IMPACTS OF ANTHROPOGENIC NOISE ON LITTER CHEMISTRY AND DECOMPOSITION PROCESSES IN A SEMI-ARID ECOSYSTEM

by

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The following individuals read and discussed the thesis submitted by student Peggy Martinez, and they evaluated her presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

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DEDICATION

For my family NMO, ESM and LCM.

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ABSTRACT

Chronic anthropogenic noise in ecosystems can change avian/arthropod/plant interactions, but it is unclear how changes in herbivory pressure affects functional traits of plants. We asked how anthropogenic noise, mediated through changes in arthropod abundance, altered timing of leaf senesce, chemical composition (i.e. C/N ratios, total phenolics) and decomposition rates of leaf litter in Wyoming big sagebrush (*Artemisia tridentata spp. wyo.)*. Additionally, we asked if changes in arthropod abundance altered secondary metabolites (i.e. monoterpenes) in foliage. We broadcasted recorded gas compressor station noise (24hrs/day) from April through October 2015 in a sagebrush steppe ecosystem of Idaho, USA. We quantified quantity, chemical composition (i.e. C/N ratios, total phenolics) and decomposition rates of leaf litter and changes to monoterpene concentrations. We found that: (1) changes to top down forces resulting from noise treatments did not impact the leaf abscission rates, the chemical composition of leaf litter or litter decomposition and (2) time of year significantly affected quantity, chemical composition (i.e. C/N ratios and phenolic concentrations) and decomposition of leaf litter. Our research indicates that increases in anthropogenic noise over one growing season does not impact litter chemistry or decomposition processes. Future research should evaluate whether prolonged noise-induced changes in herbivory lead to changes in litter chemistry and decomposition.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The United States is currently the world’s largest consumer and producer of natural gas, and this trend is projected to continue into the year 2040 (IEA, 2016). In 2015 and 2016, the U.S. increased demand and production of natural gas by 3.1%, and 5.5%, respectively (IEA, 2016). This led to the establishment of more than 555,000 active gas-producing wells (U.S. EIA, 2015). Much of this production occurs in the sagebrush-dominated landscape of the Intermountain West, U.S. (Knick et al., 2003), and future oil and gas exploration is predicted to impact 3.7 million ha of sagebrush steppe ecosystems (Copeland et al., 2009). Developing well pads for natural gas extraction requires locating gas deposits (i.e. seismic mapping), infrastructure establishment (i.e. roads, buildings), horizontal/vertical drilling (i.e. fracking) and moving liberated gas to processing plants (i.e. compressors). Through vegetation removal, road construction and noise pollution, the ecosystem becomes fragmented and degraded, and wildlife behavior can be altered (Fahrig and Rytwinski, 2009; Francis et al., 2009; Northrup and Wittemyer, 2012; Allred et al., 2015). Currently, the sagebrush steppe is less than half of the historic range, and what remains is highly fragmented from anthropogenic land-use changes such as livestock grazing, agriculture and natural gas development (Braun, 1998; Connelly et al., 2000; Knick et al., 2003; Copeland et al., 2009). Thus, natural gas development will exacerbate the effects of disturbances already operating in this ecosystem, possibly leading to irreversible changes in its structure and function.

