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LETTER

Bears benefit plants via a cascade with both antagonistic and mutualistic interactions

Joshua B. Grinath,[1,2]* Brian D. Inouye[1] and Nora Underwood[1]

[1]*Biological Science Florida State University Tallahassee, FL, 32306-4295, USA*

[2]*Rocky Mountain Biological Laboratory P.O. Box 519, Crested Butte, CO, 81224, USA*

**Correspondence: E-mail: grinath@bio.fsu.edu*

Abstract

Predators can influence primary producers by generating cascades of effects in ecological webs. These effects are often non-intuitive, going undetected because they involve many links and different types of species interactions. Particularly, little is understood about how antagonistic (negative) and mutualistic (positive) interactions combine to create cascades. Here, we show that black bears can benefit plants by consuming ants. The ants are mutualists of herbivores and protect herbivores from other arthropod predators. We found that plants near bear-damaged ant nests had greater reproduction than those near undamaged nests, due to weaker ant protection for herbivores, which allowed herbivore suppression by arthropod predators. Our results highlight the need to integrate mutualisms into trophic cascade theory, which is based primarily on antagonistic relationships. Predators are often conservation targets, and our results suggest that bears and other predators should be managed with the understanding that they can influence primary producers through many paths.

Keywords

Chrysothamnus viscidiflorus, ecological network, food web, honeydew mutualisms, indirect interactions, trophic cascades, *Ursus americanus*.

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INTRODUCTION

Food webs generally only consider antagonistic predator–prey relationships. In this context, trophic cascades occur when predators suppress herbivores, indirectly benefiting plants (Hairston *et al*. 1960; Terborgh & Estes 2010; Estes *et al*. 2011). Typically, predators in higher trophic positions are thought to create cascades by preying on intermediate predators, weakening predator–herbivore interactions and reducing primary production (Carpenter *et al*. 1987; Estes *et al*. 1998). However, the cascading influence of predators can be non-intuitive; for instance, fish can provide benefits to terrestrial plants by consuming larval dragonflies that as adults are predators of pollinators (Knight *et al*. 2005). The full influence of predators may be difficult to anticipate because cascades can be mediated by both antagonistic (negative) and mutualistic (positive) species interactions. These different types of interactions are usually measured in separate studies, ignoring potentially important links. Though mutualistic interactions are often regarded as non-trophic relationships, most mutualisms involve exchanges of resources and can be integrated with antagonistic interactions by adopting a consumer-resource perspective of ecological webs (Holland *et al*. 2005; Holland & DeAngelis 2010). To our knowledge only two studies have analysed cascades with both predators comprising a fourth trophic level and mutualistic interactions. These studies found that predator-suppression of ants engaged in a mutualism with plants can be detrimental for plants (Letourneau & Dyer 1998), and predators that increase pollinator visitation can benefit plants (Knight *et al*. 2005). Both of these studies investigated plant–animal mutualisms; the influence of animal–animal mutualisms in cascades remains unclear, especially for mutualisms that link predators and herbivores. If predators suppress predator–herbivore mutualisms, can they generate cascading effects that are beneficial for plants?

To answer this question, we investigated the potential for black bears to alter plant performance by eating ants that are mutualists of herbivores (Fig. 1). Though ants may seem like a tiny meal for large-bodied bears, ants are on the menu for many bear species including grizzly (Swenson *et al*. 1999) and sloth bears (Bargali *et al*. 2004), and black bears in the US have a large appetite for ants (Noyce *et al*. 1997; Baldwin & Bender 2009). Ants are an abundant, high-energy food source comprising almost a third of the volume of bear diets in Rocky Mountain National Park, Colorado (Baldwin & Bender 2009). We studied a montane meadow ecosystem near Almont, Colorado, where black bears forage on ants (*Formica obscuripes* Forel: Formicidae, the dominant ant in this ecosystem) by digging into nests to consume immature and adult ants (Fig. 1a).

Because ants interact with many species, bear consumption of ants has the potential to cause indirect effects across the ecological community. In this system, ants are mutualists of plant-sucking treehoppers, which provide ants with food (honeydew) in return for protection from predators (Styrsky & Eubanks 2007; Grinath *et al*. 2012). This protection is generally perceived as a non-consumptive service (Holland *et al*. 2005; Holland & DeAngelis 2010). Here, we argue that protection often involves intraguild predation (Letourneau *et al*. 2009) and should be thought of as a combination of density and trait-mediated indirect effects (Werner & Peacor 2003). Ants cooperatively attack (Fig. 1b) and prey on (Fig. 1c) other arthropod predators that would otherwise consume herbivores when undeterred by ants (Fig. 1d). Ant predation on

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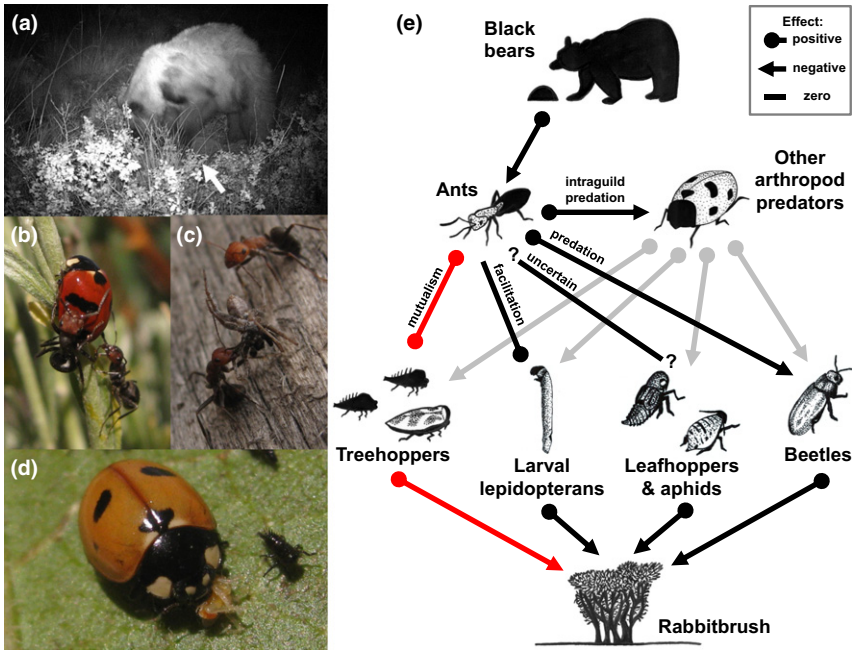

