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Chronic, low-level nitrogen deposition enhances abundances of ant-protected herbivores inhabiting an imperiled foundation species

Joshua B. Grinath [a,b,*]

[a] Department of Biological Sciences, Idaho State University, 921 S 8th Ave, Mail Stop 8007, Pocatello, ID, 83209, USA
[b] Rocky Mountain Biological Laboratory, P.O. Box 519, Crested Butte, CO, 81224, USA

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ABSTRACT

Atmospheric nitrogen (N) deposition is driving changes in plant assemblages worldwide, but animal responses are not well understood, especially in relation to current widespread rates of low-level N deposition. Big sagebrush (*Artemisia tridentata*) is a foundation species in steppe ecosystems of western North America, where elevated, but low-level N deposition is prevalent. Sagebrush hosts numerous herbivorous and predatory arthropods, some of which form mutualistic (i.e. mutually beneficial) herbivore-predator associations that may be harmful for sagebrush. Here, I evaluated the response of a sagebrush arthropod assemblage to four and nine years of low-level N enrichment in Colorado, USA. Though sagebrush cover and arthropod abundances were not different in the fourth year, by the ninth year, N additions increased arthropod abundances due to greater numbers of sap-feeding insects that are mutualist partners of predaceous ants. Ant and non-mutualist herbivore abundances did not significantly respond to N treatments in the ninth year, but non-mutualist predators were only found in ambient N plots, suggesting ants provided greater anti-predator protection for mutualist herbivores under N enrichment. These responses occurred during drought conditions, which may have increased sagebrush nutritional quality for sap-feeding insects. Sagebrush is experiencing multiple stressors that are transforming steppe ecosystems; these results suggest chronic exposure to common rates of low-level N deposition may create further stress as herbivorous insects proliferate. Additional work is needed to understand and manage the repercussions of N deposition for plant-animal assemblages, particularly in contexts including species of conservation concern and both mutualistic and antagonistic species interactions.

1. Introduction

Humans have greatly increased atmospheric nitrogen (N) deposition across large areas of Earth, fertilizing ecosystems that were historically limited by N availability (Bobbink et al., 2010). Nitrogen deposition has well-documented effects on plant assemblages, altering plant performance, competition, and diversity (Bobbink et al., 2010). However, the impact of this pollution on animals is much less understood (Stevens et al., 2018). Current evidence indicates N deposition generally has indirect effects on animals, as herbivores respond to changes in plant quality and quantity (Throop and Lerdau, 2004), and predators respond to altered prey quality and availability (Haddad et al., 2000; de Sassi et al., 2012). Yet, most of our current understanding is based on short-term experiments that simulate very high levels of N deposition (>10 kg ha^{-1} yr^{-1}) or observational studies across N deposition gradients. Though these studies are appropriate for drawing correlational inferences and assessing responses to high-level N deposition that occurs in restricted localities, they are inappropriate for making causal inferences concerning the common elevated, but low-level N deposition (<10 kg ha^{-1} yr^{-1}) that occurs across larger landscapes (Throop and Lerdau, 2004). At present, it is unclear how long-term exposure to low-level N deposition may affect herbivores and predators. This knowledge gap may be especially important to address for species of conservation concern that live in environments experiencing chronic, low-level N deposition.

In western North America, big sagebrush (*Artemisia tridentata*) is an iconic foundation species in steppe ecosystems, which are both widespread and yet imperiled due to the influence of invasive species, fragmentation, overgrazing, and other stressors (Davies et al., 2011). Elevated, but low-level rates of N deposition are widespread across this region (Fenn et al., 2003), and though N deposition has been raised as a potential concern for sagebrush conservation, this has been primarily

* Department of Biological Sciences, Idaho State University, 921 S 8thAve, Mail Stop 8007, Pocatello, ID, 83209, USA.
E-mail address: grinjosh@isu.edu.

