

PERENNIAL SHRUB AND HARVESTER ANT RESPONSES TO ENVIRONMENTAL
GRADIENTS IN SOUTHERN CALIFORNIA DESERTS

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Natural Resources

in the

College of Graduate Studies

University of Idaho

by

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May 2012

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ABSTRACT

Nitrogen deposition via airborne pollution has been shown to alter soil biogeochemical processes and plant communities in various ecosystems. However, little is known about how changes in these processes may affect higher trophic levels. Building upon previous research that revealed an atmospheric nitrogen deposition gradient from the San Bernardino Mountains through Joshua Tree National Park, we investigated the effects of increased nitrogen on plants and *Messor pergandei* (Mayr) harvester ants, which rely on plants for seed. We measured ant colony attributes (nest density, nest mound dimensions, and the number of abandoned nests), as well as shrub fruit densities, at eighteen sites along the nitrogen deposition gradient. We also measured nitrogen and carbon concentrations, along with carbon and nitrogen stable isotopes, along the nitrogen deposition gradient. Carbon and nitrogen attributes were determined in *Larrea tridentata* (DC. Coville) and *Ambrosia dumosa* (A. Gray) leaves, seeds from selected plant species, and ants. We predicted N deposition would increase both seed production and ant nests along the deposition gradient. In addition, we expected percent carbon and nitrogen and isotopes to vary along the deposition gradient. Ant nest density and *Larrea tridentata* fruits increased from low deposition to high deposition sites. In addition, ant nest diameter, ant nest height, and abandoned nests decreased as deposition increased. Nest mound size is correlated with the size and age of the colony; therefore, these results suggest nest colonization has been more frequent in areas of high deposition. Nitrogen and carbon isotope values of *Ambrosia dumosa* and *Larrea tridentata* leaves, *Ambrosia dumosa* and *Larrea tridentata* seeds, annual plant seeds, and *Messor pergandei* ants were significantly different across the nitrogen deposition gradient indicating different sources of both elements, including anthropogenically-produced

compounds. Considering that deserts are nitrogen limited, the results indicate that altered nitrogen inputs may result in cascading effects through trophic levels.

ACKNOWLEDGMENTS

I would like to thank my major professor, Dr. Beth A. Newingham, for her guidance and support throughout my time at the University of Idaho. My committee members, Drs. John D. Marshall and Sanford D. Eigenbrode, were also instrumental during this process providing me with invaluable assistance during the research process.

In addition, I would like to thank Dr. Edith Allen and Michael Bell from the University of Riverside California, Dr. Vicki Chang and Josh Hoines from Joshua Tree National Park, Dr. Al Muth from the Deep Canyon Research Station, Ginny Short from the Coachella Valley Preserve, Dr. Mark Massar from the Bureau of Land Management, and Margret Keefe from Idaho Stable Isotopes Laboratory for their assistance with project design, logistics, and field work.

Finally, I want to express my appreciation to Ryan Tsutsui, Shawn Taylor, Rebecca Johnson, Carrie Anderson, and Chris Scaroni for their help in the field and laboratory.

This project could not have been completed without the financial support from the Desert Legacy Fund, California Desert Research Program at The Community Foundation, San Bernardino, California; the Robert Lee Graduate Student Grant Program at Joshua Tree National Park; and the University of Idaho Student Grant Program.

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1. Introduction

Global changes, including altered atmospheric nitrogen deposition and precipitation regimes, are driving novel ecosystem responses. Considering both nitrogen and precipitation are limiting in numerous ecosystems, changes in these resources may have pronounced effects. Nitrogen deposition can affect soil microbial and plant available nitrogen producing alterations in ecosystem structure and function. Due to the linked relationship of soil moisture to the nitrogen cycle, altered precipitation will further modify nitrogen availability. Therefore, it is imperative we understand how altered nitrogen and water affect resource-limited systems, such as deserts.

Atmospheric nitrogen has dramatically increased over the last several decades from sources such as car exhaust, power plant emissions, industrial emissions, agricultural field fertilization, and feedlots (Vitousek *et al.*, 1997; Fenn *et al.*, 2003b; Meehl *et al.*, 2007). This nitrogen is carried in many forms, including nitric oxide (NO), nitrogen dioxide (NO₂), ammonia (NH₃), and nitric acid (HNO₃), via air currents and is deposited on the soil affecting biogeochemical processes (Rao *et al.*, 2009; Fenn *et al.*, 2003a). Nitrogen deposition occurs in either wet or dry form. The arid western US experiences primarily dry deposition, while the more mesic regions in the eastern United States receive N deposition during precipitation events (Fenn *et al.*, 2003b). Not only do emissions pollute air reducing air quality, but they also pollute the soil by increasing soil nitrogen levels (Galloway, 1998; Hooper and Johnson, 1999; and Krupa 2003; Vourlitis *et al.*, 2007).

Atmospheric N deposition can have strong effects on soil and plant communities in various ecosystems (Sirulnik *et al.*, 2007a; Sirulnik *et al.*, 2007b). Excess nitrogen in soil reduces the carbon to nitrogen ratio, which allows soil microbial populations to expand (Nave *et al.*, 2009). Following excess nitrogen depletions, those larger microbial populations

take up the majority of the nitrogen in the system and leave little plant available nitrogen before dying off. These cyclical swings of nitrogen availability can cause weedy plant invasions in desert systems, altering fire regimes and plant community composition (D'Antonio and Vitousek, 1992; Evans *et al.*, 2001; Brooks, 2003; Schwinning *et al.*, 2005). A synthesis by Bobbink *et al.* (2010) found that nitrogen is more critical in determining plant community composition than previously realized.

In addition to nitrogen inputs, altered precipitation is also likely to have substantial impacts on desert ecosystems since water and nitrogen are two primary resource limitations (Noy-Meir, 1973; Burke, 1989; Hooper and Johnson, 1999). Although the global climate models used in the 2007 IPCC (Intergovernmental Panel on Climate Change) report predict an overall decrease in precipitation for desert systems in the southwestern US, the timing, duration, and amount of rain is difficult to forecast with certainty (Loik *et al.*, 2004; Scanlon *et al.*, 2005; Christensen *et al.*, 2007; Fischlin *et al.*, 2007; IPCC, 2007). These two cycles are often coupled and changes may have reciprocal effects. For example, precipitation pulse events drive microbial processes in arid and semi-arid soils, which include nitrogen cycling (Evans and Ehleringer, 1994; Loik *et al.*, 2004; McCalley and Sparks, 2008; Yahdjian and Sala, 2010). However, many of these effects are inadequately understood due to the unknown consequences of climate change (Sirulnik *et al.*, 2007a; Sirulnik *et al.*, 2007b). Less nitrogen in an ecosystem already limited in nutrients could affect flora and fauna species (Patrick *et al.*, 2009; Rao and Allen, 2010).

Many governmental agencies currently monitor atmospheric deposition, including NO, NO₂, NH₃, and HNO₃ across the United States (Fenn *et al.*, 2003b; Porter and Johnson, 2007). Regions close to and downwind from high-density population centers and confined

animal feeding operations are especially vulnerable to N deposition and are therefore heavily monitored in the US (Rao *et al.*, 2009; Fenn *et al.*, 2003a; and Junknys *et al.*, 2007).

However, low population areas including some national parks are also vulnerable but are less monitored than urban areas. The National Park Service is concerned about the impacts of N deposition on plant biodiversity and ecosystem function and has implemented programs to monitor the effects of N deposition at selected parks (Phoenix *et al.*, 2006; Fischlin *et al.*, 2007; Porter and Johnson 2007).

Nitrogen deposition is an imminent concern in southern California. Los Angeles and nearby population centers create enormous amounts of pollution each year through fossil fuel combustion, primarily in the form of nitrogenous compounds found in or derived from automobile exhaust (Fenn *et al.* 2003a; Fenn *et al.*, 2007; Allen *et al.*, 2009). The nitrogen is carried across southern California and falls out as winds move east, creating a nitrogen deposition gradient. This N deposition gradient extends about 150 km across the Coachella Valley and Joshua Tree National Park, which provides a unique opportunity to examine the ecological effects of such a gradient.

Rao *et al.* (2009) and Allen *et al.* (2009) detailed changes in soil processes and annual plant communities following large pulses of N fertilizer in and around Joshua Tree National Park. However, little is known about how multiple trophic levels in southern California desert systems are responding to chronic N deposition. The trophic structure in the Colorado Desert is unique due to the ubiquity of seed harvesting ants (Went *et al.*, 1972; Rissing and Wheeler, 1976; Davidson, 1977). How plants and granivores react to N deposition is critical as the effects of increased N on seed production, size, and nutrient content could have large consequences for desert ecosystems (Kelrick *et al.*, 1986).