Figure 1 Photographic evidence and web diagram showing the cascade of effects from bears to plants. (a) A bear digs into an ant nest to consume ants; the white arrow is embedded to focus viewer attention on nest material pulled back by the bear. (b) The ants are mutualists of herbivores, which they benefit by interfering with other arthropod predators, such as ladybeetles. (c) This ant protection often results in ant predation of other arthropod predators. (d) Without ant suppression, arthropod predators consume herbivores, to the benefit of plants. In the diagram (e), reciprocal interactions are indicated by paths that end in circles for organisms that benefit from the interaction and arrows for organisms that are negatively affected by the interaction. In a previous study, ants had a negative net effect on plants due to the ant–treehopper mutualism and the treehopper's effect on plants (red paths) (Grinath *et al.* 2012). Interactions between non-ant arthropod predators and herbivores are shown in grey to highlight paths that may be altered by intraguild predation. The photo in (a) was taken using night-vision photography with a Bushnell Trophy XLT trail camera (Bushnell Outdoor Products, Overland Park, KS, USA).

arthropod predators creates enemy-free space for treehoppers that can facilitate other herbivores (Fritz 1983), such as larval lepidopterans (Fig. 1e) (Grinath *et al.* 2012). In addition to the positive effects of ants on herbivores, which are detrimental for plants, ants are also predators of herbivores and can indirectly benefit plants by reducing herbivory (Fig. 1e) (Styrsky & Eubanks 2007; Grinath *et al.* 2012). Thus, the net effect of ants on plants depends on the relative contribution of positive and negative component interactions. We previously found that the ant's net effect on rabbitbrush (*Chrysothamnus viscidiflorus* Nuttall: Asteraceae) plants was reduced reproduction, primarily due to the positive effect of ants on treehoppers and the treehopper's negative effect on plants (Fig. 1e). In the context of these interactions, bears can be considered a fourth trophic level predator. Though black bears are omnivorous, they do not directly consume rabbitbrush and they interact with plants indirectly through their role as predators of ants.

We used natural bear damage to ant nests and experimental manipulations to test whether bears indirectly influence plants and to decipher the mechanism responsible for this effect. We expected that bear damage to ant nests would benefit nearby rabbitbrush plants because bear damage may decrease ant protection for treehoppers and other herbivores. To test this we manipulated mutualist treehoppers and ants on rabbitbrush near damaged and undamaged ant nests, and analysed the responses of plants and arthropods to bears. Considering the mechanism for bear effects on plants, we hypothesised that predation on ants by bears allowed other arthropod predators to devour or deter herbivores, thus benefiting plants. Other mechanisms may be operating simultaneously, such as decreased herbivore sanitation when honeydew accumulates in the absence of ants (Way 1963). However, we focused on arthropod predators because ants are known to benefit treehoppers by providing protection from predators (e.g. Cushman & Whitham 1989). To assess this prediction, we used a field experiment manipulating the abundances of both foraging ants and non-ant arthropod predators, primarily ladybeetles and crab spiders, on rabbitbrush plants with treehoppers. Overall, we found that both mutualistic and antagonistic interactions are important in creating a trophic cascade.

MATERIALS AND METHODS

Experimental system

We analysed an ecological web within a mountain meadow in Almont, Colorado (meadow size = ~ 2 ha, elevation = 2769 m, latitude = 38.719, longitude = −106.816). Green rabbitbrush is common in this meadow and hosts phloem-feeding treehoppers (*Publilia modesta* Uhler: Membracidae), which form aggregations of up to several hundred individuals per plant (Reithel & Campbell 2008). The treehoppers are patchily distributed across the landscape, but are very

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abundant locally and present on many plant species (Reithel & Campbell 2008). Aphids (Aphidae) and leafhoppers (Cicadellidae) also feed on plant phloem and can be positively or negatively affected by treehopper-tending ants (Billick *et al.* 2007; Grinath *et al.* 2012). In addition, the ant–treehopper mutualism positively affects larval lepidopterans (tent caterpillars and coleophorids) and negatively affects leaf-chewing beetles (Chrysomelidae) (Grinath *et al.* 2012). Ladybeetles (Coccinellidae) and crab spiders (Thomisidae) are prevalent predators in this meadow and we refer to these species, together with active-hunting spiders and hemipteran predators, as 'other arthropod predators'. Black bears (*Ursus americanus* Pallas: Ursidae) are predators of ants that dig into nests to consume large numbers of immature and adult ants (Noyce *et al.* 1997). We have observed black bears in Almont, and bear presence in our meadow was evident from damage to ant nests, paw prints, ant carcass-filled bear faeces, autosensor trail photography (Fig. 1), and bite-marks to field equipment.

