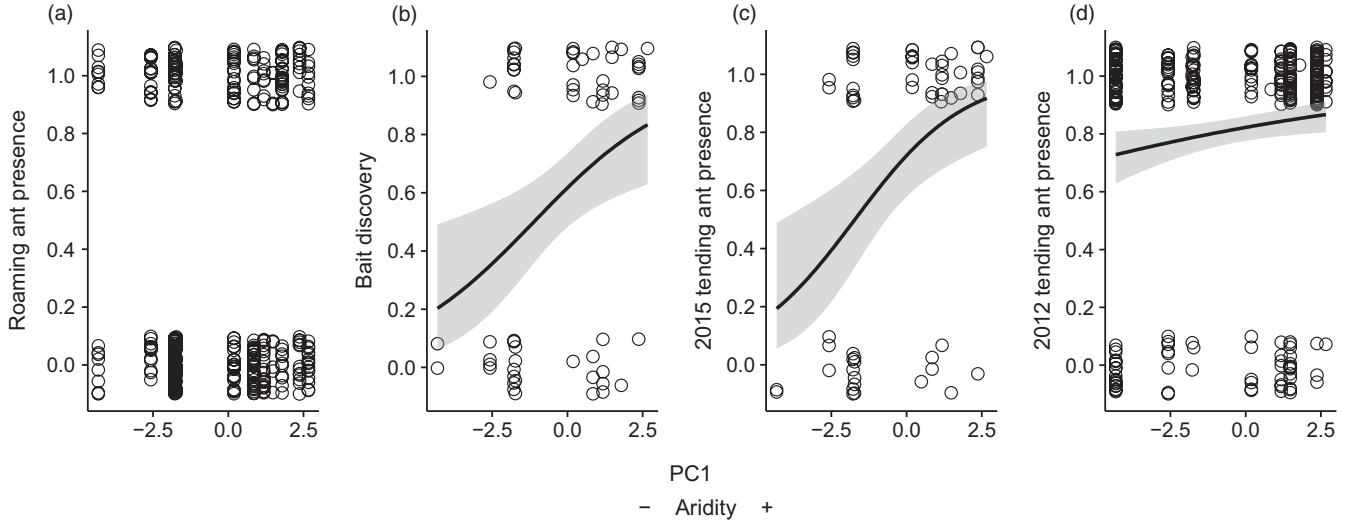

FIGURE 3 The relationship between PC1 (positively correlated with aridity; Figure 1 and Appendix S2) and (a) the presence (vs. absence) of ants in trees without aphids ("roaming ant presence"), (b) whether experimental baits were discovered (vs. undiscovered) by ants ("bait discovery") and (c) the presence (vs. absence) of tending ants ("tending ant presence") at experimentally established (2015) and (d) naturally occurring aphid colonies (2012). Points in all panels are vertically jittered to minimize overplotting

due to higher trophic levels being more sensitive to abiotic change. We detected no effects of elevational changes in aridity on aphid performance either indirectly, through changes in host plant quality (first trophic level), or directly (second trophic level). However, the strength of natural enemy effects (third trophic level) increased with aridity, with natural enemies having no effects at low aridity but suppressing aphid colony growth by 252% in the most arid sites. The strength of mutualist ant effects (fourth trophic level) also increased from the least to most arid sites, with ants discovering more aphid colonies and artificial baits, allocating more foragers per aphid, and as a result doubling aphid colony growth and causing aphid colonies to be 75% larger. Thus, increased aridity was associated with strong predator but even stronger ant mutualism effects, increasing the strength of the ant–aphid mutualism. In summary, this elevational cline in herbivore abundance was driven by a monotonic increase in trophic-level sensitivity to aridity.

There is contrasting evidence for how abiotic variation affects sap-feeding herbivores directly and through changes in host plant quality. In this study, we did not find evidence for such effects.