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with regards to positive effects on invasive annual grasses (D'Antonio and Vitousek, 1992; Chambers et al., 2014). It is not clear how N deposition may be affecting sagebrush in other ways, such as by altering abundances of insect herbivores inhabiting sagebrush. Previous studies indicate that insect herbivores, especially sap-feeding species, may frequently increase in abundance and cause greater damage to host plants following N enrichment (Throop and Lerdau, 2004). A study on a different sagebrush species (*Artemisia ludoviciana*) found that sap-feeding insects increased in abundance under high N enrichment (800 kg ha^{-1} yr^{-1}) (Strauss, 1987). Similarly, in a study in which soil nutrients (N plus other nutrients) were manipulated for big sagebrush, grasshopper growth and consumption rates were both enhanced by nutrient enrichment (Johnson and Lincoln, 1991). Yet, it is not known whether current rates of N deposition are affecting insect herbivores on big sagebrush.

Herbivore responses to N deposition can be influenced by predators, but the effect of low-level N deposition on secondary consumers remains a key knowledge gap (Stevens et al., 2018). The negative effects of herbivores on plants may be suppressed by greater predator abundances and predation intensity in nutrient-enriched conditions (Strauss, 1987). Alternatively, mutualistic relationships between predators and herbivores, such as those between sap-feeding insects that excrete 'honeydew' food for ants in exchange for protection against predators (Fig. 1), can benefit mutualist herbivores while being detrimental for co-occurring herbivores eaten by ants (Strauss, 1987; Grinath et al., 2012). In such communities, the overall effect on plants will be contingent on the relative strengths of these positive and negative interactions, where strong mutualistic interactions between herbivores and predators can result in decreased plant performance (Grinath et al., 2012). Sap-feeding insects and predaceous ants frequently form mutualistic associations on big sagebrush (Heikkinen, 1999; Takahashi and Huntly, 2010; Erickson et al., 2012) that could exacerbate herbivore damage. Thus, it may be important to consider responses of both mutualistic and non-mutualistic species of herbivores and predators when assessing the effects of N deposition on arthropod assemblages on sagebrush and other foundation species.

In this study, I evaluated whether chronic, low-level N deposition affects arthropod assemblages inhabiting big sagebrush. Building on a previous study evaluating rabbitbrush-arthropod responses to short-term N deposition (Grinath, 2018), I measured sagebrush cover and the abundances of arthropods in plots experiencing very low ambient N deposition (2 kg ha^{-1} yr^{-1}) and plots in which elevated, but low-level N deposition (7 kg ha^{-1} yr^{-1}) was simulated over nine years (data were collected in years four and nine of study). The arthropods included mutualistic sap-feeding insects and predatory ants, as well as non-mutualistic herbivore and predator species, and I assessed responses of each of these groups. Based on previous study of high-level N enrichment and arthropods inhabiting a different sagebrush species (Strauss, 1987), I hypothesized that long-term exposure to low-level N enrichment would result in greater abundances of mutualist herbivores and ants, and lower abundances of non-mutualist herbivores and predators.

In addition, the experimental site was experiencing a drought during this study. Drought conditions can increase plant susceptibility to sap-feeding herbivores (Huberty and Denno, 2004) and are expected to intensify in western North America (Seager et al., 2007). Therefore, I also conducted a climate analysis to measure drought severity to aid in understanding the context in which arthropod responses to N enrichment were measured and the potential for trends in these responses.



Fig. 1. Images depicting the mutualistic relationship between predatory ants and sap-feeding insects on big sagebrush at the Colorado study site. (a) Ants (*Formica obscuripes*) collect sugary honeydew excretions from sap-feeding insects, including aphids (*Obtusicauda frididae*). (b) Predatory arthropods consume sap-feeding insects that are mutualist partners of ants, such as this lady beetle (*Coccinella monticola*) eating an aphid (*Pleotrichophorus pseudoglandulosus*). (c) Ants defend their mutualist partners by attacking predatory arthropods, resulting in the removal of such predators from plants. Photo credit: J. B. Grinath.