Ant nest disturbance surveys

We surveyed ant nests from 2009 to 2012 to investigate patterns of disturbance to nests. In July 2009, we collected data on the incidence of bear damage to 35 focal ant nests. We also recorded ant nest activity; we defined inactive nests as those from which no more than one worker emerged when the ground next to the nest was beaten by hand. All of these nests were active in 2008. Of the 35 focal ant nests, nine were damaged by bear and eleven became inactive. Three of these nests were both bear-damaged and inactive; more nests like these may have gone undetected in our surveys if ants rebuilt their nest following bear damage and then became inactive. We also surveyed randomly selected ant nests for bear damage in the same meadow in 2010 (55 nests), 2011 (55 nests) and 2012 (50 nests). To improve our understanding of whether bear damage caused nests to become inactive, we monitored an additional 36 ant nests for damage from 2010 to 2012 and recorded nest activity in September 2012.

Ant nest disturbance experiment

To investigate the potential for bear damage to ant nests to cause cascading effects on plants, in 2009 we performed separate manipulations of treehoppers and ants on 148 rabbitbrush plants within 3 metres of the 35 focal ant nests (blocks). We manipulated treehoppers within groups of 4 plants surrounding each of 20 ant nests and manipulated ants within groups of 6 plants surrounding each of 15 ant nests; some groups had fewer observations due to plant death. Treehoppers were manipulated by adjusting (i.e. via removal or addition) initial nymph abundances (20–30 per plant) on plants on July 9. For treehopper-absent plants, we removed all treehoppers found during the experiment. We manipulated ant presence by supplying treehoppers to attract ants to experimental plants; for ants-absent plants, ants were excluded with sticky Tanglefoot barriers (Tanglefoot Company, Grand Rapids, MI, USA) at the plant's base. We trimmed bridging vegetation around each experimental plant to minimise treehopper migration and ant access from neighbouring plants. Data on insects consist of cumulative abundances from 4 surveys, conducted from mid-July to mid-August. Beetle damage was measured as the per cent of leaves with beetle-skeletonising out of 50 haphazardly selected leaves for each plant on August 10. Plant reproduction was measured by weighing seeds (mg) that were bagged in mesh on August 15 and collected on September 16; the initial number of flower buds was surveyed on July 13 to account for the plant's reproductive potential early in the growing season. Plant growth was measured as the difference in plant sizes on June 17 and August 14. The size of each plant was calculated non-destructively as the volume of a cone from measurements of plant height and surface area covered; this volume was converted to aboveground dry biomass with an allometric curve we obtained from 40 rabbitbrush from the meadow that were measured, collected and dried at 66 °C for 72 h ($g_{dry\ plant\ mass} = 0.00568\ cm^3 - 0.117$; $P < 0.001$, $R^2 = 0.94$).

We evaluated the effects of ant nest disturbance on plants and insects with generalised linear mixed-effects models (GLMM) in R v3.1.1 (Zuur *et al.* 2009; R Development Core Team 2014) (Fig. 3 and Table S1) and structural equation models (SEM) in AMOS 5.0.1 (Arbuckle 2003; Grace 2006) (Fig. 4, Tables S2–S4, and Figure S1). Because we have found that treehopper and ant manipulations have similar effects on this community and treehopper and ant abundances are interdependent (Grinath *et al.* 2012), we combined data from both manipulations to form a variable indicating the presence of the mutualism. The mutualism was present (78/148 experimental plants) when both ants and treehoppers were present, and absent otherwise. We then used GLMMs to model plant and arthropod responses as a function of presence of bear damage, nest inactivity, mutualism and their interaction, with plants nested within ant nests and ant nests included as a

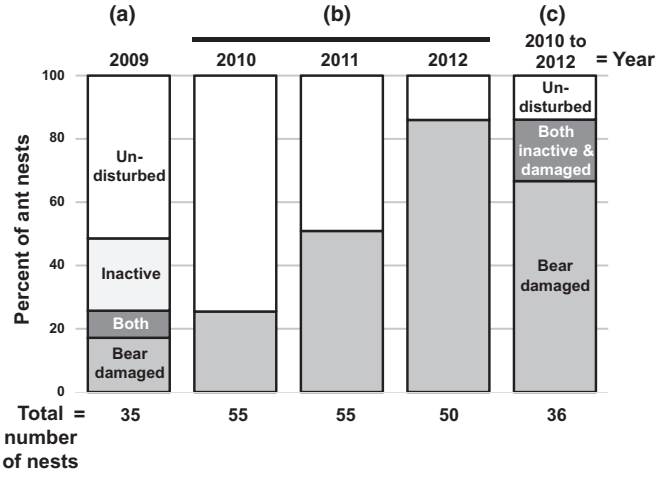

Figure 2 Per cent of ant nests that were disturbed from 2009 to 2012. (a) In 2009, we documented bear damage to ant nests and whether nests were inactive. (b) From 2010 to 2012, we identified active nests at the beginning of the summer and surveyed incidence of bear damage within each summer. (c) For a separate group of ant nests, we surveyed bear damage from 2010 to 2012 and then determined nest activity in 2012.

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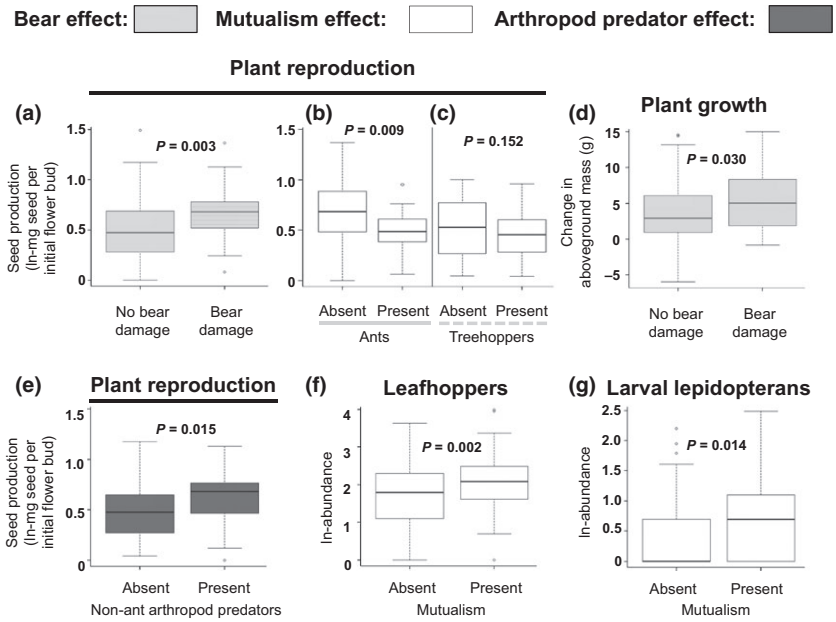