Harvester ants along with birds and rodents move, store, and consume mass quantities of seed (MacMahon *et al.*, 2000; White and Robertson 2009). Granivory and seed movement can deplete plant populations and/or shift species composition (MacMahon *et al.*, 2000; White and Robertson, 2010). However, little is known about seed production and subsequent granivory under elevated nitrogen, as well as how seed movement may affect ecosystem dynamics (Throop and Lerdau, 2004; Lewis and Gripenberg, 2008). Higher nitrogen levels typically result in increased plant biomass production and higher tissue N concentrations, which can regulate trophic structure (Cebrian *et al.*, 2009). Conifers seem to be particularly sensitive to N deposition, resulting in increased insect herbivory (Armolaitis, 1998). Throop and Lerdau (2004) found higher growth or consumption rates in leaf-feeding insects in the majority of 20 studies on insect herbivory in response to N deposition. Considering nitrogen is highly limiting for most herbivores, plants producing more seed or seed with higher nitrogen concentrations could cause an increase in granivore populations, including harvester ants (Throop and Lerdau, 2004).

The effects of an altered hydrologic and nitrogen cycle in this desert system are complex and not well understood. If declines in rainfall and soil moisture reduce nitrogen availability, plant populations and the insects and animals that depend on them could be negatively impacted. Conversely, increases in nitrogen deposition could mitigate reductions in microbially-produced nitrogen in low precipitation environments (Vourlitis *et al.* 2007). If situations arise with coupled changes in water and nitrogen, the increased nitrogen availability may promote invasive plant species adapted to high nitrogen availability (D'Antonio and Vitousek 1992; Evans *et al.* 2001; Brooks 2003; Schwinning *et al.* 2005).

Furthermore, there are other interactions that are likely affected by altered precipitation and nitrogen, including plant-microbe and plant-insect interactions.

We investigated how atmospheric nitrogen deposition and precipitation affected multiple trophic levels, including plants, seeds, and seed-harvesting ants across a N deposition and precipitation gradient in the Coachella Valley and Joshua Tree National Park, California. Our study asked: 1) Are harvester ant nest densities greater in areas with higher N deposition and precipitation? 2) Does ant nest size change in areas with higher N deposition and precipitation? 3) Is seed production increased with higher N deposition and precipitation? 4) Do areas of higher N deposition and precipitation alter $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and percent carbon and nitrogen across trophic levels?

2. Materials and Methods

2.1 Nitrogen Deposition Gradient

Nitrogen deposition values from a Models-3/Community Multiscale Air Quality (CMAQ) model (Fenn *et al.* 2003; Tonneson *et al.*, 2007) and HNO_3 atmospheric concentrations from 2010-2011 sampling efforts (Bell, *unpublished*) were used to delineate three N deposition levels along the gradient (high, medium, and low) (Figures 1 and 2). In addition, the proposed N deposition threshold of about five $\text{kg ha}^{-1} \text{ year}^{-1}$, at which invasive annual plants increase (Allen *et al.*, 2009), was used to separate the medium and low N deposition levels. Precipitation values for each site were obtained from the PRISM model (PRISM Climate Group, 2004; Figure 2).

2.2 Site Description

We examined 18 sites, which stretched from the west end of the Coachella Valley to the east side of Joshua Tree National Park; these areas are comprised of the Colorado and

Mojave deserts. Nine sites were within the park boundaries, while another nine sites were situated among urban areas between Interstate 10 and the park. We selected sites based on the presence of *Messor pergandei* (Mayr) ants and their inclusion within the established atmospheric N deposition gradient (Allen *et al.*, 2009; Rao *et al.*, 2009).

The sites were *Larrea tridentata* (DC. Coville)/*Ambrosia dumosa* (A. Gray) vegetation communities. *Larrea tridentata* are evergreen shrubs, while *A. dumosa* is a drought-deciduous shrub. Other co-occurring native shrubs included *Encelia farinosa* (A. Gray ex Torr.) and *Hymenoclea salsola* (A. Gray). Common native annual forbs were *Cryptantha*, *Corzanthe*, *Eriodinium*, and many *Aster spp.* Non-native grasses (*Schismus spp.* and *Bromus rubens* L.) and non-native forbs (ex. *Brassica tournefortii* Gouan) were also present. Soil texture at each site was either loamy sand or sand; sites were located in sandy washes, basins or bajadas, and ranged from approximately 90-715 meters above mean sea level (Table 1).

Messor pergandei are ubiquitous in the deserts of southern California and are co-dominant with *Pogonomyrmex* species. *Messor pergandei* establish large nests underground and deposit sand and soil in craters surrounding the nest entrance hole. Worker ants harvest and forage seeds in the area near the nest, carrying seeds that are processed by other workers (Went *et al.*, 1972). Seeds from annual plants are typically harvested; however, perennial shrub and grass seeds are also harvested (Went *et al.*, 1972; Wissinger, *personal observation*). Seed refuse, flowers, stems, and other debris are brought from inside the nest back to the nest entrance and deposited on the crater, creating large mounds (Went *et al.*, 1972). These mounds are correlated to the size and age of the ant colony inhabiting the nest (Gordon, 1984; Wagner *et al.*, 1997).

2.3 Field Measurements

All field measurements were taken on belt transect crosses, where we established four transects radiating out at 90° angles. We established five crosses per site and the center point of each cross was separated by 300 meters. Each segment of the cross was 100 m long by 4m wide, which allowed us to survey 1,600 m². Thus, at each site we surveyed 8,000 m².

Messor pergandei nest density was calculated by counting nests with active ants within each of the five belt transect crosses. Nests no longer in use within three meters of the active nest were considered abandoned nests. We measured active nest mound diameter at its widest point and nest mound height at its highest point.

At three of the five crosses, we measured shrub density and counted fruits and seeds. *Ambrosia dumosa* and *L. tridentata* shrubs were counted within the 1,600 m². Along each transect we located the nearest *A. dumosa* and *L. tridentata* shrubs to the centerline at 20, 40, 60, 80, and 100 meters. Buds, flowers, fruits, and seeds were then counted on the last 15cm of the closest branch to the centerline.

We collected ants from at least three randomly chosen nests at each of the five crosses and preserved them in 70% ethanol. Leaves and seeds from randomly selected *A. dumosa* and *L. tridentata* within each the 1,600 m² sampled were collected, air-dried, and stored in the laboratory. Seeds from two species of annual plants known to be harvested by ants were also collected (Wissinger, *personal observation*). In the laboratory, all plant and ant samples were cleaned, rinsed with dionized water, oven dried (50°C), and stored in airtight vials until analysis. Ant gasters were removed to eliminate undigested plant material from influencing the carbon and nitrogen analysis (Tillberg *et al.*, 2006).

Percent carbon and nitrogen along with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of leaf tissue, seeds, and ants were analyzed in the Idaho Stable Isotopes Laboratory, Moscow, Idaho. Samples were analyzed on a Finnigan-MAT, Delta+ isotope ratio mass spectrometer (IRMS) using a CE Instrument's NC 2500 elemental analyzer to combust the samples. Isotope results are reported in delta (δ) notation on a per mille (‰) basis, $\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where R is the ratio of the heavy to the light isotope (Ehleringer and Rundel, 1989).

2.4 Statistical Analysis

Response variables with homogenous variances were tested using a nested ANOVA (SAS Institute, Inc.). Tukey's HSD tests were performed to determine post-hoc differences between means. Variables with heterogeneous variances were tested using a nested PERMANOVA (permutational multivariate analysis of variance) with a multivariate version of the t-statistic (based on distances) used for post hoc tests of the means (Anderson, 2005; Anderson, 2001; McArdle and Anderson, 2001). For both types of analysis, the effect of N deposition level was tested using site as a source of error; thus, site was nested within N deposition level.

3. Results

3.1 Ant Nest Descriptions

Messor pergandei nest density was significantly higher in the high and medium N deposition levels than in the low N deposition level (Figure 3a, Table 2). Abandoned nests surrounding the active colony were not significantly different among deposition levels although there was a trend of more abandoned nests at low N deposition sites (Figure 3b Table 2). Nest mounds were wider and taller in areas of lower N deposition (Figures 3c and 3d, Table 2).

3.2 Shrub Surveys

There were no significant differences in *L. tridentata* and *A. dumosa* shrub densities among the three N deposition levels. (Figure 4, Table 3). *Larrea tridentata* fruit and seed counts were significantly different among the three levels (Figure 4, Table 3); *Larrea tridentata* produced more fruits and seeds at high N deposition levels. We were unable to obtain *A. dumosa* fruit and seed counts at all sites since some shrubs had dropped their fruits and seeds before sampling began. At eight sites, there were higher numbers of *Ambrosia dumosa* fruits and seeds at sites with high N deposition ($R^2=0.80$; $p=0.0029$).