2. Materials and methods

This study was conducted in a sagebrush-rabbitbrush steppe near Almont, Colorado (elevation = 2769 m, latitude = 38.719, longitude = −106.816). Here, big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) hosts sap-feeding aphids (Aphidae), mealybugs (Pseudococcidae) and treehoppers (Membracidae) that engage in food-for-protection mutualisms with predaceous ants (Formicidae: primarily *Formica obscuripes*; Fig. 1) (Erickson et al., 2012) (Fig. 1). Sagebrush also hosts herbivorous leafhoppers (Cicadellidae), plant bugs (Miridae), planthoppers (Issidae and Dictyopharidae), caterpillars (Lepidoptera), and leaf beetles (Chrysomelidae), and predatory beetles (Coccinellidae), spiders (Araneae), hemipterans (Hemiptera), lacewings (Neuroptera), and wasps (Hymenoptera), which are not mutualists with each other.

In 2010, 36 circular plots (5 m diameter) were established, each containing big sagebrush and a single *F. obscuripes* ant nest (Grinath, 2018). Half the plots were randomly selected to receive N treatments of 0.5 g m^{-2} slow-release ammonium nitrate pellets applied manually each summer from 2010 to 2018. In each plot, two 1 m^2 quadrats were established by blindly tossing a marker, within which plant and arthropod surveys were conducted. Big sagebrush cover and arthropod abundances were initially assessed for all plots in August 2013. Surveys were repeated for 19 plots on July 24–25, 2018; not all plots were surveyed due to worker time constraints. Surveys were conducted by first counting ants and other highly mobile arthropods on all aboveground sagebrush surfaces, moving quickly across the plants to avoid double-counting, then by counting less mobile and sedentary species. Lastly, sagebrush cover was measured by overlaying a 1 m^2 quadrat divided into 1 dm^2 cells with string placed every 10 cm. Percent cover was estimated as the number of dm^2 cells filled by sagebrush (to the nearest ¼ cell, or 0.25%) when viewed from above. Data were pooled across quadrats within plots to analyze results at the plot-scale. Further details of the study system and experimental setup are in Grinath (2018) and Erickson et al. (2012).

I gathered climate data from the National Oceanic and Atmospheric Administration's online climate database (https://www.ncdc.noaa.gov/cdo-web/datatools/findstation, accessed November 4, 2019). Data from 1910 to 2018 were downloaded for two nearby weather stations in Gunnison (USC00053662) and Crested Butte (USC00051959). Variables included monthly total precipitation (mm) and average daily maximum and minimum temperatures (C). Some values were occasionally missing, and I estimated missing values using linear regressions based on relationships between the weather stations,

which covaried. The field site occurs nearly halfway between these weather stations; therefore, I calculated average values to estimate variables at the field site. To measure drought severity, I used R v3.6.1 (R Core Team, 2019) to calculate water-balance with the standardized precipitation-evapotranspiration index ('spei' function, 'SPEI' package), using precipitation to approximate insolation in the evapotranspiration (ET0) estimate (Vicente-Serrano et al., 2010). SPEI is centered on zero, representing the long-term mean; positive and negative values indicate water-surplus and deficit, respectively, in standard deviation units. SPEI can be calculated for various lengths of time; here, values measure water-balance corresponding to summer through the previous winter (October–August).

I analyzed sagebrush cover and arthropod abundance responses to N enrichment (2-level factor) using generalized linear models (GLMs) in R. Cover was analyzed assuming Gaussian error distributions; natural log transformation (y+1) was applied to 2018 cover data to meet the assumption of normality (this transformation did not qualitatively change the inference from the model). Arthropod counts (total, mutualist/non-mutualist herbivores and predators) were analyzed by considering GLMs assuming Poisson and Negative Binomial error distributions; the most appropriate model was chosen using AIC (Zuur et al., 2009). In the original experimental setup, plots were maintained as ant enclosures in which some nests became inactive (Grinath, 2018), but enclosures were not maintained after 2013 and ants from nests outside plots could forage within. Therefore, results were analyzed separately for 2013 and 2018, and ant nest inactivity was included as a covariate (2-level factor) in the 2013 analyses. To account for potential differences in plant cover, I also analyzed arthropod densities (abundance/percent cover) by 'offsetting' by cover in the GLMs (Zuur et al., 2009). Visual inspection of SPEI indicated non-linear trends, which I addressed using a generalized additive model (GAMs: 'gam' function, 'mgcv' package) to analyze SPEI as a function of time. To understand which climate variables drove SPEI trends, I used GAMs to evaluate total precipitation and mean monthly maximum and minimum temperatures through time, in both the summer (June–August) and the previous non-growing season (October–May). Results were significant if $P \leq 0.05$. All data from this study can be found in Appendix A.