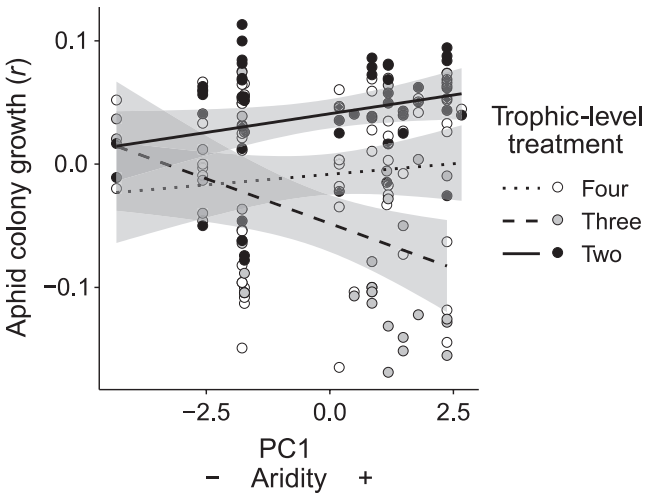

FIGURE 4 The relationship between PC1 (positively correlated with aridity; Figure 1 and Appendix S2) and aphid colony per capita growth (*r*) ("aphid colony growth") in treatments of two, three and four trophic levels

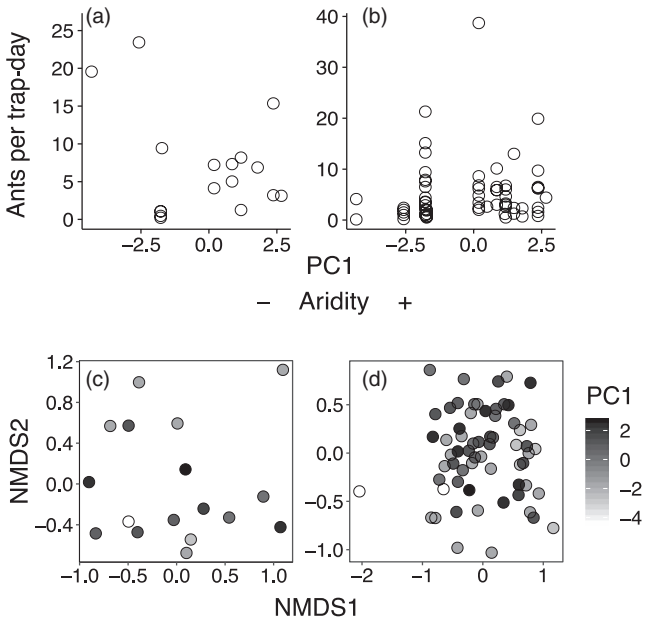

FIGURE 5 The relationship between PC1 (positively correlated with aridity; Figure 1 and Appendix S2) and the number of ants collected per trap per day within a site ("ants per trap-day") in (a) 2012 and (b) 2015. NMDS plots of ant taxonomic composition (ants per trap-day; ln+1 transformed) in (c) 2012 and (d) 2015, with PC1 values indicated by colour

Likewise, in another study in the same region, there was no evidence for the direct effects of the abiotic environment or of changes in plant quality on the performance of the aphid *Aphis helianthi* feeding on *Ligusticum porteri* (a perennial herb) (Mooney et al., 2016). However, in other systems temperature and moisture have been shown to directly increase aphid colony growth rates and densities (Barton & Ives, 2014; Pons & Tatchell, 1995). Other studies have also found evidence for elevational changes in host plant quality, in terms of both intraspecific variation (Pellissier et al., 2014) and interspecific variation (Wimp & Whitham, 2001), and aspen defensive chemistry and herbivory are known to be mediated by extreme climatic events (e.g., heat or frost events; Lindroth & St. Clair, 2013; St. Clair et al., 2009) and nutrient availability (Donaldson et al., 2006). In this study, it is possible that if plant drought stress increased with aridity, the negative effects of drought would have offset any positive direct effects of temperature on aphid performance. In addition, if our study had spanned a larger aridity gradient (with a mean monthly summer temperature and precipitation ranging greater than 3.7°C and 27 mm/month, respectively), we may have found stronger effects. For example, Barton and Ives (2014) found evidence for direct effects upon experimentally elevating temperatures by 4.87°C, and Pellissier et al., (2014) found elevational variation in plant quality when temperatures ranged by 8°C. Nonetheless, our results suggest that other factors may be more important for driving differences in herbivore abundance along environmental gradients.