While many of the disturbances associated with gas development are relatively short-term, the compressors used to move gas through pipelines can last for ten or more years, until the well runs dry. Sustained noise stemming from these compressors can alter ecosystem function through noise-induced changes in the interactions between predators, herbivores, plants, and ultimately detritivores. Anthropogenic noise disrupts distributions and community structure of wildlife, resulting in negative consequences to overall fitness and altered species abundance/composition (Francis et al., 2009; Farrell et al., 2012; Francis and Barber, 2013). Recently, studies have linked anthropogenic noise exposure to altered songbird foraging and vigilance patterns (Quinn et al., 2006; Ware et al., 2015), and avoidance of suitable habitat (Blickley et al., 2012; Ware et al., 2015, Kleist et al., 2017). Cinto-Mejia (2017) found that playback of gas compressor noise resulted in decreased songbird distribution, and that this decline in-turn lead to changes in arthropod distributions. These alterations can potentially cascade through the ecosystem to impact plant physiology, and ultimately may affect the quantity and chemical composition of litter and decomposition processes (Findlay et al., 1996; Chapman et al., 2003). Changes in decomposition processes can further feedback to alter plant community structure and the consumers depending on it (*see review* Estes et al., 2011; Bardgett and Wardle, 2010, Chomel et al., 2016), making it important to understand how noise impacts litter chemistry and decomposition. Although we know that noise pollution from gas wells will lead to loss of insectivores (i.e. songbirds), change the abundance and community composition of herbivores, and affect plant physiology (Pacioretty 2016), we are uncertain about its impacts on litter chemistry and decomposition processes in arid ecosystems.

Noise induced changes in herbivory are likely to impact leaf litter chemistry, and affect decomposition rates. Namely, herbivory affects leaf litter quality metrics such as C/N ratios, which is linked to sudden leaf abscission (Chapman et al., 2003), complex phenolics (Findlay et al., 1996) and monoterpene concentrations (Wiens et al., 1991). Changes in each one of these variables have a direct impact on microbial activity, with an increase in activity as C/N ratios and phenolic concentrations decrease (Eiland et al., 2001) and a decrease in activity with an increase in C/N ratio or phenolic or monoterpene concentrations (Hättenschwiler and Vitousek, 2000; Chomel et al., 2016). Despite these predictable impacts of changes in litter chemistry on decomposition, impacts of herbivory on litter chemistry have been highly variable among plant types, leading to both acceleration and deceleration of decomposition in response to herbivory (Chapman et al., 2006; Bardgett and Wardle, 2010).

Disparate effects of herbivory on litter quality and decomposition rates may hinge on plant life history traits (i.e. deciduous, evergreen) (Chapman et al., 2006). For example, acceleration of decomposition occurred when evergreen trees induced leaf abscission and failed to re-absorb nitrogen rich compounds thereby decreasing the C/N ratio in litter (Chapman et al., 2006). Conversely, deceleration of decomposition occurred when deciduous trees induced phenolic compounds (Findlay et al., 1996; Chapman et al., 2006). Although Chapman et al. (2006) reported increased litter quality in evergreens, others (White, 1991; Paavolainen et al., 1998) have shown evergreens induce secondary metabolite production (i.e. monoterpenes) in response to herbivory which then, in turn, decelerates decomposition (Chomel et al., 2016). These diverging responses make predicting the impacts of herbivory on sagebrush difficult. This difficulty is exacerbated by the fact that sagebrush has life history traits akin to both evergreen and deciduous trees. Namely, sagebrush is a drought deciduous shrub that also maintains persistent leaves for a year or more (Evans and Black, 1993). The net effect of both positive and negative effects of herbivory on sagebrush litter quality is uncertain. Thus, it is unclear how sagebrush litter and decomposition thereof will respond to predicted increased herbivore pressure associated with effects of anthropogenic noise.