3. Results

In 2013 (experimental year four), sagebrush cover and all measures of arthropod abundances did not significantly differ between ambient and N-enriched plots (Appendix B: Fig. B.1). In 2018 (Fig. 2), the ninth year of the experiment, sagebrush cover still did not differ between N treatments (GLM-Gaussian: estimate = −0.02, SE = 0.26, $t = -0.06$, $P = 0.951$), but total arthropod abundance was significantly greater in N-enriched plots (GLM-Negative Binomial: estimate = 1.48, SE = 0.68, $z = 2.18$, $P = 0.029$). This result was due to greater numbers of herbivores that form mutualistic relationships with predatory ants (GLM-Negative Binomial: estimate = 1.95, SE = 0.93, $z = 2.11$, $P = 0.035$); N treatments did not significantly affect abundances of ants (GLM-Negative Binomial: estimate = 0.77, SE = 0.82, $z = 0.94$, $P = 0.348$) and non-mutualist herbivores (GLM-Negative Binomial: estimate = 0.11, SE = 0.65, $z = 0.16$, $P = 0.871$). Too few non-mutualist predators were present to statistically analyze their response, but these arthropods were only found in ambient N conditions (Fig. 2). Because sagebrush cover was not different between N treatments, arthropod density results (abundance/percent cover) were qualitatively equivalent to above (Appendix B: Table B.1).

Water-balance varied greatly across the 108-year time series, especially in the first half of the twentieth century when surplus conditions were followed by severe drought during the 1930's (Fig. 3). Water-balance remained near mean conditions for the second half of the century, but the trend from 2000 to 2018 suggests that drought conditions may be becoming more prevalent. Both 2013 (SPEI: −0.71) and 2018 (SPEI: −1.56) were years of water-deficit, but 2018 was the third