Figure 3 Generalised linear model (GLM) and mixed-effects model (GLMM) results for the Ant Nest Disturbance Experiment in 2009. (a) We found an effect of bear damage on plant reproduction near ant nests (GLMM: Gaussian, $\chi^2 = 8.95$, $P = 0.003$). We also found an effect of the ant-treehopper mutualism on plant reproduction, which was primarily due to the effects of (b) ants (GLM: Gaussian, $\chi^2 = 6.75$, $P = 0.009$) and not (c) treehoppers (GLM: Gaussian, $\chi^2 = 2.05$, $P = 0.152$). Additionally, (d) bear damage to ants affected plant growth (GLMM: Gaussian, $\chi^2 = 4.69$, $P = 0.030$), and (e) the presence of non-ant arthropod predators was correlated with plant reproduction (GLM: Gaussian, $\chi^2 = 5.94$, $P = 0.015$). Abundances of (f) leafhoppers (GLMM: Gaussian, $\chi^2 = 9.29$, $P = 0.002$) and (g) larval lepidopterans (GLMM: Binomial, $\chi^2 = 6.03$, $P = 0.014$) increased in the presence of the mutualism. All contrasts are shown as box-and-whisker plots.

random variable. We used the package 'nlme' for GLMMs with Gaussian-distributed residuals and 'lme4' for GLMMs with other distributions. We chose the best model for each response variable by comparing Akaike Information Criterion (AIC) scores and visually assessing error distributions. Gaussian-distributed models were selected by comparing models with random intercepts vs. random slopes and intercepts, followed by comparing models with alternative variance structures (varIdent for each explanatory factor combination and main effect). To analyse count data, we compared models with Poisson and Negative Binomial error distributions. If an appropriate model was not found, we fitted a Gaussian-distributed model to ln(data + 1) transformed data. We used presence/absence data for arthropods with low abundances, and analysed presence/absence and proportional data with models assuming a Binomial distribution. In some cases, one to three outlying data points were removed to attain appropriate model fit. In addition, zeros were removed from aphid abundance data and extreme values over 15 g of growth were removed from plant growth data, thereby focusing on average plant growth, to achieve appropriate model fit. To aid interpretation of the GLMMs, we used generalised linear models (GLMs; package 'MASS') to analyse the effects of ant and treehopper manipulations on ants, treehoppers and plants. We also used GLMs to assess whether the presence of non-ant arthropod predators was correlated with plant responses (Table S1). All final analyses were conducted using analysis of deviance with the 'car' package to calculate GLMMs with Type II SS and GLMs with Type III SS.

We used multi-group SEM to understand the paths leading to effects on plants when ant nests were undisturbed or bear-damaged. Using our previous knowledge of the system (Grinath *et al.* 2012), we developed SEMs to examine cascading effects from ants to plants via herbivores that are influenced by ants (Figure S1). We included flower buds as a variable representing plant quality early in the season. We employed a model pruning strategy to determine whether effects of flower buds and unexplained covariances contributed to model fit (Table S2 and Figure S1). We deleted each path to examine its effect on model fit, and then replaced the deleted path before perturbing the next interaction. Following this perturbation, paths were retained if their deletion caused lack-of-fit: when χ^2 P-values < 0.10 and/or when Akaike's information criteria (AIC), root mean error of approximation (RMSEA), and expected cross-validation index (ECVI) values increased from those of the full model (for at least two of three indices). The best-fit model for the entire data set (Table S2) was used to compare species' effect sizes when ant nests were undisturbed vs. bear-damaged. Raw per capita effects, total effects, and standardised effect sizes were calculated for the best model in each group (Fig. 4, and Tables S3 and S4). We used a P-value threshold of 0.10 in the SEMs because it is analogous to interpreting one-tailed t-tests for directional effects, consistent with our previous study in this system (Grinath *et al.* 2012). Difficulty obtaining $P < 0.05$ in ecological data sets may warrant a less conservative threshold for SEMs when complementary analyses provide support (Grace 2006). We used the GLMMs as complimentary analyses to assist the

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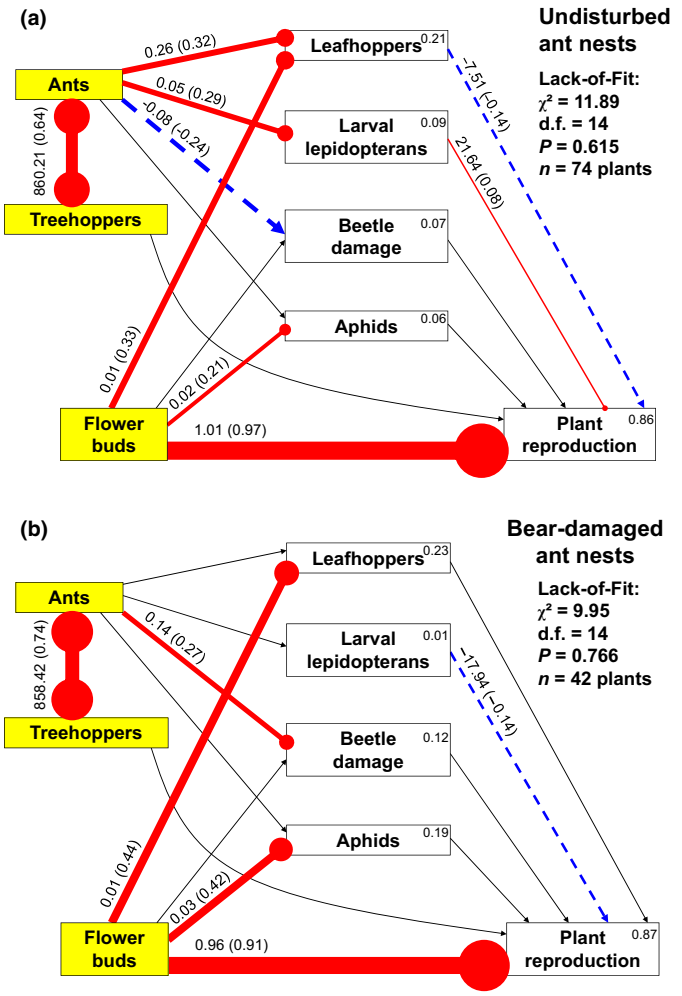

