

Title: Indirect effect of black bears on sunflowers in nitrogen-polluted and pristine steppe

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Abstract

Both antagonistic and mutualistic types of interactions between species occur in most ecosystems, and these different types of interactions can contribute to indirect effects between species, such as trophic cascades. These interactions can be altered by humans, and one major way this is occurring is via atmospheric nitrogen (N) pollution. Though research has been conducted to study how N pollution affects cascades, results have not been consistent. The objective of this experiment is to determine the indirect effect of black bears on mule's ear sunflowers through a cascade of antagonistic and mutualistic interactions, and whether N pollution could alter this cascade. This sunflower is a primary host for sap-sucking treehoppers, which can complete their entire life cycle on the plant, potentially harming plant performance. The treehoppers have a mutualistic relationship with thatch ants, which provide protection against predators while the treehoppers provide sugary food for the ants. These ants are a common food for black bears, and this predation has been shown to indirectly affect rabbitbrush plants. Building on a 15-year N enrichment study, I tested whether black bears and ants indirectly affect mule's ears sunflowers (*Wyethia magna*), and if long-term N deposition could affect this cascade. I manipulated initial treehopper nymph densities on individual plants in plots with added or ambient N and with either active or inactive (due to bear predation) thatch ant nests, and measured responses of insects and plants to these experimental conditions. I found that while treehoppers negatively affected plant water content, there was no evidence for a trophic cascade from bears to mule's ears sunflowers. However, N addition did alter ant abundance responses to treehopper density, suggesting that N pollution may weaken the mutualistic interaction between these animals. Further work is needed to account for the effects of cattle grazing and other factors to gain a clearer understanding for the effects of predators and N pollution in this ecological web.

Introduction

Species interact both antagonistically (predation, herbivory, competition) and mutualistically (mutualism, facilitation), and these interactions are fundamental to the function and structure of ecosystems around the world (Bronstein, 1994; Holland et al., 2005). These interactions contribute to indirect effects in ecological webs, such as trophic cascades (Knight et al., 2006; Grinath, Inouye, & Underwood 2015), and are important to consider together to understand the stability of ecological networks (Sauve, Fontaine, & Thebault, 2013). A trophic cascade occurs when a top predator has an indirect effect on lower trophic levels (Ripple et al., 2016). Across ecosystems, trophic cascades play critical roles in maintaining ecosystem structure

and function by regulating species interactions and population dynamics (Estes et al. 2011, Ripple et al., 2014; Ripple et al., 2016), but there is much still to learn about cascades that include both antagonistic and mutualistic interactions.

An example of a trophic cascade that includes antagonistic and mutualistic interactions is the effect of American black bears (*Ursus americanus*) on rabbitbrush plants (*Chrysothamnus viscidiflorus*) in Colorado (Grinath et al., 2015). This cascade includes a mutualistic ‘food-for-protection’ relationship between treehoppers (*Publilia modesta*) and their patrolling ants (*Formica obscuripes*). The inclusion of a mutualistic interaction in a chain of antagonistic interactions changed the prediction for how plants would respond. In trophic cascades of antagonistic species interactions, top predators are expected to be detrimental for plants across four trophic levels. With this mutualism, the top predators benefit plants across four trophic levels. It is unclear how common such cascades may be, and how humans may be altering these indirect interactions (Grinath et al., 2015; Grinath, 2018).

Human activities are altering water and nutrient cycles in ecosystems worldwide (Vitousek et al., 1997a), and these changes also impact trophic cascades. In particular, human-induced nitrogen (N) input has doubled the amount of biologically-available N on Earth (Vitousek et al., 1997b), which has greatly impacted plant assemblages in many ecosystems (Bobbink et al., 2010). The impact of this N pollution on trophic cascades is also significant. For instance, N addition in a spider-Collembola-plant litter food web decreased *Collembola* populations and spider-mediated litter decomposition (Liu et al. 2018). In a study on thatch ant-treehopper cascades on white sagebrush (*Artemisia ludoviciana*), high N levels increased cascade strength resulting in greater sagebrush reproduction (Strauss, 1987). However, a later study with lower N levels and the same ant and treehopper species showed weakened plant-herbivore interactions and a weakened cascade for rabbitbrush plants (Grinath, 2018), indicating a need for more research to understand these varying effects.