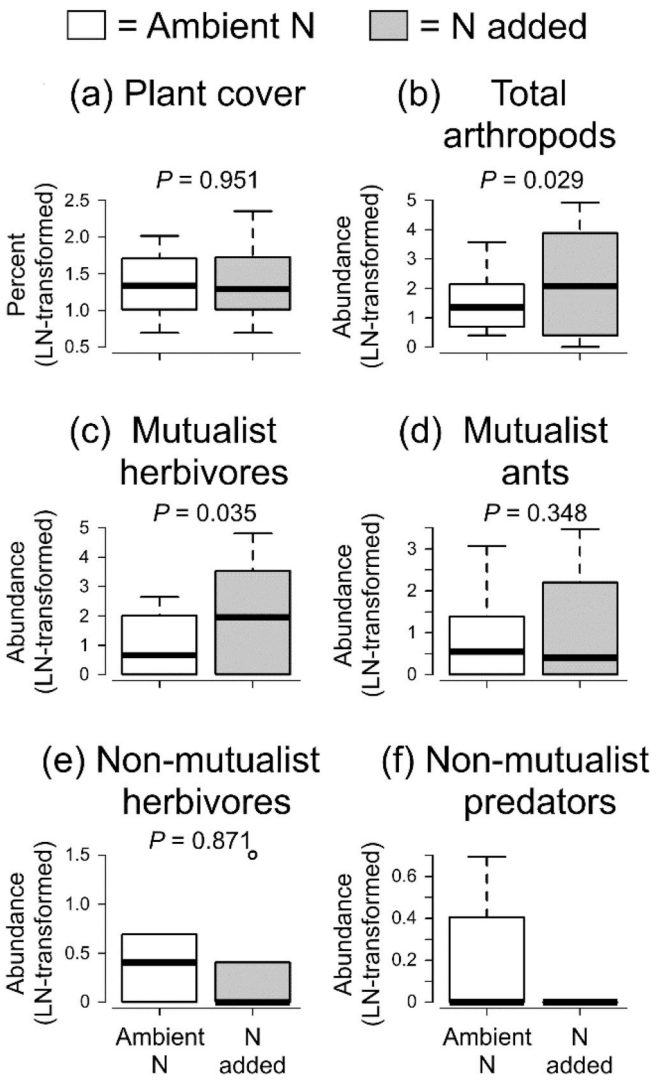

Fig. 2. Survey results from 2018 for (a) sagebrush cover, (b) total arthropod abundances, (c) mutualist herbivore abundances, (d) mutualist, predatory ant abundances, (b) non-mutualist herbivore abundances, and (f) non-mutualist predator abundances. *P*-values are from corresponding GLMs; a *P*-value is not provided for non-mutualist predators because they only occurred in ambient N conditions. All results are depicted as boxplots and with LN(y+1) to aid visualization. Data shown are for an average 1 m^2 quadrat per plot, where $n = 19$ plots: 10 with ambient N and 9 with N added.

strongest drought since 1940 (seventh lowest water-balance value across the entire 108-year record; Fig. 3). Evaluation of the component climate variables indicated that precipitation in winter and summer was at or slightly below normal (outside 95% spline confidence bands) in both 2013 and 2018, and maximum and minimum temperatures were similarly at or slightly above normal in both summers. Minimum and especially maximum temperatures prior to the summer were above normal in 2018, but not in 2013 (Fig. B.2).

4. Discussion

This study shows that chronic, low-level N deposition can increase abundances of insect herbivores that form mutualistic relationships with ants on an iconic foundation species, consistent with previous studies on other plants and high-level N deposition (Strauss, 1987; Throop and Lerdau, 2004). Big sagebrush is the namesake organism for the imperiled sagebrush steppe ecosystems of western North America, and the results shown here suggest that common rates of N deposition may

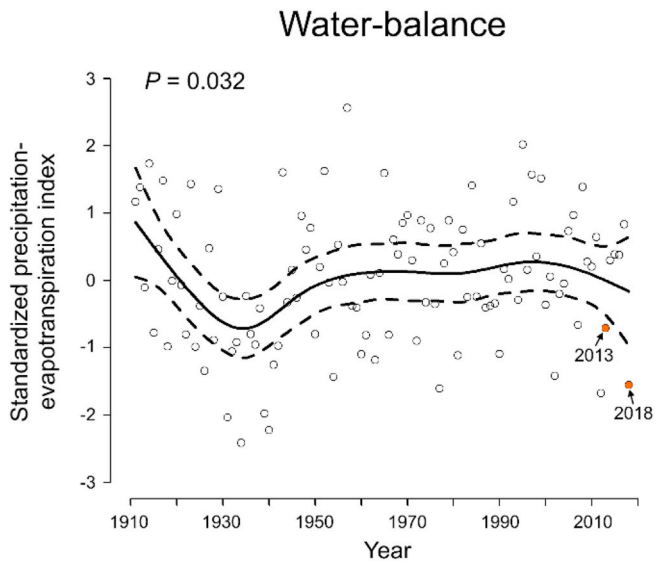

Fig. 3. Trends in water-balance from 1910 to 2018. Water-balance was measured with the standardized precipitation-evapotranspiration index (SPEI) from October to August, where positive and negative values represent water-surplus and deficit, respectively, in standard deviation units relative to the long-term mean (GAM: $F = 2.35$, $P = 0.032$, deviance explained = 15.7%). The trend is depicted with a smoothing spline (solid line) and 95% confidence bands (dashed lines) with $n = 108$ years. The years of study included in the sagebrush dataset (2013 and 2018) are indicated with closed symbols.