While we did not detect differences in natural enemy abundance, the top-down control of aphids by natural enemies increased with aridity. In other work along the same elevational gradient, we found that natural enemy abundance and top-down control of aphids (*A. varians* feeding on *C. angustifolium*) were greater at low elevations (Nelson, Pratt, et al., 2019). Predation and parasitism by invertebrates are often stronger at lower elevations (Roslin et al., 2017; Sam et al., 2015; Straw et al., 2009), and experimental warming has been found to directly affect the abundance of predators of other aphids (*Chaitophorus populicola*) feeding on aspen (Marquis, Del Toro, & Pelini, 2014). It is possible that natural enemy abundance also increased with aridity in our system, but we may not have detected such patterns because many flying natural enemies (e.g., parasitoid wasps) spend only brief amounts of time at aphid colonies. Nonetheless, we have shown that aridity can influence the top-down control of aphids by natural enemies, although stronger natural enemy effects do not explain why aphid abundance increased with aridity.

Surprisingly, elevational changes in aridity did not mediate the effects of ants on aphids through changes in ant abundance or taxonomic composition. Ants are known to generally be more abundant and diverse at lower elevations (Lessard et al., 2007; Machac et al., 2011; Sanders et al., 2007), including near RMBL (Menke et al., 2014). In addition, other studies have found the effects of ants as mutualists and predators to be stronger at lower elevations and latitudes, where ants were more abundant or had different species compositions (Koptur, 1985; Olmstead & Wood, 1990; Pellissier et al., 2012; Plowman et al., 2017; Sam et al., 2015; Zelikova, Dunn, & Sanders, 2008). While all ant taxa in this study are ground-dwelling, and pitfall trapping is a commonly accepted method for sampling ground-active ants (Lach et al., 2010), it is possible that there were differences in the ant community that we were unable to detect. For example, ant taxa may spend different amounts of time foraging in plant canopies than on the ground. However, the lack of evidence for changes in ant forager abundance or taxonomic composition suggests that additional mechanisms may also drive variation in ant protection mutualisms across environmental gradients.

Changes in aphid abundance and performance were best explained by aridity effects on mutualist ant activity. In 2012, tending ant presence increased marginally significantly with aridity, and in 2015, tending ant presence and number per aphid both increased significantly with aridity. These contrasting results (with aridity increasing ant tending in 2015 but not 2012) are likely due to differences in the nature of the studies. In 2015, we observed the performance of experimentally established aphid colonies over time, but the naturally occurring colonies that we observed in 2012 were those that had established and persisted (rather than gone extinct), and these colonies were primarily ant-tended across all sites. Due to increased ant tending, aphid colonies grew faster in more arid sites. As a result, naturally occurring colonies were 75% larger in the most (vs. least) arid sites, although colony presence and number did not vary. It is surprising that aphid colony abundance did not also increase with aridity, since larger colonies often produce more winged aphids that disperse to establish additional colonies (Müller et al., 2001). However, enhanced colony growth rates and sizes may not ultimately result in increased colony number if successful establishment is low or if ant tending limits dispersal by reducing the production of winged aphids (Oliver et al., 2007; Tegelaar & Leimar, 2014).

Our results suggest that the increased benefits with aridity of ant tending were due to intraspecific increases in ant activity. Despite no change in ant taxonomic composition, ant tending of aphids increased with aridity. In other work along the same elevational gradient (discussed in more detail below), we found that *Formica podzolica* colonies (the species that tended 44% and 72% of the ant-tended aphid colonies in this study in 2012 and 2015, respectively) are more active and as a result provide greater benefits to the aphid *A. varians* feeding on *C. angustifolium* at low elevations (Nelson, Pratt, et al., 2019). This finding thus provides a direct indication that intraspecific variation in ant activity can drive differences in aphid performance along aridity gradients. Such changes in ant activity may be driven by temperature (Fitzpatrick, Lanan, & Bronstein, 2014; Sagata & Gibb, 2016), water availability (Frizzi, Rispoli, Chelazzi, & Santini, 2016; Kaspari & Weiser, 2000), the availability of other sugar-rich resources (e.g., extrafloral nectar; Pemberton, 1998) or ant metabolic and nutritional requirements. While water may be limiting and pose desiccation risk to ants under arid conditions (Kaspari & Weiser, 2000), such effects were unlikely in this study, since ant activity increased with aridity. Instead, it is more likely that ant activity increased in direct response to temperature, with ants being cold limited at higher elevations. Stable isotope analyses have shown that along the same elevational gradient, *F. podzolica* ants consume more

carbohydrates versus proteins, possibly indicating that sugar-rich resources are more available or that ants have a faster metabolism in warmer sites (Nelson, Pratt, et al., 2019).