Here, I assessed whether black bears and ants indirectly affect mule’s ears sunflowers (*Wyethia magna*), and if long-term N deposition could affect this cascade. This work built on a long-term (15 year), low-level N enrichment experiment designed to evaluate whether N deposition alters trophic cascades involving black bears, thatch ants, treehoppers, and plants (Grinath, 2018). Over the course of this experiment, bears caused ant nests in some of the experimental plots to die. In addition to rabbitbrush, mule’s ears sunflowers are also a common host plant for treehoppers in this system (Reithel & Billick, 2006; Reithel & Campbell, 2008). Within this experiment, I manipulated treehopper density on individual mule’s ears sunflowers and measured plant and insect responses to assess effects of N pollution, bears, ants, and treehoppers on plants. I expected that plant biomass, water content, and change in cover would decrease as treehopper densities increased, which would depend on the presence of ants and whether bears had destroyed ant nests. I also expected that when N was introduced to the soil, there would be greater plant biomass and cover change. When combining the nitrogen addition with the treehopper density treatment, I anticipated two outcomes. In ambient N conditions, I

expected a decrease in plant biomass, water content, and cover as treehopper density increased. With a weakening cascade, I expected to see no change in plant performance across treehopper densities in N addition plots. In a strengthening cascade, I expected to see a very sharp decrease in plant performance as treehopper density increased in the nitrogen-rich plots.

Methods

Study System

I conducted this study within a previously established N enrichment experiment consisting of 36 circular plots (Figure 1), each 5 m in diameter (Grinath, 2018). These plots are in a montane sagebrush-rabbitbrush steppe ecosystem in Almont, Colorado (2669 m elevation; 38° 43' 29.47" N; 106° 48' 48.91" W). Nitrogen has been added to half of the plots over the past 15 years at a rate of 0.5 g N m⁻² yr⁻¹. This treatment simulated a rate of atmospheric N deposition of ~7 kg N ha⁻¹ yr⁻¹ in an area that receives an ambient rate of ~2 kg N ha⁻¹ yr⁻¹. The plots all originally encircled one thatch ant nest and were constructed with barriers of plastic landscape edging buried 5 cm into the soil to limit thatch ant movement in and out of the plots. However, thatch ants could move under or over the barriers during this study. Mule's ears sunflowers occurred in all plots, but adequate numbers of these plants were only available in 34 of 36 plots for this study. During the last 15 years, black bears have attacked the thatch ant nests within the plots, causing many of the original nests to become inactive (lacking live ants). By July 2024, active ant nests occurred in 18 of the 34 plots. The number of plots in the experimental groups with and without N addition and active thatch ant nests are summarized in Figure 2.



Figure 1. Map of the 36 plots (red points) in the original N deposition experiment.

		Active Ant Nest	
		Inactive	Active
Nitrogen	Ambient	8	10
	Added	8	8

Figure 2. The number of plots in conditions of added or ambient nitrogen and with inactive or active thatch ant nests.

In each of the 34 plots, I selected three similar-sized mule's ear sunflower plants and estimated the initial cover of all plants using a quadrat. In order to calculate the size of each plant, we counted how many 10 x 10 cm squares the plant fit in when the quadrat was laid on top, to the nearest quarter of a square. The quadrat used was 1 meter squared and each plant measurement was in decimeters squared. Using plastic stakes with metal tags, each plant was given a designated identification number. When each plant was chosen, the amount of leaves, stems, flowers, and insects on the plant was recorded. This was done June 14th and the 19th. After choosing our initial *Wyethia*, cows ate 11 of our plants. To fix this, we chose different plants to replace the eaten ones and remeasured cover on July 3rd.