3.3 Leaf, Seed, and Ant Isotopes

As N decreased across the gradient, $\delta^{13}\text{C}$ values were more enriched. *Ambrosia dumosa* and *L. tridentata* leaf $\delta^{13}\text{C}$ values were significantly different in each deposition level; $\delta^{13}\text{C}$ values increased from high to low N deposition (Figure 5a, Table 4). Seeds from *A. dumosa*, *L. tridentata*, and annuals also had significant patterns of $\delta^{13}\text{C}$ enrichment across the deposition levels from high N to low N (Figure 5b, Table 4). In addition, the $\delta^{13}\text{C}$ of ants was significantly different among the three deposition levels, also becoming more enriched as N decreased (Figure 5c, Table 4).

Ambrosia dumosa and *L. tridentata* leaf $\delta^{15}\text{N}$ values were also significantly different among the deposition levels becoming more enriched across the gradient from high to low N deposition (Figure 5d, Table 4). *Larrea tridentata* seed $\delta^{15}\text{N}$ followed the same pattern as leaves (Figure 5e, Table 4). *Ambrosia dumosa* and annual seed $\delta^{15}\text{N}$ values were also significantly different among deposition levels (Figure 5e, Table 4), where seeds were more enriched in the medium N level than in the high and low N levels. *Messor pergandei* were

also more enriched in the medium and low N compared to high N deposition (Figure 5f, Table 4).

3.4 Leaf, Seed, and Ant Percent Carbon and Nitrogen

Nitrogen deposition had no effect on percent carbon within trophic levels. Percent carbon in *L. tridentata* leaves was not significantly different among the three N deposition levels (Figure 6a, Table 5). *Ambrosia dumosa* leaf percent carbon was similar across the three N levels (Figure 6a, Table 5). Percent carbon in seeds from *L. tridentata*, *A. dumosa*, and annual plants were not significantly different among the three N levels (Figure 6b, Table 5). There were also no significant differences in percent carbon in ants from high to low N deposition (Figure 6c, Table 5).

Patterns of percent N were similar to percent carbon. Percent N in *A. dumosa* leaves was not significantly different among the three N levels (Figure 6c, Table 5). *Larrea tridentata* leaves had slightly lower percent N at medium deposition sites (Figure 6c, Table 5). As with percent carbon, percent N in seeds of *L. tridentata*, *A. dumosa*, and annual plants were similar among the three N deposition levels (Figure 6e, Table 5). Percent N in ants was also not significantly different across the N deposition gradient (Figure 6f, Table 5).

4. Discussion

4.1 Nitrogen and Precipitation Gradients

We confirmed previously established patterns of higher N deposition on the western side of our study area. We also detected a precipitation gradient that follows this N deposition gradient. Desert productivity is limited by both nitrogen and water (Hooper and Johnson, 1999; Harpole *et al.*, 2007) and studies have found that increased water and nitrogen availability may result in increases in plant production in arid ecosystems (Rao and Allen,

2010, Yang *et al.*, 2011); therefore, we predict that precipitation enhances the nitrogen cycle throughout the region. Although long term averages indicate precipitation on the western end of the N deposition gradient is higher than on the eastern side of the gradient, rain amounts on the west side are still extremely low. Separating the influence of precipitation from the effects of increased nitrogen will require more detailed studies; however, the reliance of the nitrogen cycle on precipitation suggests that higher nitrogen levels are having positive effects on both plants and *M. pergandei*.

4.2 Ant Nest and Shrub Characteristics

While shrub density did not vary along the N deposition gradient, *L. tridentata* seed production was higher in high N deposition and precipitation areas. In addition, based on analysis and field observations, *A. dumosa* seed production patterns suggested that N deposition and precipitation increased fruit and seed production. We also predict from these patterns that annual plants (not measured in this study) would have increased seed production in areas of high N deposition based on increases in annual plant production during regional fertilization trials (Rao and Allen, 2010). *Messor pergandei* built more nests in areas with higher N deposition, which may be a function of the increased food availability with high seed production.

A larger food supply for ants may promote early colony success and decreased competition after colony establishment (Gordon and Kulig, 1996; Wagner and Gordon, 1997). Foundress queen success in harvester ants is dependent on several factors, including seed resources (Johnson, 2001). *Messor pergandei* nuptial flights and colony establishment occur after late winter rains in southern California and workers begin to harvest annual plant seeds during early spring (Went *et al.*, 1972; Johnson, 2001). Harvester ants will travel long

distances (tens of meters) to collect seeds, but abundant nearby seeds would provide easily attainable food sources promoting establishment of the young colonies (Gordon, 1995; Went *et al.*, 1972; Johnson, 2001) and help ensure colony longevity.

Competition among established *M. pergandei* colonies could also be a factor in nest density across the N deposition gradient. Ant colonies may be released from resource competition in areas with more nitrogen and precipitation due to larger amounts of seed production. Increased N could also raise the carrying capacity and thus ant colony density contributing to greater stable ant populations. *Messor pergandei* are adapted for high temperatures and sparse desert landscapes (Went *et al.*, 1972); however, more seed allows harvester ants to reduce foraging time in adverse conditions. Reduced competition for seeds throughout a colony's lifetime in high N deposition areas may result in increased ant nest density.

While ant nest density increased with increasing nitrogen, the size of ant nest mounds decreased with increasing nitrogen. Previous work on *Pogonomyrmex barbatus* and *Pogonomyrmex occidentalis* has demonstrated that colony age is correlated with colony size, specifically the size of the seed refuse mound at the nest entrance (Gordon and Kulig, 1996; Wagner and Gordon, 1997). In our study, ant nest mounds were taller and wider as nitrogen decreased. This result suggests that colonies in areas with lower nitrogen were older and more established. At sites with higher nitrogen, colonies were smaller and thus presumed to be younger and more recently established.

Group colony founding (pleometrosis) is common *M. pergandei* when resources are scarce in order to improve early colony success and usually leads to large colonies (Rissing and Pollock, 1987). Cahan (2001) investigated pleometrosis at sites similar in location to the

present study in the Coachella Valley and Joshua Tree National Park and found an increase of group colony founding in areas of low plant productivity where we also measured larger nest mounds in low nitrogen deposition areas. Our nest mound dimension patterns support the idea that there are older, larger colonies in the areas with low nitrogen. The colonies in areas with higher nitrogen deposition are more numerous, have established more recently and are smaller.

4.3 Carbon and Nitrogen Isotope Patterns

The patterns of $\delta^{13}\text{C}$ enrichment across the nitrogen and precipitation gradients (from high resources to low) indicated that plants were water stressed at the low precipitation end of the gradient. Plants discriminate against the heavier carbon isotope, ^{13}C , during stomatal conductance of CO_2 for photosynthesis (Dawson *et al.*, 2002; Fry, 2006). Plants in drought conditions decrease the time stomates are open resulting in more enriched CO_2 being used during photosynthesis (Fry, 2006). Our results follow similar patterns of $\delta^{13}\text{C}$ enrichment in water stressed conditions in conifer seedlings (Dawson *et al.*, 2002; Pinto *et al.*, 2011).

The differences in ^{13}C values among the three deposition levels could also signify different sources of carbon (Fry, 2006). Fossil fuel combustion $\delta^{13}\text{C}$ values are more depleted than the atmosphere and when mixed with the atmosphere they lower atmospheric $\delta^{13}\text{C}$ (Djuricin *et al.*, 2010). Air currents that deliver the atmospheric nitrogen deposition also deliver carbon pollution from urban fossil fuel combustion on the west side of the Coachella Valley. As plants across the valley take up carbon and as the air currents move from west to east, the polluted carbon sources become less concentrated in the east and are not taken up as readily by the plants. Depletion of the $\delta^{13}\text{C}$ values at the high N sites suggests plants are sourcing carbon from fossil fuel combustion pollution on the west side of the gradient.

Enrichment in $\delta^{15}\text{N}$ values for leaves and seeds with decreasing N contrasts results found in more mesic hardwood and conifer forests, which revealed a positive correlation with $\delta^{15}\text{N}$ and N deposition (Pardo *et al.*, 2006; Pardo *et al.*, 2007; Talhelm *et al.* 2012). The increase in $\delta^{15}\text{N}$ with increased N deposition in these other ecosystems may be due to N saturation and increased nitrification (Pardo *et al.*, 2006). Our results suggest that this desert ecosystem has not reached N saturation along the N deposition gradient due to the depleted $\delta^{15}\text{N}$ values in areas of high N deposition.

Differences in $\delta^{15}\text{N}$ could also be due to specific source $\delta^{15}\text{N}$ values along the gradient (Pardo *et al.*, 2006). Assuming that the air currents that brought the polluted carbon also delivered the nitrogen, it is possible that atmospheric nitrogen from the urban areas is eventually being taken up by harvester ants. The differences in $\delta^{15}\text{N}$ values for leaves, seeds, and ants among the deposition levels suggest that the sources of nitrogen are different or that the nitrification process is different across the gradient (Fry, 2006; Pardo *et al.*, 2006; Pardo *et al.*, 2007).