The results from this study complement and extend the generality of the results from a recent study (Nelson, Pratt, et al., 2019) of another aphid-plant system along the same aridity gradient. Studying the ant *Formica podzolica* alone, Nelson, Pratt, et al. (2019) showed that ant tending and mutualist effects on aphids (*Aphis varians*) were stronger at more arid, lower elevation sites, while experimentally controlling for variation in most other factors. The study manipulated ant access to aphids feeding on potted plants (*Chamerion angustifolium*) placed adjacent to *F. podzolica* mounds, assessing ant tending of aphids, diet (through stable isotopes) and effects on aphid performance. At the same time, plant genetic variation and environmental effects on plant quality were controlled for by consistently watering potted greenhouse-grown plants sourced from the same seeds. In addition, ant colonies were selected to be of uniform size, and variance due to the process of aphid discovery and competitive interactions with other ants was eliminated by placing potted plants immediately adjacent to ant colonies. Accordingly, Nelson, Pratt, et al. (2019) explicitly demonstrated that with increasing aridity, *F. podzolica* interest in aphid tending and mutualist effects on aphid performance increased. Furthermore, although natural enemy access to aphids was not manipulated, they were more abundant at lower elevations. Thus, Nelson, Pratt, et al. (2019) complement the current study in demonstrating that aridity increases ant propensity to tend aphids and that the ant-mediated positive effects of aridity on aphids superseded the parallel negative effects of increasing natural enemy abundance. Together, these two studies provide strong evidence for a progressive sensitivity of trophic levels to climate.

Because ants are dominant species in many terrestrial ecosystems, variation in ant activity may have widespread cascading effects. As we have shown here, ants are important drivers of aphid abundance in temperate regions. Other work has shown that myrmecophilous (vs. non-myrmecophilous) treehopper (Olmstead & Wood, 1990), lycaenid (Pellissier et al., 2012) and extrafloral nectary-bearing plant (Pemberton, 1998) species are also generally less common in colder environments associated with decreased ant attendance, likely because ants are less abundant or active. Although aphids become less common towards the tropics, such effects are likely not due to decreased ant tending but rather the difficulty of locating suitable host plants with increased plant diversity (Dixon, Kindlmann, Leps, & Holman, 1987).

In summary, this study provides evidence that changes in species abundance along environmental gradients can be driven by a trophic gradient in sensitivity to abiotic change. While elevational changes in aridity did not affect aphids directly or indirectly through changes in host plant quality (second trophic level), natural enemy (third trophic level) and mutualist ant effects (fourth trophic level) both increased with aridity. These results are consistent with two other studies of ant–aphid systems in the same region (*Aphis helianthi* feeding on *Ligusticum porteri* [Mooney et al., 2016] and *Aphis varians* feeding on *Chamerion angustifolium* [Nelson, Pratt, et al., 2019]) that show a progressive sensitivity of higher trophic levels to temperature, with effects on higher (natural enemies and ants) but not lower (host plant quality or aphids directly) trophic levels. Such trophic gradients in sensitivity to abiotic change may be widespread and have also been observed, for example, in aquatic systems (Kishi, Murakami, Nakano, & Maekawa, 2005). Overall, our work contributes to a growing body of literature showing that in order to predict the effects of climate change on community structure, we must assess the effects on multiple, and particularly higher, trophic levels.

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AUTHORS' CONTRIBUTIONS

K.A.M. and A.S.N. designed the study; A.S.N., C.T.S. and M.J.H. collected the data; A.S.N. analysed the data and wrote the manuscript; and A.S.N. and K.A.M. revised the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j6kn128 (Nelson, Symanski, Hecking, & Mooney, 2019).

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REFERENCES

Abdala-Roberts, L., Agrawal, A. A., & Mooney, K. A. (2012). Ant–aphid interactions on *Asclepias syriaca* are mediated by plant genotype and caterpillar damage. *Oikos*, *121*(11), 1905–1913.

Abdala-Roberts, L., & Mooney, K. A. (2013). Environmental and plant genetic effects on tri-trophic interactions. *Oikos*, *122*(8), 1157–1166. https://doi.org/10.1111/j.1600-0706.2012.00159.x

Barton, B. T., Beckerman, A. P., & Schmitz, O. J. (2009). Climate warming strengthens indirect interactions in an old-field food web. *Ecology*, *90*(9), 2346–2351. https://doi.org/10.1890/08-2254.1

Barton, B. T., & Ives, A. R. (2014). Direct and indirect effects of warming on aphids, their predators, and ant mutualists. *Ecology*, *95*(6), 1479–1484. https://doi.org/10.1890/13-1977.1

Benaglia, T., Chauveau, D., Hunter, D. R., & Young, D. S. (2009). Mixtools: An R package for analyzing finite mixture models. *Journal of Statistical Software*, *32*(6), 1–29.