The objectives of this study were to gain a better understanding of how noise-induced changes in herbivory pressure affects the chemical composition of sagebrush leaf litter and foliage. We played back recorded compressor station noise in a sagebrush-dominated ecosystem southwest of Boise, Idaho from April-October 2015. Through creating a \`phantom\` natural gas field, we were able to uncouple the effects of noise from other sources of disturbance (i.e. roads, proximity to humans, habitat fragmentation) caused by natural gas fields (Northrup and Wittemyer, 2012). In addition to noise manipulation, we created vertebrate insectivore exclusions to prevent predator access to arthropods (Bridgeland et al., 2010; Maas et al., 2013), thereby implementing a positive control for arthropod herbivory. We tested three hypotheses: 1) anthropogenic noise and exclusion of vertebrate insectivores will reduce litter C/N ratio because shrubs will abscise leaves damaged by arthropod herbivory (Chapman et al., 2006, Bardgett and Wardle, 2010), thus accelerating decomposition 2) anthropogenic noise and exclusion of insectivores will increase total phenolics because shrubs induce chemical defenses in response to herbivory (Wiens et al., 1991; Chapman et al., 2006), thus decelerating decomposition and 3) shrubs will induce chemical defenses (i.e. monoterpenes) in leaf tissue because volatiles released from damaged tissue (i.e. experimental clipping) reduce herbivory (Karban et al., 2006; Shiojiri et al., 2012). To assess effects of herbivory on senesced leaf litter we collected Wyoming big sagebrush (*Artemisia tridentata spp. wyo*) leaves monthly and measured quantity of litter-fall, quality metrics (i.e. %C, %N, total phenolics) and decomposition rates. To assess effects of herbivory on foliage (i.e. monoterpenes), we experimentally clipped sagebrush in April and again in October because sagebrush respond to volatile cues in response to herbivory (Karban et al., 2006; Shiojiri et al., 2012). Understanding how anthropogenic noise cascades through trophic levels is critical to the effective management and preservation of ecosystem services for lands currently being tapped for energy exploration.

METHODS

Experimental Design

The study was conducted at the Orchard Combat Training Center (OCTC), approximately 24 km south of Boise, ID, USA on the central portion of the Snake River Plain and the Mountain Home Plateau. The area is located within the Morley Nelson Snake River Birds of Prey Conservation Area and has been used by the Idaho Air National Guard and serves as a major training site for Idaho Army National Guard since the early 1950's. Study sites are dominated by Wyoming big sagebrush (*Artemisia tridentata spp. wyo*) with patches of rubber rabbitbrush (*Ericameria nauseosa*), Sandberg's bluegrass (*Poa secunda*) and red threeawn (*Aristida pupurea*). Common mammals include the Piute ground squirrel (*Urocitellus mollis*), coyote (*Canis latrans*), black-tailed jackrabbit (*Lepus californicus*), and American badger (*Taxidea taxus*). Common insectivorous birds include Brewer's sparrow (*Spizella breweri*), sagebrush sparrow (*Artemisiospiza nevadensis*), Western meadowlark (*Sturnella neglecta*) and horned lark (*Eremophila alpestris*).

Soils are characterized as sandy-clay loam, with up to 40% clay content. Mean annual temperature ranges from 7.2°C-10°C with a mean annual precipitation of 23.5cm (USDANRCS 2015).

In 2015, we constructed six control sites (n=6) that lacked noise playback (hereafter, control) and six treatment (n=6) sites where we broadcasted compressor noise (hereafter, noise). These sites were 100m x 100m and were located at least 1km apart and at least 500m from secondary roads. At noise sites we mounted omni-directional speakers (Octasound SP820A; 35–20,000 Hz ±10dB) and subwoofers (Octasound OS2X12; 25–20,000 Hz ±10dB) driven by Class T amplifiers (Lepai LP-2020A 20W, 4-ohm) to 2m tall metal support towers. Amplifiers were powered by solar array systems and sound was broadcast using Olympus LS-7 (MP3) players. We played synthetic compressor noise, created in Audacity from an average of 3 compressor stations recorded in the San Juan basin, NM and Green River Basin, WY. Compressor stations were recorded with a Sennheiser ME66 microphone (40–20,000Hz; ±2.5dB) and Roland R-05 recorder (sampling rate 48 kHz) at 40m. We created a 3-hour playback file that was repeated 24hr/day. It is important to note that the compressor stations we recorded very likely produced energy below 20Hz (22), the lower limit of our microphone (Cinto-Mejia, 2017). For control sites we attached empty five gallon buckets to 2m tall metal support towers to represent speakers and used glass mounted on top of blue-painted plywood to represent solar panels, thereby controlling for potential alterations caused by our infrastructure.