Interpreting the nitrogen isotope values are more difficult since microbial communities fractionate nitrogen before plants discriminate against the heavier isotope during nitrogen acquisition (Evans, 2001; Evans, 2007). Soil $\delta^{15}\text{N}$ values from different parts of the nitrogen cycle are not easily identifiable due to these fractionations. Furthermore, our inability to measure carbon and nitrogen isotopic values and percent composition in the soil samples collected limits our ability to link sources of plant and ant nitrogen across the gradient. Future research into the effects of atmospheric N deposition on the soil nitrogen cycle will increase our capacity to understand how atmospheric nitrogen deposition affects desert organisms.

Differences in $\delta^{15}\text{N}$ values among trophic levels are more evident. Ant $\delta^{15}\text{N}$ values are about three per mille more enriched than the $\delta^{15}\text{N}$ values of the annual seeds in each nitrogen deposition level. This enrichment difference follows the $\Delta \delta^{15}\text{N}$ of three ‰ thought to be the nitrogen fractionation for each trophic level in a system starting with the first level herbivores (DeNiro and Epstein, 1981; McCutchan Jr. *et al.*, 2003). *Larrea tridentata* seed $\delta^{15}\text{N}$ values are nearly identical to the ant $\delta^{15}\text{N}$ values in the high and medium N levels and seed values are more enriched than the ants in the low N level, suggesting that *L. tridentata* seeds are not a primary food source for *M. pergandei* across the N gradient. Although several studies have demonstrated that herbivores in desert ecosystems have elevated $\delta^{15}\text{N}$ values due to physiological means, Hartman (2010) demonstrated that $\delta^{15}\text{N}$ values of two desert bovids were likely caused by diet and not physiology due to a $\Delta \delta^{15}\text{N}$ of three ‰ between the diet and animal tissues. Our study corroborates this finding, as the ants were separated from the annual seeds with $\Delta \delta^{15}\text{N}$ of three per mille between the two trophic levels.

The similarities in percent nitrogen for plants and ants across the N deposition gradient indicate that nitrogen deposition is not increasing plant available nitrogen. The high N level areas in this study receive about $20 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Fenn *et al.*, 2007; Allen *et al.*, 2009), while typically experimental studies that examine the effects of nitrogen deposition fertilize study plots with levels much higher than natural rates (e.g. Rao and Allen, 2010; Rao *et al.*, 2009; Schwinning *et al.*, 2005). Thus, this level of nitrogen deposition is possibly too low for additions to the nitrogen cycle to occur without adequate amounts and timing of soil moisture. Precipitation pulse events could also drive compensatory population growth of nitrogen cycling bacteria resulting in excess nitrogen being added to the system becoming immobilized instead of mineralized. (Yahdjian and Sala, 2010). The amount of nitrogen in

plants and insects can also be influenced by other factors, including temperature and phosphorus availability (Fagan *et al.*, 2002; Jones and Power 2012).

Each organism's ability to regulate carbon and nitrogen may reduce any patterns across the gradient (Sturner and Elser, 2002). Other studies in *L. tridentata*/*A. dumosa* communities have found only small or no changes in percent nitrogen of vegetation in response to atmospheric N deposition (Smith *et al.*, 2009; Hall *et al.*, 2011). In addition, as the nitrogen deposition has been occurring for many decades, plants and their granivores may have already adapted to the increase in nitrogen. This adaptation could have happened early in the history of the N deposition gradient and adjustments to ecological stoichiometry are no longer apparent.

Further studies on higher trophic levels, including harvester ant predators, would provide more clarity on how ant colony competition is affected by resource limitation. Ant nest density could be regulated by predators; however, increases in precipitation and nitrogen resulted in higher food resources and higher ant nest density suggesting that harvester ant population densities' are controlled by resource availability.

5. Conclusion

Altered nitrogen inputs to desert systems are predicted to have cascading effects through trophic levels. We found higher seed production, higher ant nest densities, and smaller nests in high deposition areas suggesting that N deposition may be increasing food supplies for harvester ants and promoting colonization of new nests. In addition, variation in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across the N deposition gradient reveal sources of carbon and nitrogen

across the gradient are different and influenced by anthropogenic activities. Our results suggest that plants and harvester ants are taking up nitrogen from polluted regions.

Harvester ants are one of the primary ecosystem engineers in desert ecosystems. How they adjust to global changes, including N deposition, will affect desert plant biodiversity and health. The harvester ant's ability to move seed rivals that of any desert animal. With annual invasive plants predicted to increase with higher nitrogen paired with changes in precipitation patterns (Rao and Allen, 2009), harvester ant movement of those seeds could create considerable invasions in sensitive desert regions. In addition, native perennial shrubs, such as *L. tridentata* and *A. dumosa*, may be affected by increased competition from annual plants and growing fire risk from larger fuel loads (Rao and Allen, 2009). This competition could reduce their dominance in the deserts of southern California and shift the native plant community from perennial shrubs to invasive annual plants. The critical role of harvester ants and perennial shrubs in desert ecosystems reflects the importance of understanding how they will adapt to N deposition.

LITERATURE CITED

- Allen, E.B., L.E. Rao, R.J. Steers, A. Bytnerowicz, and M.E. Fenn. 2009. Impacts of atmospheric nitrogen deposition on vegetation and soils in Joshua Tree National Park. In: Webb, R.H., L.F. Fenstermaker, J.S. Heaton, D.L. Hughson, E.V. McDonald, and D.M. Miller (Eds.). *The Mojave Desert: Ecosystem Processes and Sustainability*. University of Nevada Press, Las Vegas, USA.
- Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.
- Anderson, M.J. 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand.
- Armolaitis, K. 1998. Nitrogen pollution on the local scale in Lithuania: vitality of forest ecosystems. *Environmental Pollution* 102:55-60.
- Bobbink, R., K. Hicks, J. Galloway, T. Spranger, R. Alkemade, M. Ashmore, M. Bustamante, S. Cinderby, E. Davidson, F. Dentener, B. Emmett, J.-W. Erisman, M. Fenn, F. Gilliam, A. Nordin, L. Pardo, and W. De Vries. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* 20:30-59.
- Brooks, M.L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* 40:344-353.
- Burke, I.C. 1989. Control of nitrogen mineralization in a sagebrush steppe landscape. *Ecology* 70:1115-1126.
- Cahan, S.H. 2001. Ecological variation across a transition in colony-founding behavior in the ant *Messor pergandei*. *Oecologia* 129:629-635.
- Cebrian, J., J.B. Shurin, E.T. Borer, B.J. Cardinale, J.T. Ngai, M.D. Smith, W.F. Fagan. 2009. Producer nutritional quality controls ecosystem trophic structure. *Plos One* 4:1-5.
- D'Antonio, C.M., Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- Davidson, D.W. 1977. Foraging ecology and community organization in desert seed-eating ants. *Ecology* 58:725-737.
- Dawson, T.E., S. Mambelli, A.H. Plamboeck, P.H. Templer, and K.P. Tu. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33:507-559.

- DeNiro, M.J. and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45:341-351.
- Djuricin, S., D.E. Pataki, and X. Xu. 2010. A comparison of tracer methods for quantifying CO₂ sources in an urban region. *Journal Geophysical Research* 115:D11303.
- Ehleringer, J.R. and P.W. Rundel. 1989. Stable isotopes: history, units, and instrumentation. In: Rundel, P.W., J.R. Ehleringer, and K.A. Nagy (Eds.). *Stable Isotopes in Ecological Research*. Springer-Verlag, New York, USA.
- Evans, R.D. 2001. Physiological mechanisms influencing plant nitrogen isotope composition. *Trends in Plant Sciences* 6:121-126.
- Evans, R.D. 2007. Soil nitrogen isotope composition. In Michener RM and Lajtha K (eds), *Stable Isotopes in Ecology and Environmental Science* 2nd Edition. Blackwell Scientific, Oxford, England.
- Evan, R.D. and J.R. Ehleringer. 1994. Water and nitrogen dynamics in an arid woodland. *Oecologia* 99:233-242.
- Evans, R.D., R. Rimer, L. Sperry, J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* 11:1301-1310.
- Fagan, W.F., E. Sieman, C. Mitter, R.F. Denno, A.F. Huberty, A. Woods, J.J. Elser. 2002. Nitrogen in insects: implications for trophic complexity and species diversification. *The American Naturalist* 160:784-802.
- Fenn, M.E., J.S. Baron, E.B. Allen, H.M. Rueth, K.R. Nydick, L. Geiser, W.D. Bowman, J.O. Sickman, T. Meixner, D.W. Johnson, and P. Neitlich. 2003a. Ecological effects of nitrogen deposition in the western United States. *BioScience* 53:404-420.
- Fenn, M.E., R. Haeuber, G.S. Tonnesen, J.S. Baron, S. Grossman-Clarker, D. Hope, D.A. Jaffe, S. Copeland, L. Geiser, H.M. Rueth, and J.O. Sickman. 2003b. Nitrogen emission, deposition, and monitoring in the western United States. *BioScience* 53:391-403.
- Fischlin, A., G.F. Midgley, J.T. Price, R. Leemans, B. Gopal, C. Turley, M.D.A. Rounsevell, O.P. Dube, J. Tarazona, A.A. Velichko. 2007: Ecosystems, their properties, goods and services. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson, Eds., Cambridge University Press, Cambridge, 211-272.
- Fry, B. 2006. *Stable isotope ecology*. Springer, New York, USA.