To test the effect of treehoppers on plants, I manipulated the abundance of nymphs found on each plant on July 3rd. In order to do this, I took nymphs from outside the plot and used a paint brush to add a designated number onto each plant. Within each plot, one plant had 0 nymphs added, one had 20, and the last had 80 placed on the plant. These designations were randomly assigned. Over the course of our experiment, I took multiple surveys, once a week, of the abundances of treehoppers and ants found on each plant, starting July 10th and ending July 25th. Each survey kept track of the number of thatch ants, treehopper adults, treehopper nymphs, and other ants and arthropods, and I totaled the abundances across surveys to measure cumulative abundances. I maintained the zero-treehopper density treatment on associated plants during the surveys as well. I also measured the number of leaves and flowers, and grazing damage as the number of plant parts (flowering stems, leaves) removed. My first and last survey included the number of flowering stalks and cow damage to each plant.

On July 26th, I collected all of the insects on each plant and placed them into labeled vials, which were frozen (-20 C) for future analysis. I also collected the aboveground portion of each plant by cutting at the soil surface. I placed the cut plants into pre-weighed plastic bags and sealed them to prevent moisture loss. Back at the lab, I measured the wet mass (grams) of each plant and placed each into separate, labeled paper bags. I then dried the plants in an oven at 60 C

for 3 days. After 3 days, I took all the paper bags out of the oven and weighed each plant to obtain aboveground dry mass (grams). Plant aboveground water content was calculated as a percent of dry mass by subtracting dry mass from wet mass, dividing by dry mass, and then multiplying by 100 (Pollet & Brown, 2007; Zhang & Zhou, 2019). I measured plant change in cover as the cover estimated on July 3rd minus cover estimated on July 25th.

Data Analysis

We used the generalized linear mixed effects models (GLMMs) to analyze the data. We used this type of test because we needed to account for there being multiple plants within each plot. These plants are not independent of each other because they are grouped together spatially. All of the GLMMs were performed in R version 4.2.2 using the packages ‘lme4’ and ‘car’, using Type II sums of squares to account for different sample sizes across treatment groups. Our data include counts of treehoppers, thatch ants, and plant parts removed (stems/leaves removed by grazing), and these variables were analyzed with GLMMs for count data (using a Poisson distribution). We also have data for plant water content, aboveground dry biomass, and change in cover, which were analyzed with GLMMs for continuous data (using a Gaussian distribution). All the GLMMs included plot identity as a random factor. Cumulative treehopper abundances were analyzed as a function of the treehopper density treatment. All other response variables were analyzed as functions of the treehopper density treatment, the N addition treatment, the presence of active thatch ant nests, and the interactive effects of these categorical factors. Results were considered significant when $P \leq 0.05$.

Results

First, we evaluated whether the treehopper density treatment had the intentional effect on treehopper abundances (Figure 3). The treehopper density treatment successfully created a gradient of cumulative treehopper abundances, with abundances increasing from the 0 to 20 to 80 density treatment groups (Table 1). This indicates that we successfully created a gradient of treehopper abundances, and therefore the manipulation technique worked.

Next, we tested thatch ant cumulative abundance responses to treehopper density, the nitrogen treatment, and whether there was an active ant nest in July (Table 2). There was a significant interactive effect of all three predictor variables, indicating that all three of these predictors influenced the abundances of thatch ants together. In general, thatch ants were more abundant in plots with active nests. There was also a significant interactive effect of treehopper density and nitrogen treatment, which is shown in Figure 4. We found that the 80-treehopper density group attracted the most thatch ants in the ambient N conditions. In the enriched N conditions, there was no difference between the 80-treehopper density group and the group where treehoppers were removed. This suggests that nitrogen pollution may alter the interaction between treehoppers and ants.

We then evaluated the water content of each plant and found that none of the experimental factors significantly affected water content (Table 3). Even though there was not an effect of the initial treehopper density treatment, we further evaluated whether greater cumulative treehopper abundances resulted in lower water content. This expectation was supported with a significant negative regression slope (slope = -0.136, $t = -2.14$, $P = 0.035$), which can be seen in Figure 5. This shows that greater treehopper abundances did result in lower water content.

Next, we evaluated plant aboveground dry biomass, finding no significance response to the experimental factors (Table 4). We also found no significant responses in plant growth over time, measured as change in plant cover (Table 5).