Blackman, R. L., & Eastop, V. F. (2018). *Aphids on the world's plants*. Retrieved from http://www.aphidsonworldsplants.info/

Bretfeld, M., Franklin, S. B., & Peet, R. K. (2016). A multiple-scale assessment of long-term aspen persistence and elevational range shifts in the Colorado Front Range. *Ecological Monographs*, *86*(2), 244–260. https://doi.org/10.1890/15-1195.1

Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, *17*(7), 881–890. https://doi.org/10.1111/ele.12279

Chamberlain, S. A., & Holland, J. N. (2009). Quantitative synthesis of context dependency in ant–plant protection mutualisms. *Ecology*, *90*(9), 2384–2392. https://doi.org/10.1890/08-1490.1

Coley, P. D., & Barone, J. A. (1996). Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, *27*(1), 305–335. https://doi.org/10.1146/annurev.ecolsys.27.1.305

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Dixon, A. F. G. (1985). Structure of aphid populations. *Annual Review of Entomology*, *30*(1), 155–174. https://doi.org/10.1146/annurev.en.30.010185.001103

Dixon, A. F. G., Kindlmann, P., Leps, J., & Holman, J. (1987). Why there are So few species of aphids, especially in the tropics. *The American Naturalist*, *129*(4), 580–592. https://doi.org/10.1086/284659

Donaldson, J. R., Kruger, E. L., & Lindroth, R. L. (2006). Competition- and resource-mediated tradeoffs between growth and defensive chemistry in trembling aspen (*Populus tremuloides*). *New Phytologist*, *169*(3), 561–570.

Fitzpatrick, G., Lanan, M. C., & Bronstein, J. L. (2014). Thermal tolerance affects mutualist attendance in an ant-plant protection mutualism. *Oecologia*, *176*(1), 129–138. https://doi.org/10.1007/s00442-014-3005-8

Frizzi, F., Rispoli, A., Chelazzi, G., & Santini, G. (2016). Effect of water and resource availability on ant feeding preferences: A field experiment on the Mediterranean ant *Crematogaster scutellaris*. *Insectes Sociaux*, *63*(4), 565–574. https://doi.org/10.1007/s00040-016-0500-4

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, *25*(6), 325–331. https://doi.org/10.1016/j.tree.2010.03.002

Kaspari, M., & Weiser, M. D. (2000). Ant activity along moisture gradients in a neotropical forest. *Biotropica*, *32*(4), 703–711.

Kishi, D., Murakami, M., Nakano, S., & Maekawa, K. (2005). Water temperature determines strength of top-down control in a stream food web. *Freshwater Biology*, *50*(8), 1315–1322. https://doi.org/10.1111/j.1365-2427.2005.01404.x

Koptur, S. (1985). Alternative defenses against herbivores in *Inga* (Fabaceae: Mimosoideae) over an elevational gradient. *Ecology*, *66*(5), 1639–1650. https://doi.org/10.2307/1938026

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, *22*(11), 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Lach, L., Parr, C., & Abbott, K. (Eds.) (2010). *Ant ecology*. New York, NY: Oxford University Press.

Lessard, J.-P., Dunn, R. R., Parker, C. R., & Sanders, N. J. (2007). Rarity and diversity in forest ant assemblages of Great Smoky Mountains National Park. *Southeastern Naturalist*, *6*, 215–228. https://doi.org/10.1656/1528-7092(2007)6[215:RADIFA]2.0.CO;2

Lindroth, R. L., & St. Clair, S. B. (2013). Adaptations of quaking aspen (*Populus tremuloides* Michx.) for defense against herbivores. *Forest Ecology and Management*, *299*, 14–21. https://doi.org/10.1016/j.foreco.2012.11.018

Machac, A., Janda, M., Dunn, R. R., & Sanders, N. J. (2011). Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. *Ecography*, *34*(3), 364–371. https://doi.org/10.1111/j.1600-0587.2010.06629.x

Marquis, M., Del Toro, I., & Pelini, S. L. (2014). Insect mutualisms buffer warming effects on multiple trophic levels. *Ecology*, *95*(1), 9–13. https://doi.org/10.1890/13-0760.1

McCain, C. M. (2007). Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography*, *16*(1), 1–13. https://doi.org/10.1111/j.1466-8238.2006.00263.x

Menke, S. B., Harte, J., & Dunn, R. R. (2014). Changes in ant community composition caused by 20 years of experimental warming vs. 13 years of natural climate shift. *Ecosphere*, *5*(1), 1–17.