- Galloway, J.N. 1998. The global nitrogen cycle: changes and consequences. *Environmental Pollution* 102:15-24.
- Gordon, D.M. 1984. The harvester ant (*Pogonomyrmex badius*) midden: refuse or boundary? *Ecological Entomology* 9:403-412.
- Gordon, D. 1995. The development of ant colony's foraging range. *Animal Behavior* 49:649-659.
- Gordon, D.M and A.W. Kulig. 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology* 77:2393-2409.
- Hall, S.J., R.A. Sponseller, N.B. Grimm, D. Huber, J.P. Kaye, C. Clark, and S. Collins. 2011. *Ecological Applications* 21:640-660.
- Harpole, W.S., D.L. Potts, and K.N. Suding. 2007. Ecosystem responses to water and nitrogen amendment in a California grassland. *Global Change Biology* 13:2341-2348.
- Hartman, G. 2011. Are elevated $\delta^{15}\text{N}$ values in herbivores in hot and arid environments caused by diet or animal physiology? *Functional Ecology* 25:122-131.
- Hooper, D.U. and L. Johnson. 1999. Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry* 46:247- 293.
- IPCC (Intergovernmental Panel on Climate Change). 2007. *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]. IPCC, Geneva, Switzerland, 104 pp.*
- Jones, A.G. and S.A. Power. 2012. Field-scale evaluation of effects of nitrogen deposition on the functioning of heathland ecosystems. *Journal of Ecology* 100:331-342.
- Johnson, R.A. 2001. Biogeography and community structure of North American seed-harvester ants. *Annual Review of Entomology* 46:1-29.
- Juknys, R., J. Zaltauskaite, V. Stakenas. 2007. Ion fluxes with bulk and throughfall deposition along an urban-suburban-rural gradient. *Water, Air, and Soil Pollution*. 178:363-372.
- Kelrick, M.I., J.A. MacMahon, and R.R. Parmenter. 1986. Native seed preferences of shrub-steep rodents, birds and ants - the relationships of seed attributes and seed use. *Oecologia* 68:327-337.
- Krupa, S.V., 2003. Effects of atmospheric ammonia (NH_3) on terrestrial vegetation: a review. *Environmental Pollution* 124:179-221.

- Lewis, O.T. and S. Gripenberg. 2008. Insect seed predators and environmental change. *Journal of Applied Ecology* 45:1593-1599.
- Loik, M.E., D.D. Breshears, W.K. Laurenroth, and J. Belnap. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141:269-281.
- MacMahon, J.A., J.F. Mull, and T.O. Crist. 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics* 31:265-291.
- McArdle, B.H. and M.J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290-297.
- McCalley, C.K. and J.P. Sparks. 2008. Controls over nitric oxide and ammonia emissions from Mojave Desert soils. *Oecologia* 156:871-881.
- McCutchan Jr., J.H., W.M. Lewis Jr., C. Kendall, and C.C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102: 378-390.
- Meehl, G.A., T.F. Stocker, W.D. Collins, P. Friedlingstein, A.T. Gaye, J.M. Gregory, A. Kitoh, R. Knutti, J.M. Murphy, A. Noda, S.C.B. Raper, I.G. Watterson, A.J. Weaver and Z.-C. Zhao, 2007: Global Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Nave, L.E., E.D. Vance, C.W. Swanston, and P.S. Curtis. 2009. Impacts of elevated N inputs on north temperate forest soil C storage, C/N, and net N-mineralization. *Geoderma* 153:231-240.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25-51.
- Pardo, L.H., P.H. Templer, C.L. Goodale, D. Duke, P.M. Groffman, M.B. Adams, P. Boeckx, J. Boggs, J. Campbell, B. Colman, J. Compton, B. Emmett, P. Gundersen, J. Kjonaas, G. Lovett, M. Mack, A. Magill, M. Mbila, M.J. Mitchell, McGee, S. McNulty, K. Nadelhoffer, S. Ollinger, D. Ross, H. Rueth, L. Rustad, P. Schaberg, S. Schiff, P. Schleppi, J. Spoelstra, and W. Wessel. 2006. Regional assessment of N saturation using foliar and $\delta^{15}\text{N}$. *Biogeochemistry* 80:143-171.
- Pardo, L.H., S.G. McNulty, J.L. Boggs, and S. Duke. 2007. Regional patterns in foliar $\delta^{15}\text{N}$ across a gradient of nitrogen deposition in the northeastern US. *Environmental Pollution*

149:293-302.

Patrick, L.D., K. Ogle, C.W. Bell, J. Zak, and D. Tissue. 2009. Physiological responses of two contrasting desert plant species to precipitation variability are differentially regulated by soil moisture and nitrogen dynamics. *Global Change Biology* 15:1214-1229.

Phoenix, G.K., K.W. Hicks, S. Cinderby, J.C.I. Kuylenstierna, W.D. Stock, F.J. Dentener, K.E. Giller, A.T. Austin, R.D.B. Lefroy, B.S. Gimeno, M.R. Ashmore, and P. Ineson. 2006. Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. *Global Change Biology* 12:470-476.

Pinto, J.R., J.D. Marshall, R.K. Dumroese, A.S. Davis, and D.R. Cobos. 2012. Photosynthetic response, carbon isotopic composition, survival, and growth of three stock types under water stress enhanced by vegetative competition. *Canadian Journal of Forestry Research* 42:333-344.

Porter, E., S. Johnson. 2007. Translating science into policy: Using ecosystem thresholds to protect resources in Rocky Mountain National Park. *Environmental Pollution* 149:268-280.

PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 4 Feb 2004.

Rao, L.E., D.R. Parker, A. Bytnerowicz, and E.B. Allen. 2009. Nitrogen mineralization across an atmospheric nitrogen deposition gradient in Southern California deserts. *Journal of Arid Environments* 73:920-930.

Rao, L.E. and E.B. Allen 2010. Combined effects of precipitation and nitrogen deposition on native and invasive annual production in California deserts. *Ecosystem Ecology* 162:1035-1046.

Rissing, S.W. and G.B. Pollock. 1985. Mating season and colony foundation of the seed-harvester ant, *Veromessor pergandei*. *Psyche* 92:125-134.

Rissing, S.W. and J. Wheeler. 1976. Foraging responses of *Veromessor pergandei* to changes in seed production. *The Pan-Pacific Entomologist* 52:63-72.

Scanlon, B.R., D.G. Levitt, R.C. Reedy, K.E. Reese, M.J. Sully, R.E. Dickinson. 2005. Ecological controls on water-cycle response to climate variability in deserts. *PNAS* 102:6033-6038.

Schwinning, S., B.I. Starr, N.J. Wojcik, M.E. Miller, J.E. Ehleringer, and R.L. Sanford Jr. 2005. Effects of nitrogen deposition on an arid grassland in the Colorado Plateau cold desert. *Rangeland Ecology and Management* 58:565-574.

- Sirulnik, A.G., E.B. Allen, T. Meixner, M.F. Allen. 2007a. Changes in N cycling and microbial N with elevated N in exotic annual grasslands of southern California. *Applied Soil Ecology* 36:1-9.
- Sirulnik, A.G., E.B. Allen, T. Meixner, M.F. Allen. 2007b. Impacts of anthropogenic N additions on nitrogen mineralization from plant litter in exotic annual grasslands. *Soil Biology and Biochemistry* 39:24-32.
- Smith, S.D., T.N. Charlet, L.F. Fenstermaker, and B.A. Newingham. 2009. Effects of Global Change on Mojave Desert Ecosystems. In R.H. Webb, L.F. Fenstermaker, J.S. Heaton, D.L. Hughson, E.V. McDonald, and D.M. Miller (eds), *The Mojave Desert: Ecosystem Processes and Sustainability*. University of Nevada Press, Reno, Nevada.
- Sterner, R.W. and J.J. Elser. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, New Jersey, USA.
- Throop, H.L. and M.T. Lerdau. 2004. Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. *Ecosystems* 7:109-133.
- Talhelm, A.F., K.S. Pregitzer, A.J. Burton, and D.R. Zak. Air pollution and the changing biogeochemistry of northern forests. *Frontiers in ecology and the environment* 10:181-185.
- Tillberg, C.V., D.P. McCarthy, and A.G. Dolezal. 2006. Measuring the trophic ecology of ants using stable isotopes. *Insectes Sociaux* 53:65-69.
- Tonnesen, G., Z. Wang, M. Omary, and C.J. Chien. 2007. Assessment of nitrogen deposition: modeling and habitat assessment. California Energy Commission, PIER Energy-Related Environmental Research. CEC-500-2005-032.
- Vitousek, P.M., H.A. Mooney, J. Luchenco, and J.M. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277:494-499.
- Vourlitis, G.L., G. Zorba, S.C. Pasquini, R. Mustard. 2007. Chronic nitrogen deposition enhances nitrogen mineralization potential of semiarid shrubland soil. *Soil Science Society of America Journal* 71:836-842.
- Wagner, D. and D.M. Gordon. 1997. Neighborhood density and reproductive potential in harvester ants. *Oecologia* 109:556-560.
- Went, F.W., J. Wheeler, and G.C. Wheeler. 1972. Feeding and digestion in some ants (*Veromessor and Manica*). *BioScience* 22:82-88.
- White, J.P. and I.C. Robertson. 2009. Intense seed predation by harvester ants on a rare mustard. *Ecoscience* 16:508-513.