Lastly, we conducted an additional analysis to assess whether cows could have influenced the interpretation of our results by removing parts of the experimental plants. To do so, we evaluated whether the experimental factors affected the number of plant leaves and stems removed by cattle grazing (Table 6). Interestingly, while there was no effect of the treehopper density treatment or ant nest activity for this response variable, the number of parts removed was higher for plants in enriched N plots compared to ambient N plots (Figure 6). This suggests that grazing herbivores (cows) preferentially consumed plants in N-polluted plots. In addition, of the 11 plants that needed to be replaced following cattle grazing, 9 occurred in N addition plots.

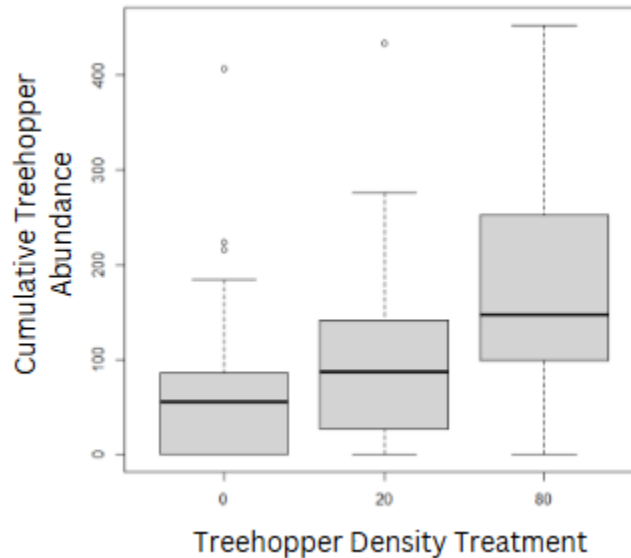


Figure 3. Cumulative treehopper abundances in each experimental treehopper density group.

Table 1. Statistical results for cumulative treehopper densities.

Explanatory Factor	Chi-squared	Degrees of freedom	P-Value
Treehopper Density	1601.8	2	<0.001

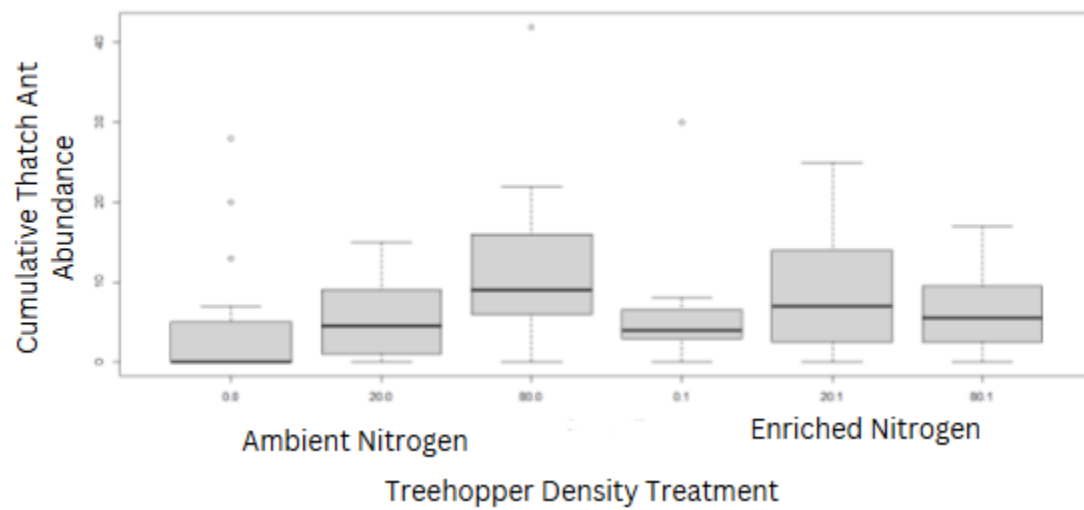


Figure 4. Cumulative thatch ant abundances across treehopper density groups in conditions with ambient (left) and enriched (right) nitrogen.

Table 2. Statistical results for cumulative thatch ant abundances.