At each study site three pairs of Wyoming big sagebrush shrubs (total of six shrubs) were chosen for physiology measurements and leaf litter collection. The shrubs were located at a 50m radius from speakers in each cardinal direction (W, N, E). In each pair of shrubs, one was covered with netting (netted) to exclude vertebrate insectivores (i.e. bird/bat) and one was left uncovered (un-netted). To create vertebrate insectivore exclusions, four rebar posts were driven vertically into the ground and exclusion netting (DuPont 14’x14’) was stretched around the posts and secured with zip ties (Figure 2). The netting prevented vertebrate access to arthropods, but allowed for free movement of arthropods. This experimental design allowed us to compare noise/control treatments, as well as netted/un-netted treatments. Additionally, two pairs of shrubs, 50m from speakers in cardinal directions North and South, were selected for clipping treatments. In each pair, one shrub was covered with vertebrate insectivore exclusion netting and one left uncovered. These four shrubs allowed us to evaluate changes in monoterpene concentrations. Figure 1 provides a schematic for the experimental design.

Arthropod abundance

Detailed methods for arthropod collection and analysis are provided in Cinto-Mejia (2017). Briefly, arthropod collections were completed using a variety of techniques (i.e. Beat netting, Japanese flying and pit fall traps) from April-June 2015, since arthropod abundance greatly decreases in the sagebrush-steppe in June (Takahashi and Huntly, 2010). Arthropods were identified down to lowest possible taxonomic group using a dissecting scope and placed into one of six trophic groups (grazers, sap-feeders, predators, scavengers, detritivores, parasites, and undetermined) based on their adult feeding strategies.

Foliage collection and analysis

We clipped foliage with scissors from four sagebrush plants at each control and noise sites on April 15th, 2015. One of the clipped shrubs was then covered with bird exclusion netting as described above. Clippings were transported on ice inside Ziploc bags and stored at -20°C until further processing. At the end of the field season on October 15th, 2015, foliage was again clipped with scissors and transported on ice inside Ziploc bags and stored at -20°C. These clippings were used for volatile compound analysis.

Clippings were prepared for analysis by grinding leaves to a fine powder with a mortar and pestle in liquid nitrogen to minimize volatilization of monoterpenes. Ground samples (100 mg) were placed into a glass headspace vial and sealed with aluminum crimp style caps. Samples were stored at -20°C until being processed on Agilent 7694 headspace auto-sampler coupled with Agilent 6890N gas chromatograph. Headspace vials were heated to 100°C for 20 min to reach vial equilibrium. Headspace gas (1 mL) was injected into a capillary column using a carrier gas. Volatile compounds were identified using chromatographs compared to known standards. A correlation matrix was used to identify highly correlated compounds, allowing us to trim our data set before statistical analysis. Percent change was calculated from the first clipping event (April) to the end clipping event (October) for eight individual volatile compounds.

Litter Collection and analysis

Litter was collected from each shrub using litter traps composed of fiberglass insect screen that was wrapped around the base of each shrub and loosely secured with zip ties around the circumference of the shrub. The litter traps were installed in April (15th -20th) 2015, and we collected senesced litter from the traps on the 1st through the 4th day of each month, May through September, 2015, using a hand-held vacuum (DustBuster). Litter was not collected in April due to extremely low leaf litter amounts. Litter was transported in Ziploc bags on ice then stored at -20°C until further processing.

The litter was sieved through a 2mm mesh to remove small debris (i.e. lichen, sticks, ants, etc.), then meticulously sorted by hand to remove any remaining non-leaf litter particles. The air dried litter was massed and stored at room temperature for future analysis. The formula for an ellipsoid was used to standardize amount of litter collected by the size of shrub (Cleary et al., 2008). Sorted litter from netted (vertebrate insectivore exclusion) and non-netted shrubs were composited within site, air dried and ground using a Wiley mill (2mm attachment) and pulverized to a fine powder with a ball mill. Litter C and N concentrations were determined using a Thermo Electron Flash EA 1112 CN analyzer at Boise State University. Samples were run in duplicate using peach leaves as calibration and internal standards.