- Yahdjian, L. and O.E. Sala 2010. Size of precipitation pulses controls nitrogen transformation and losses in an arid Patagonian ecosystem. *Ecosystems* 13:575-585.
- Yang, L., Y. Haijun, and X. Jianyang. 2011. Effects of increased nitrogen deposition and precipitation on seed and seedling production of *Potentilla tanacetifolia* in a temperate steppe ecosystem. *Plos One* 6:e28601.

TABLES

Table 1. Site descriptions across the nitrogen deposition study area with distance from Cabazon, site type, soil texture, and elevation.

Site	Distance from Cabazon, CA (km)	Site Type	Soil Texture	Elevation (m)
Snow Creek	10	Sandy Wash	Sand	369
N. Indian Canyon	22	Basin	Loamy Sand	454
Windy Meadows	23	Basin	Sand	234
Palm Drive	27	Basin	Loamy Sand	180
Mtn. View/20th	29	Basin	Sand	240
Long Canyon	31	Bajada	Loamy Sand	392
Wide Canyon	37	Bajada	Loamy Sand	523
Willis Palms	44	Bajada	Sand	91
TNC 1	44	Bajada	Loamy Sand	232
Fan Hill	50	Bajada	Loamy Sand	533
Indio Hills	53	Bajada	Loamy Sand	405
Berdoo Canyon	58	Bajada	Loamy Sand	280
Magic Circle	88	Basin	Loamy Sand	540
JT South	94	Basin	Loamy Sand	528
Pinto Basin	96	Basin	Loamy Sand	715
Cadiz Valley	128	Bajada	Loamy Sand	542
Coxcombcell	136	Bajada	Loamy Sand	375
Aqueduct	140	Bajada	Loamy Sand	360

Table 2. Nested ANOVA and PERMANOVA (*) results for ant nest density, abandoned nests, nest mound diameter, and nest mound height in the three deposition levels across the N deposition gradient.. Significant P-values are bolded where $\alpha = 0.05$.

	Source					
	N Deposition Level			Site(N Deposition Level)		
	DF	F	P value	DF	F	P value
Ant Nest Density*	2,89	6.1	0.0052	15,89	4.62	0.0002
Abandoned Nests	2,89	3.21	0.0692	15,89	5.15	<0.0001
Nest Mound Diameter*	2,89	4.16	0.0278	15,89	4.23	0.0002
Nest Mound Height	2,89	4.82	0.0242	15,89	1.67	0.0759

Table 3. Nested ANOVA and PERMANOVA (*) results for *Larrea tridentata* and *Ambrosia dumosa* shrub densities and *L. tridentata* fruit and seed count in the three deposition levels across the N deposition gradient. Significant P-values are bolded where $\alpha = 0.05$.

	Source					
	N Deposition Level			Site(N Deposition Level)		
	DF	F	P value	DF	F	P value
<i>L. tridentata</i> Shrub Density*	2,53	1.06	0.3658	15,53	3.37	0.0004
<i>A. dumosa</i> Shrub Density*	2,53	0.87	0.5046	15,53	3.6	0.0002
<i>L. tridentata</i> Fruit and Seed Count	2,53	5.81	0.0135	15,53	13.24	<0.0001

Table 4. Nested ANOVA results for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Ambrosia dumosa* and *Larrea tridentata* leaves, *Ambrosia dumosa* and *Larrea tridentata* seeds, annual plant seeds, and *Messor pergandei* ants in the three deposition levels across the N deposition gradient. Significant P-values are bolded where $\alpha = 0.05$.

$\delta^{13}\text{C}$	Source					
	N Deposition Level			Site(N Deposition Level)		
	DF	F	P value	DF	F	P value
<i>A. dumosa</i> Leaves	2,53	28.97	<0.0001	15,53	4.08	0.0003
<i>L. tridentata</i> Leaves	2,53	17.1	0.0001	15,53	6.13	<0.0001
<i>A. dumosa</i> Seeds	2,53	40.39	<0.0001	15,53	4.86	<0.0001
<i>L. tridentata</i> Seeds	2,53	31.46	<0.0001	15,53	3.36	0.0014
Annual Plant Seeds	2,53	35.6	<0.0001	15,53	7.23	<0.0001
<i>M. pergandei</i>	2,53	21.18	<0.0001	15,53	15.65	<0.0001
$\delta^{15}\text{N}$						
<i>A. dumosa</i> Leaves	2,53	8.05	0.0042	15,53	1.55	0.1403
<i>L. tridentata</i> Leaves	2,53	4.94	<0.0001	15,53	5.97	<0.0001
<i>A. dumosa</i> Seeds	2,53	3.15	0.072	15,53	2.96	0.0038
<i>L. tridentata</i> Seeds	2,53	8.86	0.0029	15,53	2.22	0.0249
Annual Plant Seeds	2,53	4.03	0.0398	15,53	3.71	0.0006
<i>M. pergandei</i>	2,53	8.96	0.0028	15,53	2.33	0.0189

Table 5. Nested ANOVA results for % carbon and % nitrogen values of *Ambrosia dumosa* and *Larrea tridentata* leaves, *Ambrosia dumosa* and *Larrea tridentata* seeds, annual plant seeds, and *Messor pergandei* ants in the three deposition levels across the N deposition gradient. Significant P-values are bolded where $\alpha = 0.05$.

%C	Source					
	N Deposition Level			Site(N Deposition Level)		
	DF	F	P value	DF	F	P value
<i>A. dumosa</i> Leaves	2,53	0.4	0.6758	15,53	1.76	0.0817
<i>L. tridentata</i> Leaves	2,53	3.59	0.053	15,53	3.59	0.0005
<i>A. dumosa</i> Seeds	2,53	0.63	0.5476	15,53	1.96	0.0488
<i>L. tridentata</i> Seeds	2,53	1.46	0.2638	15,53	2.24	0.0242
Annual Plant Seeds	2,53	1.17	0.3386	15,53	1.17	0.3386
<i>M. pergandei</i>	2,53	1.21	0.3244	15,53	1.3	0.2532
%N						
<i>A. dumosa</i> Leaves	2,53	0.97	0.4031	15,53	3.23	0.002
<i>L. tridentata</i> Leaves	2,53	0.25	0.7814	15,53	2.39	0.0163
<i>A. dumosa</i> Seeds	2,53	1.46	0.2632	15,53	1.4	0.2014
<i>L. tridentata</i> Seeds	2,53	1.43	0.2699	15,53	0.7	0.771
Annual Plant Seeds	2,53	0.69	0.516	15,53	3.83	0.0005
<i>M. pergandei</i>	2,53	2.42	0.1229	15,53	0.78	0.6947