Explanatory Factor	Chi-squared	Degrees of freedom	P-Value
Nitrogen	0.13	1	0.711
Active Thatch Ant	1.46	1	0.226
Treehopper Density	35.61	2	< 0.001
Nitrogen vs Active Thatch Ant	0.24	1	0.622
Nitrogen vs Treehopper Density	37.60	2	< 0.001
Active Thatch Ant vs Treehopper Density	3.43	2	0.179
Nitrogen vs Active Thatch Ant vs Treehopper Density	29.42	2	< 0.001

Table 3. Statistical results for plant water content.

Explanatory Factor	Chi-squared	Degrees of freedom	P-Value
Nitrogen	0.04	1	0.828
Active Thatch Ant	1.14	1	0.284
Treehopper Density	1.35	2	0.507
Nitrogen vs Active Thatch Ant	0.47	1	0.492
Nitrogen vs Treehopper Density	4.99	2	0.082
Active Thatch Ant vs Treehopper Density	0.76	2	0.681
Nitrogen vs Active Thatch Ant vs Treehopper Density	3.67	2	0.159

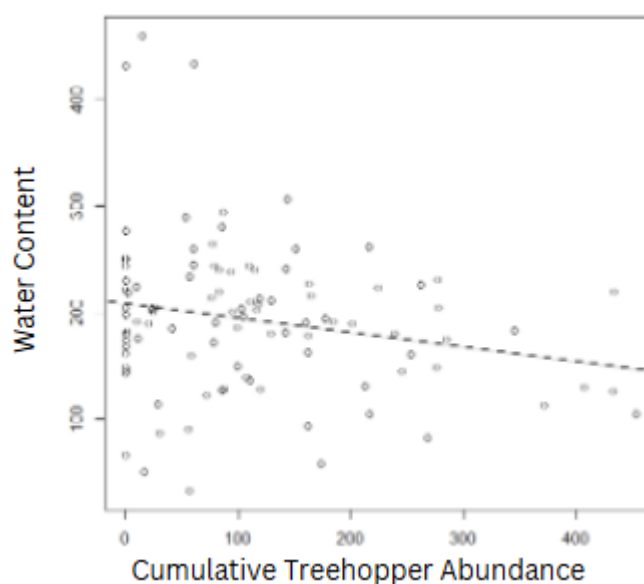


Figure 5. Plant percent water content across cumulative treehopper abundance.

Table 4. Statistical results for the plant dry mass.

Explanatory Factor	Chi-squared	Degrees of freedom	P-Value
Nitrogen	1.98	1	0.158
Active Thatch Ant	1.18	1	0.277
Treehopper Density	0.67	2	0.712
Nitrogen vs Active Thatch Ant	0.00	1	0.974
Nitrogen vs Treehopper Density	5.44	2	0.065.
Active Thatch Ant vs Treehopper Density	0.66	2	0.717

Nitrogen vs Active Thatch Ant vs Treehopper Density	0.15	2	0.927
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Table 5. Statistical results for change in plant cover.

Explanatory Factor	Chi-squared	Degrees of freedom	P-Value
Nitrogen	1.51	1	0.218
Active Thatch Ant	0.02	1	0.864
Treehopper Density	1.67	2	0.432
Nitrogen vs Active Thatch Ant	1.52	1	0.216
Nitrogen vs Treehopper Density	1.76	2	0.413
Active Thatch Ant vs Treehopper Density	3.77	2	0.151
Nitrogen vs Active Thatch Ant vs Treehopper Density	0.84	2	0.656