further increase stress on this species. Greater insect herbivore abundances may be important for steppe conservation because these herbivores can substantially suppress sagebrush reproductive performance. Takahashi and Huntly (2010) studied big sagebrush that were between approximately 0.25 and 2 m^3 in size and had 25.24 herbivores per plant on average, primarily consisting of sap-feeding insects. They found that herbivore removal increased the growth of reproductive shoots and resulted in an 11.5-fold increase in seed production (Takahashi and Huntly, 2010). In the present study, sagebrush cover ranged from 0.01 to 0.095 m^2 and mutualist herbivore abundances were 7.1 in ambient N conditions and 49.9 in N-enriched conditions on average. These results suggest that mutualist insect herbivore abundances in N-enriched conditions were nearly two or more times those that have been previously shown to impact sagebrush reproduction (Takahashi and Huntly, 2010). If these mutualist sap-feeding insects have similar negative effects on their host plants, then they could greatly impact sagebrush population persistence and regeneration after disturbance. Nitrogen deposition could stimulate plant growth and compensation for herbivory (Grinath, 2018), but this was not evident in a sagebrush cover response here. Cover may not have changed or there may have been dynamics not captured that occurred between the two years of study. Additional study is required to clarify how sagebrush performance responds to both N enrichment and insects and the resulting consequences for sagebrush populations.

Changes in mutualist herbivores were not matched by predatory ant and non-mutualist herbivore responses. These results suggest that ant predation did not increase enough to indirectly benefit plants (Strauss, 1987), or that there is a lag period before this response occurs. Non-mutualist herbivores can also benefit from enemy-free space created by ants, which could have contributed to the lack of a significant result (Grinath et al., 2015). Ant abundances may not have changed because ants were from nests that gained resources by foraging both within and outside the experimental plots. However, the results suggest that foraging ants had a negative net effect on sagebrush through their mutualistic relationship with herbivores (Grinath et al., 2012). In addition, non-mutualist predators were absent in N-enriched conditions, suggesting that these predators provide weak indirect benefits for sagebrush under N deposition. Even without changes in ant abundances, lower abundances of non-mutualist predators could have occurred if ants were more aggressive protectors of mutualist sap-feeding insects (Heikkinen, 1999; Grinath et al., 2015), perhaps in response to high quality 'honeydew' in N-enriched conditions. To understand the stresses facing sagebrush and other foundation species, further research is needed to evaluate how low-level N deposition affects herbivores and predators, and both the mutualistic and antagonistic relationships linking species across trophic levels (Grinath, 2018; Stevens et al., 2018).

This study occurred in the context of a drought that may have influenced plant-herbivore interactions (Huberty and Denno, 2004), and such conditions are expected to become more frequent in this region (Seager et al., 2007). Sap-feeding insects, such as many mutualist partners of ants, often increase in abundance during drought conditions because water-stressed plants have higher nutritional quality (Huberty and Denno, 2004; Tariq et al., 2012). Plant proteins are frequently hydrolyzed under water stress, resulting in greater amino acid availability for herbivores compared to non-stressful conditions when plants have operational protein metabolism (Huberty and Denno, 2004; Tariq et al., 2012). Though herbivore abundances were lower in 2018 than 2013, drought could have aided in developing the relatively greater numbers of herbivores on sagebrush in N-enriched plots if these plants had higher nutritional quality due to greater concentrations of hydrolyzed proteins. While herbivore abundances may have increased in prior years that were not surveyed (2014–2017), it is clear that higher abundances were maintained on sagebrush experiencing low-level N enrichment during the 2018 drought. As climate change ensues, higher temperatures like those in 2018 will increase evapotranspiration and the likelihood of water-deficits, regardless of changes in precipitation (Vicente-Serrano et al., 2010). Drought conditions combined with greater herbivory due to low-level N deposition may be important to consider among the multiple stressors threatening sagebrush and other steppe ecosystems, which deserves additional study. Research is revealing that nearly any elevated level of atmospheric N deposition can have adverse effects on recipient ecosystems (Bobbink et al., 2010). Greater regulation of N-containing pollutants may be required to prevent further unwanted ecosystem changes.

Author contributions

JBG performed all parts of this study.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary materials to this article can be found online at https://doi.org/10.1016/j.actao.2021.103706.