Figure 4 Structural equation model (SEM) results for the Ant Nest Disturbance Experiment in 2009. A multi-group analysis showed differences between cascades of effects when ant nests were (a) undisturbed and (b) damaged by bears. In the SEMs, independent variables are yellow boxes, and dependent variables are white boxes with R^2 values in the top corner. Single-headed paths represent direct effects and double-headed paths (i.e. between independent variables) are unresolved covariances/correlations. Significant paths ($P < 0.10$) are shown in colour with raw (and standardised) per capita effect sizes. Positive effects are solid red paths that end in circles, negative effects are dashed blue paths that end in arrowheads, and non-significant effects are thin black paths without coefficients. Significant paths are weighted by standardised effect size.

interpretation of paths in the SEMs. To understand how the cascade was influenced by ant nest disturbance, we also evaluated cascading effects by fitting the same SEM to data from all disturbed ant nests (i.e. nests that were bear-damaged and/or inactive) and calculated raw and standardised effect sizes (Tables S3 and S4, and Figure S1).

Arthropod predator-effect experiment

To test whether the mechanism for the cascade is through ant suppression of arthropod predators, in 2010 we factorially crossed manipulations of foraging ants and abundances of other arthropod predators on individual rabbitbrush. A total of 90 rabbitbrush were selected, in groups of six surrounding each of 15 active ant nests. Treehopper nymph abundances were adjusted to 60 initial treehoppers per plant on July 13 and neighbouring vegetation was trimmed to restrict treehopper and ant movement. We established three levels of ant attendance: a nearly ant-free treatment for which we used sticky barriers on plant stems; a 'few ants' treatment, for which we removed all ants in weekly surveys; and a control with 'many ants'. Because *F. obscuripes* foragers return daily to the same honeydew-producer aggregations (McIver & Yandell 1998) and ant attendance increases slowly after ant-removals, we expected that the ant-removals would create periods of predator vulnerability for treehoppers and other herbivores that benefit from ant presence. Reduced or elevated abundances of other arthropod predators were manipulated by excluding or enclosing predators on plants enclosed within fibrous 'breather' bags (Palm Tree Packaging, Apopka, FL, USA). Each bag had one opening at the bottom to allow ant access to the plant, and neighbouring vegetation was trimmed to minimise migration by insects and spiders. We sweep-netted vegetation in the surrounding meadow to add adult ladybeetles (1 per week for 5 weeks) and crab spiders (1 per week for 4 weeks) to plants in the 'many arthropod predators' treatment. All arthropod predators other than ants were removed from plants in the 'few arthropod predators' treatment during weekly surveys. For predator-addition plants, predators were added 3–4 days before each data survey. Data on all insects and spiders are cumulative abundances from 5 surveys from mid-July to mid-August. Plant reproduction was measured from seeds bagged on August 17 and collected September 14; flower bud abundance was surveyed on June 28. Plant growth was measured using the non-destructive technique described above as the difference between aboveground plant mass on June 22 and August 15.

The cascade of effects from ants and other arthropod predators to plants was analysed with multi-group SEM (Fig. 5, Tables S5–S7, and Figure S1) and GLMs (Table S8) to compare arthropod predator effects when there were no, few, or many ants. The SEM focused on arthropod predator effects on herbivores that benefit from ant presence (treehoppers, larval lepidopterans, and leafhoppers) and the herbivores' effects on plants. Flower bud abundance was included as a covariate. We chose to represent treehoppers with the variable 'change in treehoppers' because many treehoppers were initially supplied to plants; this variable represents treehopper survival (Grinath *et al.* 2012). Change in treehoppers was calculated as abundance in the last survey minus abundance at the start of the experiment. We found a best SEM using all the 2010 data and the pruning strategy described above (Table S5), and calculated raw per capita effects, total effects, and standardised effects for the best model in all three groups (Fig. 5, and Tables S6 and S7). Complimentary GLMs were used to analyse effects on plant traits and arthropod abundances. We used ant abundance as a continuous explanatory variable in the GLMs; this variable was binned into treatment groups to improve model fit for the plant variables. For count data, we compared models with Poisson or Negative Binomial