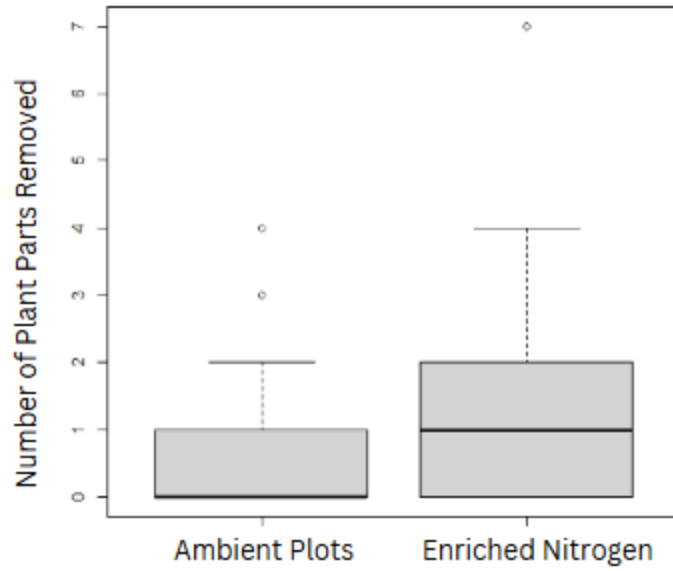


Figure 6. Plant parts (leaves, stems) removed by cows in ambient and enriched N conditions.

Table 6. Statistical results for plant parts (leaves, stems) removed by grazing cows.

Explanatory Factor	Chi-squared	Degrees of freedom	P-Value
Nitrogen	5.11	1	0.023
Active Thatch Ant	0.41	1	0.519
Treehopper Density	0.51	2	0.771
Nitrogen vs Active Thatch Ant	1.10	1	0.293
Nitrogen vs Treehopper Density	3.51	2	0.172
Active Thatch Ant vs Treehopper Density	1.10	2	0.574
Nitrogen vs Active Thatch Ant vs Treehopper Density	2.42	2	0.297

Discussion

My two questions were: do black bears have cascading effects on mule's ear sunflowers and will nitrogen be a determining factor in this cascade? While we found that our manipulation of treehopper nymphs on the experimental plants was successful, we did not find evidence for a trophic cascade from bears to mule's ear sunflower plants. However, we did find that the N and treehopper treatments had an interactive effect on thatch ant abundances, indicating that chronic, low-level rates of atmospheric N pollution may alter the mutualism between treehoppers and ants. In this case, it appears that the mutualistic interaction is weak in N-enriched conditions. Further work is needed to understand whether changes to the mutualism could affect other organisms in this ecological web, and if other factors could have influenced our interpretation of these results.

Grazing by cows added complications to our experiment. Cows removed the entire aboveground portion of some experimental plants, requiring us to find replacement plants within the plots. For many other experimental plants, cows grazed stems and leaves to ground-level, leaving only a portion of the plant with which we could work. This caused complications in our measurement of plant cover change over time, as baseline conditions early in the experiment were altered by grazing.

In addition, treehopper laid egg in many of the experimental plants, and many of these eggs hatched after the initial treehopper densities were established. Over the course of our experiment, I needed to remove new treehoppers from the plants in the zero-treehopper density group. This also complicated differences in abundances of treehoppers in the twenty and eighty density groups, which I did not further manipulate after starting conditions. This contributed to wide variation in treehopper abundances across the density treatment groups.

Lastly, some of the plots were not completely enclosed, allowing thatch ants to enter and exit the plots. This was potentially problematic for plants in plots that we designated as having inactive nests due to bear predation. This factor was not well established because thatch ants from outside the plots frequently tended treehoppers on our experimental plants, which would not have occurred if the plot barriers were effective.

Conclusion

We have learned the mutualistic relationship between treehoppers and thatch ants is being affected by N pollution. In the third year of this long-term experiment, N addition weakened interactions between plants and herbivores (Grinath 2018). Here, we found that greater treehopper abundances negatively affect water content of mule's ears sunflowers. This indicates that thatch ants had a negative indirect effect on host plants, similar to previous work with

rabbitbrush in this study system (Grinath 2012). However, further work is needed to understand how interactions across trophic levels are responding to N enrichment.

We also learned that cows preferred to graze on mule's ears sunflowers in nitrogen enriched conditions. Further data analysis is needed to account for cattle grazing in this experiment. Also, further analyses can be conducted to evaluate how proximity to ant nests outside the plots could influence the results. Going forward we will explore using proximity to ant nests as a continuous variable instead of using the categorical variable of whether or not an active nest occurred within the plots. Overall, additional work needs to be conducted to determine if black bears have cascading effects on mule's ears sunflowers.

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