FIGURES

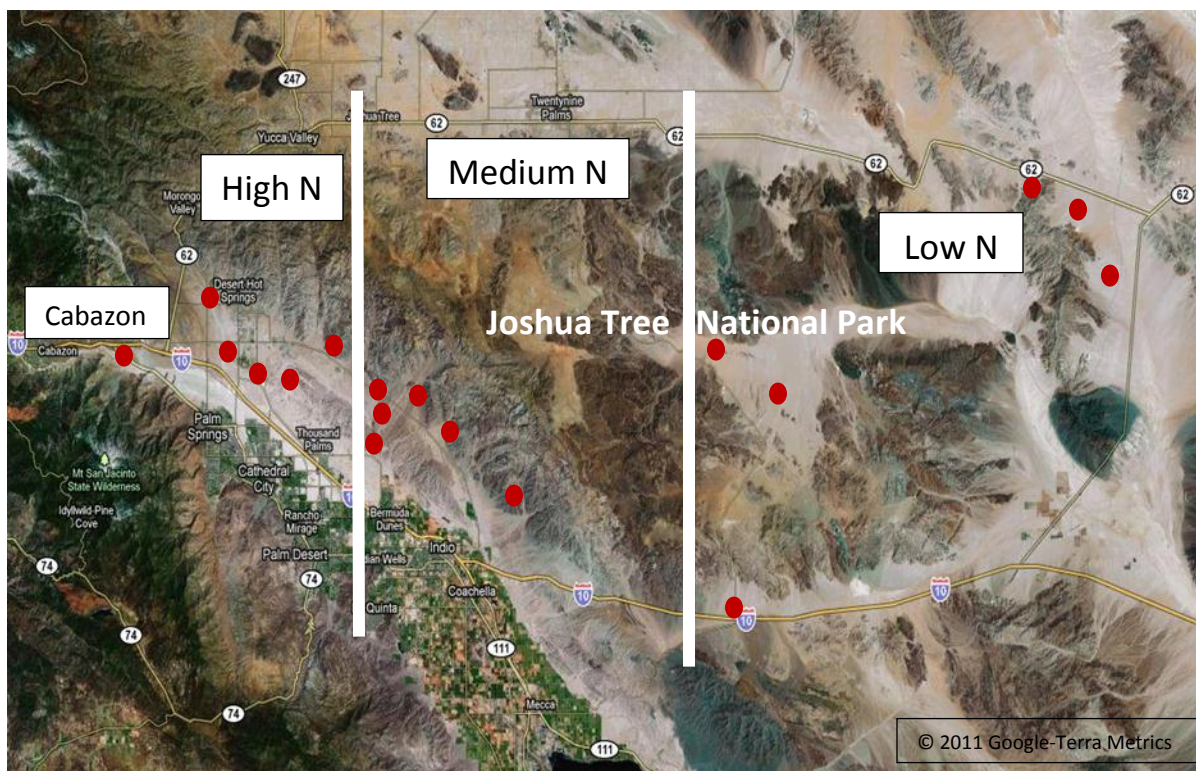


Figure 1. Map of study sites across the N deposition gradient in southern California. Sites (red circles) were grouped into three N deposition levels (high, medium, and low); six sites are within each deposition level.

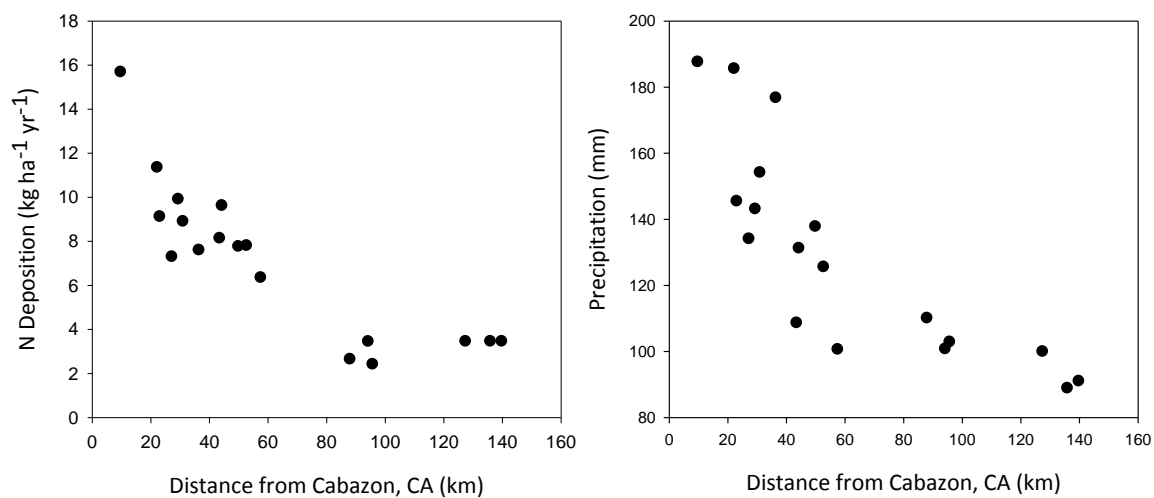


Figure 2. Nitrogen deposition and precipitation values for each of 18 sites across the Coachella Valley and Joshua Tree National Park, CA. Each site is measured as the distance from Cabazon, CA, which is the farthest town on the west side of the gradient. Nitrogen deposition values were calculated from modeled N deposition (Center for Conservation Biology, UC Riverside). Precipitation values are the yearly average precipitation from 2000 through 2011 and were calculated by the PRISM model (Oregon State University).

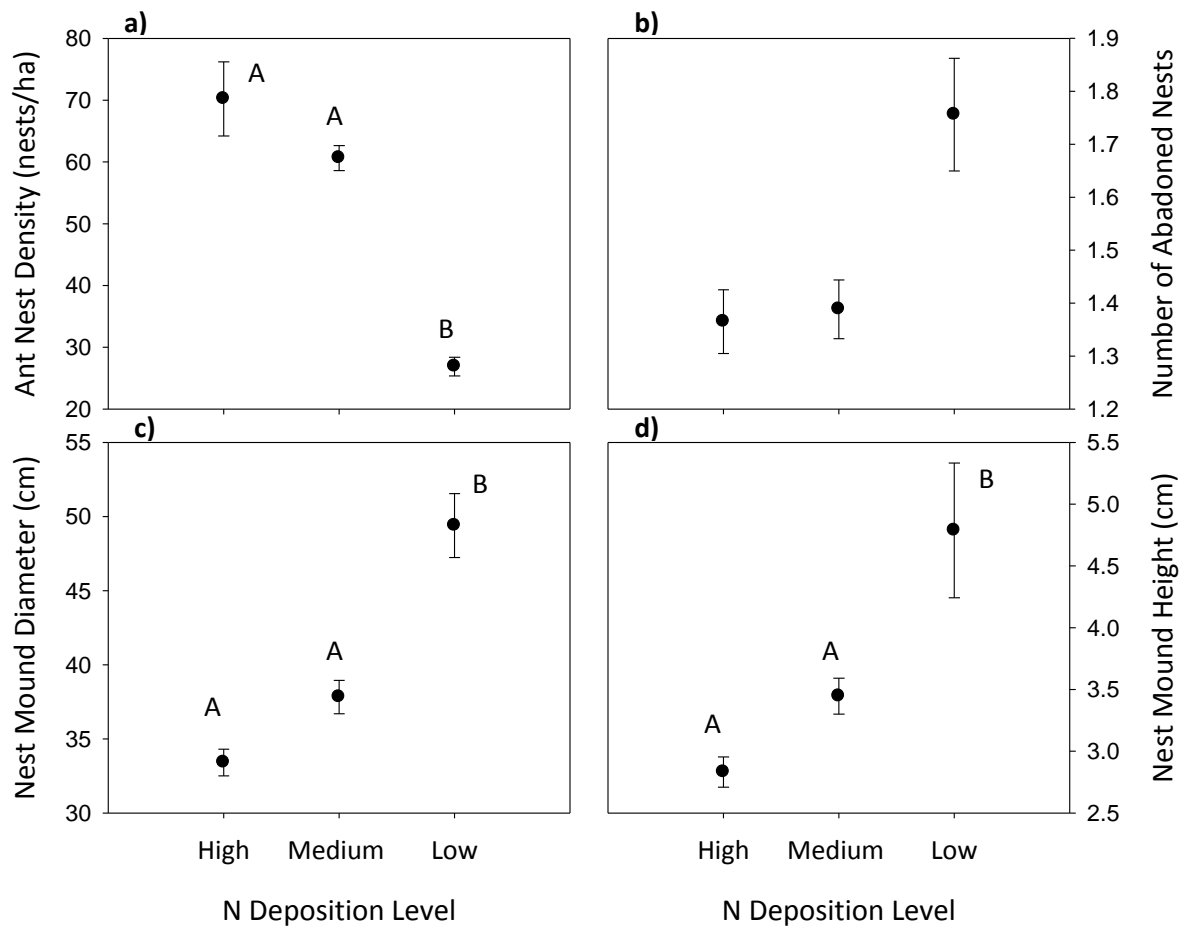


Figure 3. *Messor pergandei* nest density, number of abandoned nests, nest mound diameter and height in three N deposition levels across the gradient. Each deposition level consists of six sites. Capital letters signify significant differences between N deposition levels. Error bars represent \pm SEM.