References

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecol. Appl. 20, 30–59.

Chambers, J.C., Bradley, B.A., Brown, C.S., D'Antonio, C., Germino, M.J., Grace, J.B., Hardegree, S.P., Miller, R.F., Pyke, D.A., 2014. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17, 360–375.

D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. Rev. Ecol. Systemat. 23, 63–87.

Davies, K.W., Boyd, C.S., Beck, J.L., Bates, J.D., Svejcar, R.J., Gregg, M.A., 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biol. Conserv. 144, 2573–2584.

de Sassi, C., Staniczenko, P.P.A., Tylianakis, J.M., 2012. Warming and nitrogen affect size structuring and density dependence in a host-parasitoid food web. Philos. Trans. Roy. Soc. B 367, 3033–3041.

Erickson, D.M., Wood, E.A., Oliver, K.M., Billick, I., Abbot, P., 2012. The effect of ants on the population dynamics of a protective symbiont of aphids, *Hamiltonella defensa*. Ann. Entomol. Soc. Am. 105, 447–453.

Fenn, M.E., Haeuber, R., Tonnesen, G.S., Baron, J.S., Grossman-Clarke, S., Hope, D., Jaffe, D.A., Copeland, S., Geiser, L., Rueth, H.M., Sickman, J.O., 2003. Nitrogen emissions, deposition, and monitoring in the western United States. Bioscience 53, 391–403.

Grinath, J.B., 2018. Short-term, low-level nitrogen deposition dampens a trophic cascade between bears and plants. Ecol. Evol. 8, 11213–11223.

Grinath, J.B., Inouye, B.D., Underwood, N., Billick, I., 2012. The indirect consequences of a mutualism: comparing positive and negative components of the net interaction between honeydew-tending ants and host plants. J. Anim. Ecol. 81, 494–502.

Grinath, J.B., Inouye, B.D., Underwood, N., 2015. Bears benefit plants via a cascade with both antagonistic and mutualistic interactions. Ecol. Lett. 18, 164–173.

Haddad, N.M., Haarstad, J., Tilman, D., 2000. The effects of long-term nitrogen loading on grassland insect communities. Oecologia 124, 73–84.

Heikkinen, M.W., 1999. Negative effects of the western thatching ant (Formica obscuripes) on spiders (Araneae) inhabiting big sagebrush (Artemisia tridentata). Great Basin Nat. 59, 380–383.

Huberty, A.F., Denno, R.F., 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology 85, 1383–1398.

Johnson, R.H., Lincoln, D.E., 1991. Sagebrush carbon allocation patterns and grasshopper nutrition: the influence of CO_2 enrichment and soil mineral limitation. Oecologia 87, 127–134.

R Core Team, 2019. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.-P., Harnik, N., Leetmaa, A., Lau, N.-C., Li, C., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316, 1181–1184.

Stevens, C.J., David, T.I., Storkey, J., 2018. Atmospheric nitrogen deposition in terrestrial ecosystems: its impact on plant communities and consequences across trophic levels. Funct. Ecol. 32, 1757–1769.

Strauss, S.Y., 1987. Direct and indirect effects of host-plant fertilization on an insect community. Ecology 68, 1670–1678.

Takahashi, M., Huntly, N., 2010. Herbivorous insects reduce growth and reproduction of big sagebrush (*Artemisia tridentata*). Arthropod-Plant Inte. 4, 257–266.

Tariq, M., Wright, D.J., Rossiter, J.T., Staley, J.T., 2012. Aphids in a changing world: testing the plant stress, plant vigour and pulsed stress hypotheses. Agric. For. Entomol. 14, 177–185.

Throop, H.L., Lerdau, M.T., 2004. Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. Ecosystems 7, 109–133.

Vicente-Serrano, S.M., Begueria, S., Lopez-Moreno, J.I., 2010. A multi-scalar drought index sensitive to global warming: the Standardized Precipitation Evapotranspiration Index – SPEI. J. Clim. 23, 1696–1718.

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. Springer, New York.