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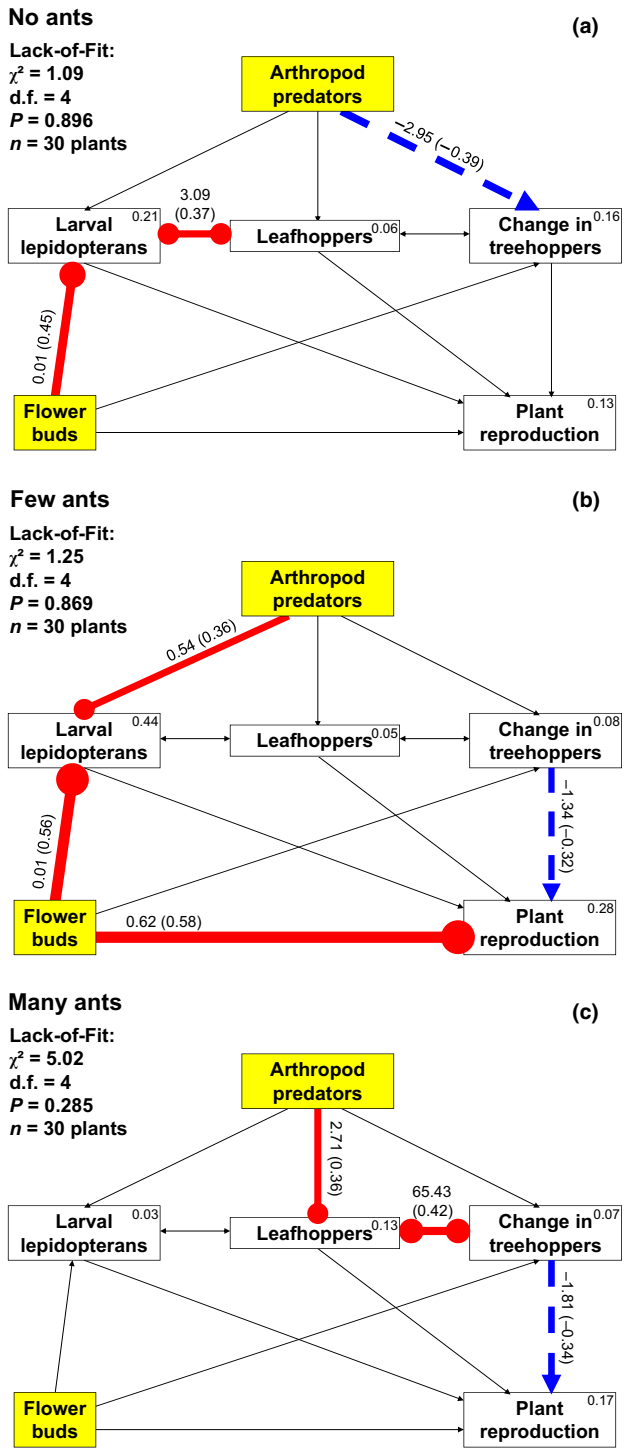

Figure 5 Structural equation model (SEM) results for the Arthropod Predator-Effect Experiment in 2010. Multi-group SEMs show how arthropod predators affected herbivores and plants when there were (a) no, (b) few, or (c) many ants. The SEMs are interpreted as in Fig. 2, with the additional note that double-headed arrows between herbivores are unresolved covariances/correlations.

distributions. If the models did not fit well, then variables were ln-transformed and analysed assuming Gaussian-distributed errors.

RESULTS

Incidence of bear damage to ant nests was highly variable across years. Black bears attacked 26% of the focal ant nests in 2009 (Fig. 2a) and a similar percentage in 2010 (Fig. 2b). This rose to 51% and 86% of nests receiving bear damage in 2011 and 2012 respectively. Additionally, we asked whether bear damage caused nests to become inactive (see methods for definition), because inactive nests have few foraging workers that might influence nearby plant success. Of the focal nests in 2009, 31% became inactive (Fig. 2a). Tracking bear damage to ant nests each summer from 2010 to 2012, we found that only nests attacked by bears became inactive (Fig. 2c).

We used the bear damage to ant nests in 2009 as a natural experiment to investigate the potential for cascading effects from bears to plants. Using GLMM (Table S1), we found that plants had significantly greater seed production near bear-damaged ant nests relative to undamaged nests (Fig. 3a). Plant reproduction was also significantly lower when the ant–treehopper mutualism was present (GLMM: Gaussian, $\chi^2 = 7.74$, $P = 0.005$). This response was due to the indirect effect of ants on plants through species other than treehoppers (Fig. 3b); mutualist treehoppers did not affect plant reproduction (Fig. 3c), suggesting that other facilitated herbivores were responsible for the ant effect. We also found that plants grew more when bears damaged nearby ant nests (Fig. 3d); there was some evidence that this effect may have been influenced by interactions among bear damage, nest inactivity, and the ant-treehopper mutualism (GLMM: Gaussian, 3-way interaction, $\chi^2 = 3.10$, $P = 0.078$).

Unlike plants, the GLMMs indicate that arthropods did not respond to the main effect of bear damage to ants; arthropod abundances were affected solely by the ant–treehopper mutualism (Table S1). Other predators were absent from plants more often when the mutualism was present (GLMM: Binomial, $\chi^2 = 4.79$, $P = 0.029$). Interestingly, the presence of arthropod predators correlated positively with plant reproduction (Fig. 3e). Similarities between this relationship and the effect of bear damage on seed production (Fig. 3a) suggest that non-ant arthropod predators contributed to the bear damage effect. In addition, abundances of leafhoppers (Fig. 3f) and larval lepidopterans (Fig. 3g) increased when the mutualism was present, indicating that ant effects on plants may have been caused by facilitation of these herbivores. Aphid abundances and beetle damage were unaffected by the factors in the GLMMs (Table S1).

Our multi-group SEM (Grace 2006) measured the effects of ants on insect herbivores and plant reproduction under varying conditions of ant nest disturbance (Tables S2–S4, and Figure S1). When ant nests were undisturbed (neither damaged by bears nor inactive; Fig. 4a), ants indirectly reduced plant reproduction. The negative effect of ants on plants was dominated by the ant's significant positive influence on herbivorous leafhoppers and the leafhoppers' negative effect on plant reproduction. Ants were strongly associated with mutualist treehoppers, but treehoppers did not directly affect plant reproduction. Moreover, ants had moderately strong beneficial effects on larval lepidopterans and potentially influenced plants via the lepidopterans' unexpected positive association with plant

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reproduction. As in our previous study (Grinath *et al.* 2012), ants weakly reduced chrysomelid beetle damage to plants, but this did not result in a measurable benefit to plants.