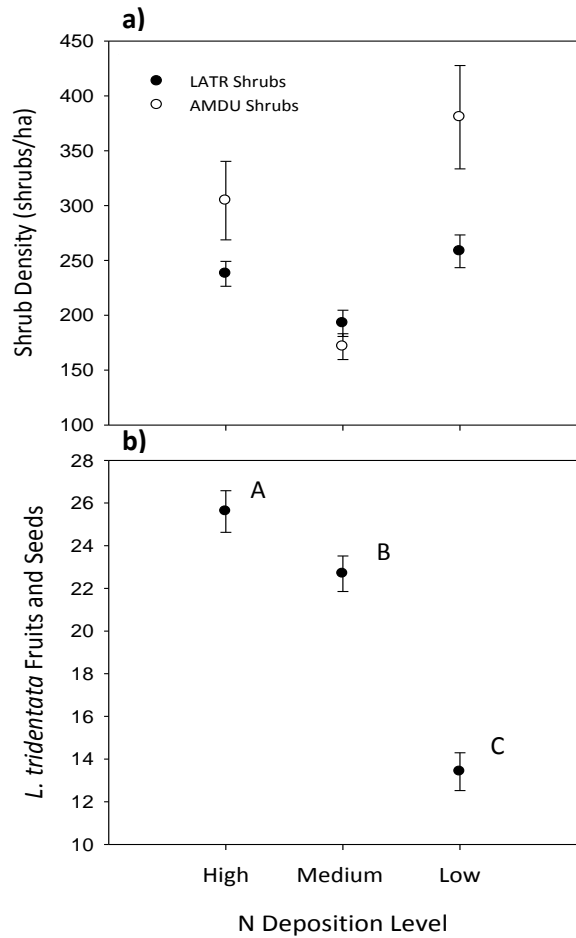


Figure 4. *Larrea tridentata* and *Ambrosia dumosa* shrub densities and *L. tridentata* fruit and seed count in three N deposition levels across the gradient. Each deposition level consists of six sites. Capital letters signify significant differences between N deposition levels. Error bars represent \pm SEM.

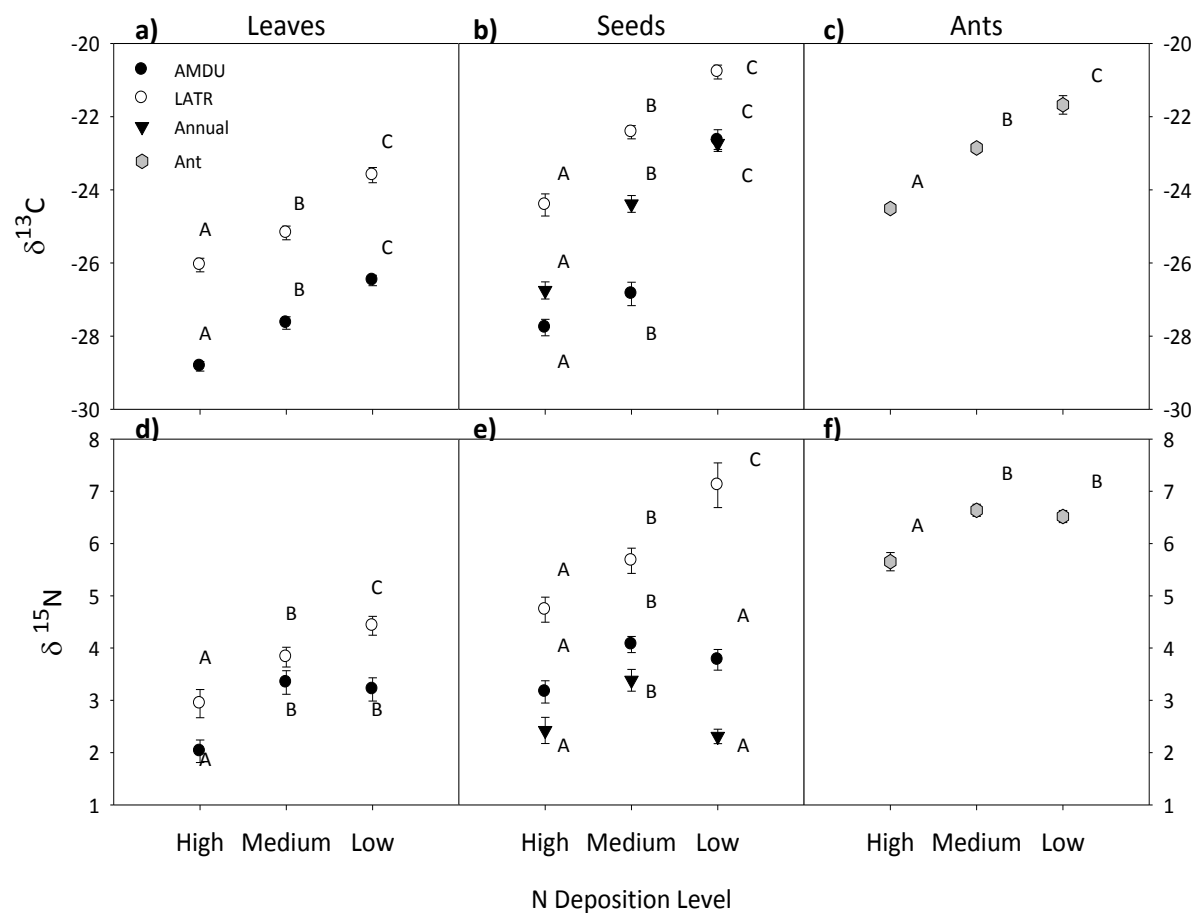


Figure 5. $\delta^{13}\text{C}$ (top panel) and $\delta^{15}\text{N}$ (bottom panel) values for leaves, seeds and ants in three N deposition levels across the gradient. Each deposition level consists of six sites. Capital letters signify significant differences between N deposition levels. Error bars represent \pm SEM.

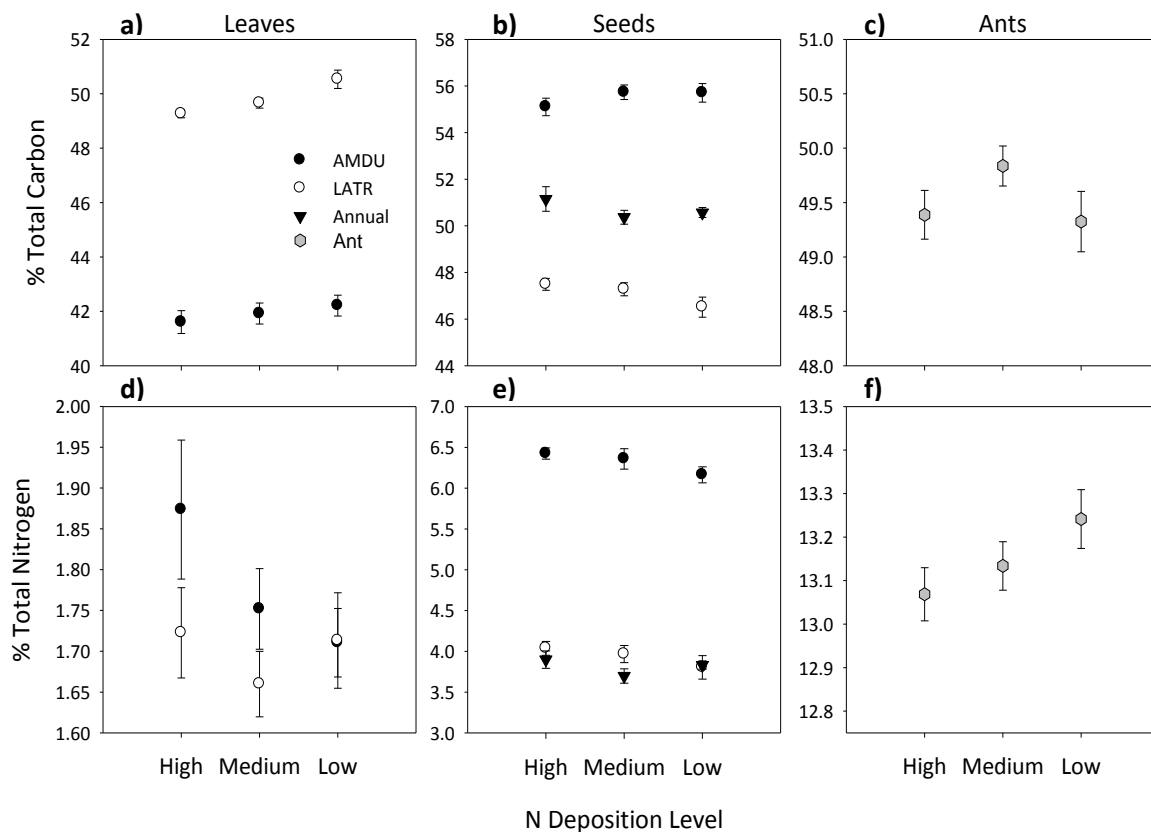


Figure 6. Percent carbon (top panel) and percent nitrogen (bottom panel) values for leaves, seeds and ants in three N deposition levels across the gradient. Each deposition level consists of six sites. Capital letters signify significant differences between N deposition levels. Error bars represent \pm SEM. Note differences in scale among the different types of tissue analyzed.