Moles, A. T., Bonser, S. P., Poore, A. G. B., Wallis, I. R., & Foley, W. J. (2011). Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology*, *25*(2), 380–388. https://doi.org/10.1111/j.1365-2435.2010.01814.x

Moles, A. T., & Ollerton, J. (2016). Is the notion that species interactions are stronger and more specialized in the tropics a zombie idea? *Biotropica*, *48*(2), 141–145. https://doi.org/10.1111/btp.12281

Mooney, E. H., Phillips, J. S., Tillberg, C. V., Sandrow, C., Nelson, A. S., & Mooney, K. A. (2016). Abiotic mediation of a mutualism drives herbivore abundance. *Ecology Letters*, *19*(1), 37–44. https://doi.org/10.1111/ele.12540

Moreira, X., Petry, W. K., Mooney, K. A., Rasmann, S., & Abdala-Roberts, L. (2018). Elevational gradients in plant defences and insect herbivory: Recent advances in the field and prospects for future research. *Ecography*, *41*(9), 1485–1496. https://doi.org/10.1111/ecog.03184

Müller, C. B., Williams, I. S., & Hardie, J. (2001). The role of nutrition, crowding and interspecific interactions in the development of winged aphids. *Ecological Entomology*, *26*(3), 330–340. https://doi.org/10.1046/j.1365-2311.2001.00321.x

Nelson, A. S., Pratt, R. T., Pratt, J. D., Smith, R. A., Symanski, C. T., Prenot, C., & Mooney, K. A. (2019). Progressive sensitivity of trophic levels to warming underlies an elevational gradient in ant–aphid mutualism strength. *Oikos*, *128*, 540–550. https://doi.org/10.1111/oik.05650

Nelson, A. S., Symanski, C. T., Hecking, M. J., & Mooney, K. A. (2019). Data from: Elevational cline in herbivore abundance driven by a monotonic increase in trophic level sensitivity to aridity. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.j6kn128

Oliver, T. H., Mashanova, A., Leather, S. R., Cook, J. M., & Jansen, V. A. A. (2007). Ant semiochemicals limit apterous aphid dispersal. *Proceedings of the Royal Society of London B: Biological Sciences*, *274*(1629), 3127–3131.

Olmstead, K. L., & Wood, T. K. (1990). Altitudinal patterns in species richness of Neotropical treehoppers (Homoptera: Membracidae): The role of ants. *Proceedings of the Entomological Society of Washington*, *92*(3), 552–560.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Pellissier, L., Litsios, G., Fiedler, K., Pottier, J., Dubuis, A., Pradervand, J.-N., … Guisan, A. (2012). Loss of interactions with ants under cold climate in a regional myrmecophilous butterfly fauna. *Journal of Biogeography*, *39*(10), 1782–1790. https://doi.org/10.1111/j.1365-2699.2012.02743.x

Pellissier, L., Roger, A., Bilat, J., & Rasmann, S. (2014). High elevation *Plantago lanceolata* plants are less resistant to herbivory than their low elevation conspecifics: Is it just temperature? *Ecography*, *37*(10), 950–959.

Pemberton, R. W. (1998). The occurrence and abundance of plants with extrafloral nectaries, the basis for antiherbivore defensive mutualisms, along a latitudinal gradient in East Asia. *Journal of Biogeography*, *25*(4), 661–668. https://doi.org/10.1046/j.1365-2699.1998.2540661.x

Petchey, O. L., McPhearson, P. T., Casey, T. M., & Morin, P. J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, *402*(6757), 69–72.

Petry, W. K., Perry, K. I., & Mooney, K. A. (2012). Influence of macronutrient imbalance on native ant foraging and interspecific interactions in the field. *Ecological Entomology*, *37*(3), 175–183. https://doi.org/10.1111/j.1365-2311.2012.01349.x

Petry, W. K., Soule, J. D., Iler, A. M., Chicas-Mosier, A., Inouye, D. W., Miller, T. E. X., & Mooney, K. A. (2016). Sex-specific responses to climate change in plants alter population sex ratio and performance. *Science*, *353*(6294), 69–71.