In contrast to the undisturbed conditions, when ant nests were damaged by bears (Fig. 4b) ants had a weaker influence on herbivores and did not affect plant reproduction. Near bear-damaged nests effects of ants on leafhoppers and larval lepidopterans, as well as effects of leafhoppers on plants, were not detected. Ants had a counterintuitive positive effect on beetle damage to plants, but beetles did not affect plant reproduction. The ant-treehopper mutualism (represented by an unresolved correlation) remained strong under all conditions of ant nest disturbance, but the directionality of this effect is unclear. When we fit this SEM to data from plants near all the disturbed ant nests (bear-damaged and/or inactive nests) we found a lack of cascading effects from ants to plants (Tables S3 and S4, and Figure S1). These results show that black bears can indirectly benefit plants by reducing the positive effects of ants on herbivores.

Additional manipulations of ants and non-ant arthropod predators showed that a plausible mechanism for the cascade is that plants benefitted when arthropod predators suppressed herbivores. Using a multi-group SEM (Tables S5–S7, and Figure S1), we compared effects of arthropod predators on plants when there were no, few or many ants. When there were no ants (Fig. 5a), we found that arthropod predators suppressed treehoppers. When few or many ants were present (Fig. 5b ,c), arthropod predators did not suppress treehoppers and treehoppers reduced plant reproduction, the latter effect becoming stronger with more ants. Neither leafhoppers nor larval lepidopterans affected plant reproduction. These 2010 results contrast with the 2009 data, which showed that ant-facilitated herbivores influenced plant reproduction, but mutualist treehoppers did not affect plants. Counter to expectation, non-ant arthropod predators were positively associated with leafhoppers and lepidopterans.

Complimentary GLMs support the SEM conclusion that herbivores and plants were influenced by interactions between ants and other arthropod predators (Table S8). Ants and non-ant predators interacted to affect treehopper abundances (Fig. 6a), and leafhoppers were more abundant on plants with greater ant abundances (Fig. 6b). Additionally, plants had lower reproduction as foraging ants became more abundant (Fig. 6c) and tended to have greater growth when non-ant predators were present (Fig. 6d). Initial flower bud abundance was a poor indicator of seed production in 2010 (Fig. 5), which may explain why there was not a significant interaction between ants and non-ant predators in the GLM for plant reproduction, for which seeds were standardised by bud abundance. Using flower buds as a separate covariate, the SEM indicates that ant and non-ant arthropod predator treatments did interact to affect seed production. Altogether, our results indicate that bear predation on ants allowed arthropod predators to suppress herbivores and thus benefit plants.

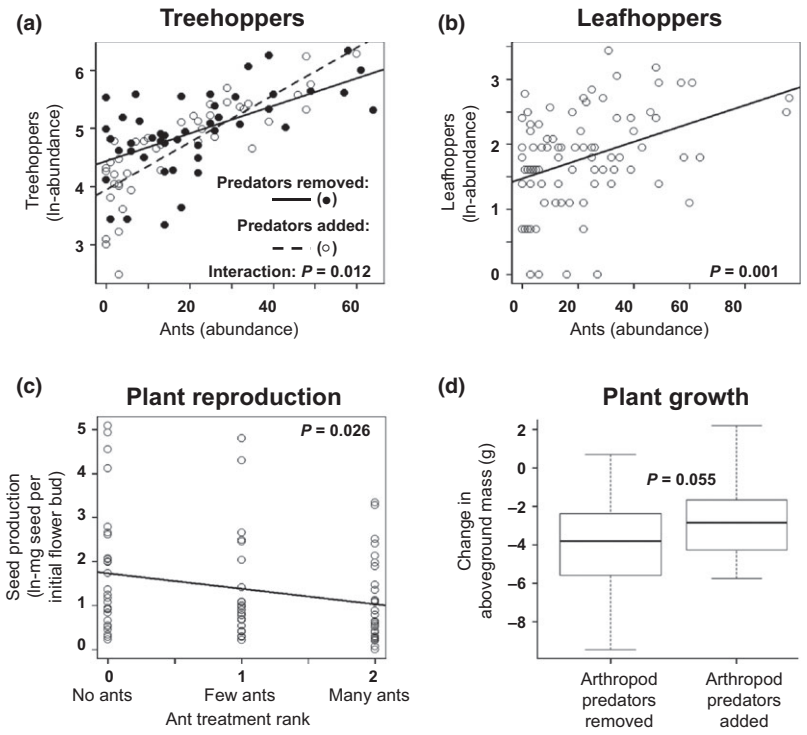

Figure 6 Generalised linear model (GLM) results for the Arthropod Predator-Effect Experiment in 2010. (a) Non-ant arthropod predators altered the benefits that treehoppers received from ants (GLM: Gaussian, $\chi^2 = 6.35$, $P = 0.012$). (b) Ants also had an effect on leafhopper abundances (GLM: Gaussian, $\chi^2 = 11.75$, $P = 0.001$). (c) Ants indirectly affected plant reproduction (GLM: Gaussian, $\chi^2 = 4.98$, $P = 0.026$), (d) whereas other arthropod predators marginally affected plant growth (GLM: Gaussian, $\chi^2 = 3.68$, $P = 0.055$). The regressions shown are post-hoc linear models; all were significant at $P < 0.05$. Data in (d) are provided as box-and-whisker plots.