Total phenolics from air dried leaf litter were extracted by weighing 5 grams of ground (<2 mm) samples into 2mL micro centrifuge tubes and eluting samples with 1.0 mL (100%) HPLC-grade methanol. Washed samples were then placed in a sonicating water bath (25°C) for three minutes (two times), with a two minute rest period between each sonication. Samples were then centrifuged at 13,000 rpm for five minutes at room temperature (20°C). Supernatant was filtered through glass wool and stored in glass vials at -20°C. After extraction, total phenolic content was assessed using adapted procedures from Ainsworth and Gillespie (2007) and Zhang et al. (2006). Samples (40 µL) were diluted to a total volume of 100 µL (1:2.5 dilution) in HPLC grade methanol. Diluted samples (20 µL) were then pipetted in triplicate into 96-well plates. Each sample was reacted with 10 % Folin-Ciocalteu reagent and 7.5% sodium carbonate solution. After thoroughly mixing reagents with samples, 96 well plates were covered with aluminum foil and incubated at room temperature for two hours. Microplates were read on Biotek SynergyMX multi-mode micro-plate spectrophotometer at absorbance 765 nm. Each plate was ran with known standards of Gallic Acid ranging from 0-1.0 mg/mL.

Potential Decomposition Assay

Air dried soil collected from Orchard Combat Training Center was sieved through 2 mm mesh and picked free of roots and other organic materials. Water holding capacity (WHC) of soil was determined by adding water dropwise until saturation had occurred (100% WHC). Water was added to each replicate to obtain 60% of this water holding capacity. Ground (<2 mm) sagebrush litter (0.3 g) was mixed with prepared soil (30 g) in 120 mL specimen cups. Litter collected in May, June and September were used for incubation to capture peak times of arthropod abundance (i.e. May and June) and the full treatment time (i.e. September). Un-amended soil (soil only) was incubated in triplicate to account for CO_2 production of pre-existing soil C. Additionally, blanks containing only water were run in triplicate to account for background CO_2 evolution (de Graaff et al., 2004). Specimen cups were placed in 1.89 L Mason jars and 3 mL of water was added to the bottom of the jar to slow soil drying and to prevent condensation from dripping into treatments. Septa were installed in lids to take air samples from headspace using a 20mL syringe and needle. Samples were kept at room temperature (~20°C) and CO_2 respiration measurements were taken on days 1, 3, 7, 14, 29 and 60 following initial wetting event. Headspace gas samples of either 1 or 2 mL (depending on headspace concentration) were injected into LiCor (Li 7000) CO_2/H_2O analyzer, using online metronome set at 44 bpm to ensure consistent flow. Standard curve was established using medical grade CO_2 (2000 ppm; NORCO supplier). After sampling, jars were opened to flush out CO_2 for 30 minutes outside the room. After 30 min flush out period, if soil moisture fell below 2% of the 60% water holding capacity, water was added.

Statistical Analysis

We built linear mixed-effects models representing several *a priori* hypotheses that tested the effects of noise and/or net on litter quantity and quality. Models for quantity and quality (i.e. C/N ratio, total phenolics and eight individual non-correlated volatile compounds) included various combinations of decibel level (dB), netted vs. non-netted shrubs and quadratic effects of month. For incubation data, models included combinations of dB, netted vs. non-netted shrubs, linear effects of month, and day the sample was collected (i.e. 1, 3, 7, 14, 29, 60). All models included site as a random effect. Several of the models included interaction effects between net and dB to determine if effect of net on the response variable differed for varying values of dB. We ranked and compared the models using Akaike's Information Criterion (AIC) (Akaike, 1974) corrected for small sample size (AICc) (Hurvich and Tsai, 1989). When data was non-normally distributed they were log transformed. We used repeated measures mixed effect models to test *A posteriori* hypotheses that quantity and quality varied by month, using site as the random effect. Post hoc pairwise comparisons with Bonferroni correction was used to determine which months were different. A post hoc linear regression model was used to establish a relationship between C/N ratio and C efflux. All linear and mixed models were built in program R v. 3.3.1 (R Code Team, 2016) using packages lme4 (Bates et al., 2015) and ez (Lawrence, 2016) and were fit using maximum likelihood.