Plowman, N. S., Hood, A. S. C., Moses, J., Redmond, C., Novotny, V., Klimes, P., & Fayle, T. M. (2017). Network reorganization and breakdown of an ant–plant protection mutualism with elevation. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1850), 20162564. https://doi.org/10.1098/rspb.2016.2564

Pons, X., & Tatchell, G. M. (1995). Drought stress and cereal aphid performance. *Annals of Applied Biology*, *126*(1), 19–31. https://doi.org/10.1111/j.1744-7348.1995.tb05000.x

Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., … Slade, E. M. (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, *356*(6339), 742–744.

Sagata, K., & Gibb, H. (2016). The effect of temperature increases on an ant-Hemiptera-plant interaction. *PLoS ONE*, *11*(7), e0155131. https://doi.org/10.1371/journal.pone.0155131

Sam, K., Koane, B., & Novotny, V. (2015). Herbivore damage increases avian and ant predation of caterpillars on trees along a complete elevational forest gradient in Papua New Guinea. *Ecography*, *38*(3), 293–300. https://doi.org/10.1111/ecog.00979

Sanders, N. J., Lessard, J.-P., Fitzpatrick, M. C., & Dunn, R. R. (2007). Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography*, *16*(5), 640–649. https://doi.org/10.1111/j.1466-8238.2007.00316.x

Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M., & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *The Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 245–269. https://doi.org/10.1146/annurev.ecolsys.39.110707.173430

St. Clair, S. B., Monson, S. D., Smith, E. A., Cahill, D. G., & Calder, W. J. (2009). Altered leaf morphology, leaf resource dilution and defense chemistry induction in frost-defoliated aspen (*Populus tremuloides*). *Tree Physiology*, *29*(10), 1259–1268. https://doi.org/10.1093/treephys/tpp058

Staab, M., Blüthgen, N., & Klein, A.-M. (2015). Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment. *Oikos*, *124*(7), 827–834. https://doi.org/10.1111/oik.01723

Stadler, B., & Dixon, A. F. G. (2005). Ecology and evolution of aphid-ant interactions. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 345–372. https://doi.org/10.1146/annurev.ecolsys.36.091704.175531

Straw, N. A., Timms, J. E. L., & Leather, S. R. (2009). Variation in the abundance of invertebrate predators of the green spruce aphid *Elatobium abietinum* (Walker) (Homoptera: Aphididae) along an altitudinal transect. *Forest Ecology and Management*, *258*(1), 1–10. https://doi.org/10.1016/j.foreco.2009.03.032

Tegelaar, K., & Leimar, O. (2014). Alate production in an aphid in relation to ant tending and alarm pheromone. *Ecological Entomology*, *39*(5), 664–666. https://doi.org/10.1111/een.12130

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*(12), 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Vasseur, D. A., & McCann, K. S. (2005). A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *The American Naturalist*, *166*(2), 184–198. https://doi.org/10.1086/431285

Vidal, M. C., & Murphy, S. M. (2018). Bottom-up vs. top-down effects on terrestrial insect herbivores: A meta-analysis. *Ecology Letters*, *21*(1), 138–150. https://doi.org/10.1111/ele.12874

Voigt, W., Perner, J., Davis, A. J., Eggers, T., Schumacher, J., Bährmann, R., … Sander, F. W. (2003). Trophic levels are differentially sensitive to climate. *Ecology*, *84*(9), 2444–2453. https://doi.org/10.1890/02-0266

Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1549), 2019–2024.

Wimp, G. M., & Whitham, T. G. (2001). Biodiversity consequences of predation and host plant hybridization on an aphid–ant mutualism. *Ecology*, *82*(2), 440–452.

Zelikova, T. J., Dunn, R. R., & Sanders, N. J. (2008). Variation in seed dispersal along an elevational gradient in Great Smoky Mountains National Park. *Acta Oecologica*, *34*(2), 155–162. https://doi.org/10.1016/j.actao.2008.05.002

Zhang, S., Zhang, Y., & Ma, K. (2015). Mutualism with aphids affects the trophic position, abundance of ants and herbivory along an elevational gradient. *Ecosphere*, *6*(12), 1–11. https://doi.org/10.1890/ES15-00229.1

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer. https://doi.org/10.1007/978-0-387-87458-6_11

SUPPORTING INFORMATION

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

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