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DISCUSSION

This study demonstrates that a trophic cascade can depend on the structure and strengths of multiple types of interspecific interactions. Though ecological webs are mostly composed of weak interactions (Wootton & Emmerson 2005; Vazquez *et al.* 2012), the mutualism in our study system is strong and is a driver of community dynamics (Grinath *et al.* 2012). Strong positive effects of ants on herbivores arise because ants suppress potentially strong predator effects on herbivores, via intraguild predation and interference. If protection-service mutualisms frequently disrupt strongly interacting natural enemies, then these mutualisms will influence the cascading effects of predators. Protection-service mutualisms are ubiquitous interactions that range from endosymbiont bacteria protecting their aphid hosts from minute parasitoids (Oliver *et al.* 2003) to ants that protect host trees from elephant damage (Stanton & Palmer 2011), and occur in both terrestrial and marine (Sonnenholzner *et al.* 2011) systems. There are likely many as yet unidentified cascades that depend on protection-service mutualisms. Mutualisms need to be integrated into trophic cascade theory to understand the often non-intuitive cascades that occur in webs with multiple types of species interactions (Goudard & Loreau 2008; Ings *et al.* 2009; Fontaine *et al.* 2011; Pocock *et al.* 2012). This integration may be accomplished by acknowledging that mutualisms involve consumer–resource relationships and can be considered along with antagonistic interactions in a consumer–resource perspective of ecological webs (Holland *et al.* 2005; Holland & DeAngelis 2010). Trophic cascades including mutualisms are likely to be important because, in theory, the interplay between antagonistic and mutualistic interactions increases the stability of ecological webs (Mougi & Kondoh 2012).

Our results suggest that the cascade from bears to plants varies from year to year. Incidence of bear damage to ant nests was highly variable among years of study, which likely altered cascade strength. Years with high percentages of damaged nests coincided with climatic conditions that may have caused a scarcity of other food sources for bears (a late spring in 2011, drought in 2012). This suggests that bears forage more heavily on ants in harsh environments, indicating the potential for strong cascades in these conditions. Additionally, many species are involved in the ecological web connecting bears and plants, and changes in interactions among component species will contribute to variation in the cascade. For instance, though the net effect of ants on plants was mediated by treehoppers in a previous experiment (Grinath *et al.* 2012), here we found that indirect effects on plants were mediated by leafhoppers in 1 year and treehoppers in the next. This variation is likely the result of changes in enemy-free space for herbivores, which could be due to differences in effects of individual arthropod predator species or in ant aggressiveness towards predators and herbivores across years. However, if ants consistently create enemy-free space for herbivores and these herbivores reduce plant performance, then bear damage to ants would consistently benefit plants. Also, though we attempted to consider all important species, rare species may have gone unnoticed and contributed to the variability we observed.

Several of our results were counter to expectation; some paths in the SEMs that we expected to be negative were found to be positive. For the effect of larval lepidopterans on plant reproduction, this positive association could have arisen from plants responding with compensatory seed production, or from herbivores benefiting from plants with greater seed production. For effects of ants on beetle damage and of non-ant predators on lepidopterans and leafhoppers, such positive paths could have occurred if predators alleviated competition between prey, or if predators were attracted to plants with these prey. Further study is required to explain these relationships and resolve the direction of causality (Grace 2006).

We found evidence suggesting that bears benefitted plants by allowing non-ant arthropod predators to suppress herbivores, but other mechanisms may have contributed to the cascade. For instance, bear damage could alter the nutritional demands of ant colonies. As ants rebuild nests following bear damage, ant colonies may demand greater amounts of protein to feed new larval production. This could increase predation by ants on herbivores and cause facilitation to switch to predation. Alternatively, bear damage to nests could alter ecosystem engineering by ants. This ant species builds nests composed of twigs, leaves and other plant material (Weber 1935), creating a patchy distribution of plant litter. After bear damage, ants may modify their demand for plant material to reconstruct nests and thereby alter the soil environment in ways that benefit plants. For example, sagebrush is co-dominant with rabbitbrush at our field site and is known to have allelopathic properties (Preston *et al.* 2002). Ants may increase collection of sagebrush litter following bear damage and alter allelopathic effects on rabbitbrush. Additional study is necessary to decipher the relative contribution of multiple potential mechanisms for generating this cascade.

We found an effect of black bears on plants through a surprising cascade of interactions. Disturbances to predators can destabilise food webs (May 1973; O'Gorman & Emmerson 2009) and alter ecosystem functioning (Terborgh & Estes 2010; Estes *et al.* 2011), and disturbances to black bears may have similar consequences. Black bear populations are affected by human encroachment and hunting, as well as by provisioning of food from humans. In recent decades bears in Colorado have increased their consumption of human-derived foods while decreasing their consumption of insects (Baldwin & Bender 2009). We expect that in locations where bears rely heavily on food from humans or decrease in abundance, the strength of cascades on plants may weaken, potentially shifting plant diversity. The ant, treehopper and plant species that we studied are common throughout western North America (Cushman & Whitham 1989; Jurgensen *et al.* 2005; Tilley & St. John 2012). Additionally, the treehopper species in our study feeds, and is tended by ants, on over 15 plant species (Reithel & Campbell 2008), and numerous herbivore species (e.g. aphids, scales) on other plants are mutualistic partners with the ants we studied. Thus, bears could have indirect effects on the majority of plant species in this ecosystem, and may influence coexistence among plant species via pathways that depend on multiple types of ecological interactions. Rabbitbrush plants reproduce only by seed, and our results suggest that bears are important for maintaining high seed

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production and potentially the local dominance of this plant, though whether rabbitbrush recruitment is seed or site limited is unknown. Land managers should be mindful that, like many predators (Terborgh & Estes 2010; Estes *et al.* 2011; Ripple *et al.* 2014), bears can cause cascading effects on plants.

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STATEMENT OF AUTHORSHIP

J.B.G. designed the research, performed research and analysed data; J.B.G, B.D.I. and N.U. wrote the paper. Artwork was composed by J.B.G.

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