RESULTS

Litter Quantity and Quality

Litter quantity was not affected by noise and/or net treatments (Fig. 3-4), but did vary by month. May, June and August showed no differences in amount of litter collected, but July litter mass was significantly higher and September litter mass was significantly lower than all other months ($p<0.001$; Fig. 5).

Noise and/or net treatments did not affect C/N ratio (Fig. 6-7), however litter C/N ratios differed by month. In relation to May, June increased +27%, July +49%, August +64% and September +31%. June and September did not differ from each other, however all other months did (Fig. 8; Table 1).

Total phenolic concentration (mg GA equiv. /g dry wt.) of senesced litter was not affected by noise and/or net treatments (Fig. 9-10), but there were differences among months. Whereas, May, July and September did not significantly differ from one another, June and August had significantly higher total phenolic concentration (+30% and +19%, respectively) than the other months tested. June and August differed significantly from each other, with July having 13% higher concentration of total phenolics (Fig. 11; Table 1). There was no effect of noise and/or net treatments on volatile compounds (Table 2).

Potential Decomposition

There was no effect of noise and/or net treatments on soil C respiration derived from litter collected in May, June or September (Fig. 12a-c), but there were significant differences among different months and day samples were taken (Fig. 12d, Table 3). May and September significantly differed in C efflux for all days samples were collected (Table 4). There was a significant negative relationship between C/N ratio and C efflux ($p<0.001$, Fig. 13). There were no significant effects of total phenolic concentrations on C efflux.

DISCUSSION

To our knowledge, this study is the first to assess if anthropogenic noise has top down effects on the functional traits of plants in semi-arid ecosystems. Our study focused on how anthropogenic noise impacts the quantity, chemical composition (i.e. C/N ratios, phenolic concentrations, or monoterpene concentrations) and decomposition of sagebrush leaf litter, through altered plant-arthropod interactions. The study built on results generated by others in the same experiment, including noise impacts on songbird and arthropod distributions, and shrub physiology (Pacioretty, 2016; Cinto-Mejia, 2017). Our study yielded two main results: (1) changes in top down forces resulting from noise treatments did not impact the leaf abscission rates, the chemical composition of leaf litter or litter decomposition and (2) time of year significantly affected quantity, chemical composition (i.e. C/N ratios and phenolic concentrations) and decomposition of leaf litter.

Noise decreased songbird distribution (-26%), increased the abundance of some arthropod guilds (i.e. grazers (+33.7%), omnivores (+30%), sap feeders (+30%), parasite (+18.8%), predator (+16.4%), parasite (18.8%); Cinto-Mejia, 2017; Table 5), enhanced photosynthesis and respiration of sagebrush shrubs (Pacioretty 2016, thesis), but did not affect leaf litter chemistry or litter decomposition. Despite the increase in grazing arthropod guilds, Pacioretty (2016) found no increase in bite marks in noise sites. Furthermore, she did not find an increase in bite marks in the netted shrubs that served as positive controls, notwithstanding the increase in Cicadelliade (i.e. leafhoppers belonging to the grazer guild) in these treatments. These results indicate that the increase in abundance of grazers was not accompanied by an increase in grazing pressure. This may explain why we found no changes in litter chemistry or litter decomposition. However, the increase in photosynthesis and respiration suggests compensatory growth, which is a widely accepted response of plants when exposed to insect herbivory (McNaughton, 1983; Nowak and Caldwell, 1984; Thomson et al., 2003). Based on these results, Pacioretty (2016) postulated that increased herbivory did happen at noise sites, and that sap-feeding guilds (+33% in noise) rather than grazers were responsible for this response. Given the apparent increase in herbivory, the lack of a response of leaf litter chemistry was surprising, because increased herbivory in semi-arid ecosystems generally leads to changes in litter chemistry (Wiens et al., 1991; Karban et al., 2004; Karban et al., 2006).

In many ecosystems, increased herbivory can affect leaf litter chemistry by promoting early leaf abscission (Findlay et al., 1996; Chapman et al., 2003; Ohgushi, 2005). Sudden leaf abscission resulting from herbivory leads to a decrease in litter C/N ratios (Chapman et al., 2006) because plants fail to re-absorb nitrogen rich compounds prior to abscission. These changes may further lead to an acceleration of litter decomposition, thus increasing the cycle of nutrients in ecosystems (Eiland et al., 2001). Given the increase in sap-feeding guilds (~30%), accompanied by apparent compensatory growth, we expected to observe a change in leaf abscission rates in sagebrush (Findlay et al., 1996; Chapman et al., 2003; Ohgushi, 2005). Further, we expected that this would lead to a decrease in litter C/N ratios and accelerated litter decomposition. Yet, the amount of leaf litter collected did not differ between noise treatments, nor did C/N ratios or decomposition. Thus we found no evidence to support our hypothesis that increased herbivory in sagebrush following noise exposure feeds back to increase nutrient cycling in semi-arid ecosystems. This lack of response in leaf abscission agrees with a previous study by Shiojiri and Karban (2008) who found no evidence that sagebrush abscise leaves in response to herbivory. Most likely, this is due to the semi-deciduous nature of sagebrush shrubs, which indicate sagebrush would be more likely to induce chemical defenses (i.e. phenolics and terpenes), than induce abscission (thereby decreasing C/N ratios) in response to herbivory (Wiens et al., 1991; Karban et al., 2004; Karban et al., 2006; Chapman et al., 2006).

We found no evidence that increased herbivory enhances chemical defenses, such as total phenolics and terpenes. This observation contradicts other studies conducted in sagebrush (Wiens et al., 1991; Karban et al., 2004; Karban et al., 2006). It may be that the Folin–Ciocalteu method for quantification of total phenolics lacked sufficient specificity to detect small differences in individual phenolic compounds between treatments (Appel et al., 2001; Chomel et al., 2016). Alternatively, we may have missed the effects of herbivory on terpene concentrations in sagebrush because folivores feed on ephemeral leaves (Takahashi and Huntly, 2010), and feeding decreases as the summer progresses (Karban et al., 2006). We collected samples for terpene analysis in October, well after ephemeral leaves had senesced with the onset of drought (Figure 3), thereby missing the key time frame in which folivores would induce a chemical response from sagebrush. Although our quantification of total phenolics and terpenes may have been hindered by assay specificity or timing of sample collection, our data on litter decomposition solidify our conclusion that the animal communities’ reorganization due to noise exposure did not affect litter chemistry in this experiment. We found no difference in potential litter decomposition rates between noise and control sites. This strongly suggests that total phenolic concentrations did not change, because it has been well established that increased phenolic concentrations in leaf litter reduces decomposition rates (*see review* Chomel et al., 2016). Thus, it appears that noise pollution does not affect plant-soil interactions in these ecosystems via its impacts on leaf litter chemistry changes.

Our experiment ran for one growing season, and it is possible that this time frame was insufficient to elicit a measurable response in leaf abscission, leaf litter chemistry or leaf litter decomposition from sagebrush. In addition, the relative change in herbivory between noise and control sites may have not passed a critical threshold to lead to significant changes in ecosystem function. For example, Wiens et al. (1991) reported significant relationships between arthropod abundance and concentrations of secondary compounds (i.e. sesquiterpenes, alcohols, hydrocarbons, ketones and monoterpenes), however, they used insecticide to completely remove arthropods, an extreme manipulation that was outside the normal fluctuations of arthropod abundance to achieve their results. In our experiment, the ~30% increase in omnivore, grazers and sap feeder guilds could have been tempered by the coinciding increase of arthropod predators (~16%), thereby reducing the magnitude of herbivory (Cinto-Mejia, 2017), and accompanying changes in leaf litter chemistry and litter decomposition. Additionally, Wiens et al. (1991) conducted their experiment over a period of 56 weeks, whereas our study only ran for 28 weeks. Our results, coupled with Wiens et al. (1991) indicate sagebrush may have a threshold of herbivory that needs to be met to induce chemical defenses. Further research should include long-term insectivore exclusions and/or arthropod removal experiments to determine if herbivory induces chemical changes and if so, how these chemical shifts alter decomposition rates. Possibly, the changes we observed in arthropod diversity and plant physiology, compounded over time, could result in changes to leaf litter chemistry, decomposition and ultimately, ecosystem function.

Our study showed that leaf litter senescence, its C/N ratio and phenolic concentrations were highly variable across the growing season, with significant implications for potential litter decomposition rates. Similar to previous studies, we collected the greatest amount of litter in July when ephemeral, floral and persistent leaves abscise with onset of drought conditions (Miller and Shultz, 1987; Evans and Black, 1993), (Table 6, Figure 5). While other studies have documented seasonal variability in phenology and chemical profiles in live leaf tissue of sagebrush (Kelsey et al., 1982; Miller and Shultz, 1987; Wilt and Miller, 1992; Evans and Black, 1993), this is the first study to document changes in litter input, chemistry and decomposition. We found a significant negative correlation between litter decomposition rates and litter C/N ratio (Figure 13, $p<0.001$). These data indicate that litter C/N ratio is an important predictor of litter decomposition rates, a result supported by many previous studies (e.g. Aerts, 1997; Eiland et al., 2001; Chomel et al., 2016). However, litter decomposition rates also differed between litter collected in June and September, although litter C/N ratio was similar (Figure 6, Table 1). This result could not be explained by differences in phenolics, because total phenolics, or the interaction between C/N ratio and total phenolics did not predict litter decomposition rates. Since photo-degradation strongly controls decomposition rates in semi-arid ecosystems (Austin and Vivanco, 2006), it is likely that the divergence in litter decomposition rates can be explained by the difference in photoperiod from June to September. Together, our results indicate that litter decomposition fluctuates during the growing season. These fluctuations are controlled by leaf senescence rates that control litter C/N ratios. Our data suggest that if changes in climate affect leaf senescence rates, leading to a change in timing of litter fall, this may significantly affect litter decomposition rates. These abiotic forces may be an underappreciated force in regulating decomposition rates in semi-arid ecosystems. A longer-term study is warranted to confirm this assertion.

CONCLUSION

By experimentally altering the acoustic environment of the sagebrush steppe ecosystem we sought to evaluate if anthropogenic noise affects litter chemistry and decomposition rates, mediated by changes in vertebrate/arthropod/plant dynamics. Although noise decreased bird distribution, altered arthropod distributions (Cinto-Mejia, 2017) and affected plant physiology (Pacioretty, 2016), we were unable to detect changes in the chemical composition (i.e. C/N ratio, total phenolics, monoterpenes) of sagebrush leaf litter or decomposition thereof, over one growing season. Therefore, our research does not support our hypotheses that anthropogenic noise alters decomposition processes, and thus the cycling of nutrients in this ecosystem. However, changes in litter chemistry and decomposition may occur in the long-term with prolonged experimental noise exposure that alter vertebrate/arthropod/plant interactions. With large scale energy development increasing in the sagebrush steppe ecosystem, it is important to continue to monitor changes in trophic cascades that may alter the function and eventually structure of these vulnerable ecosystems.

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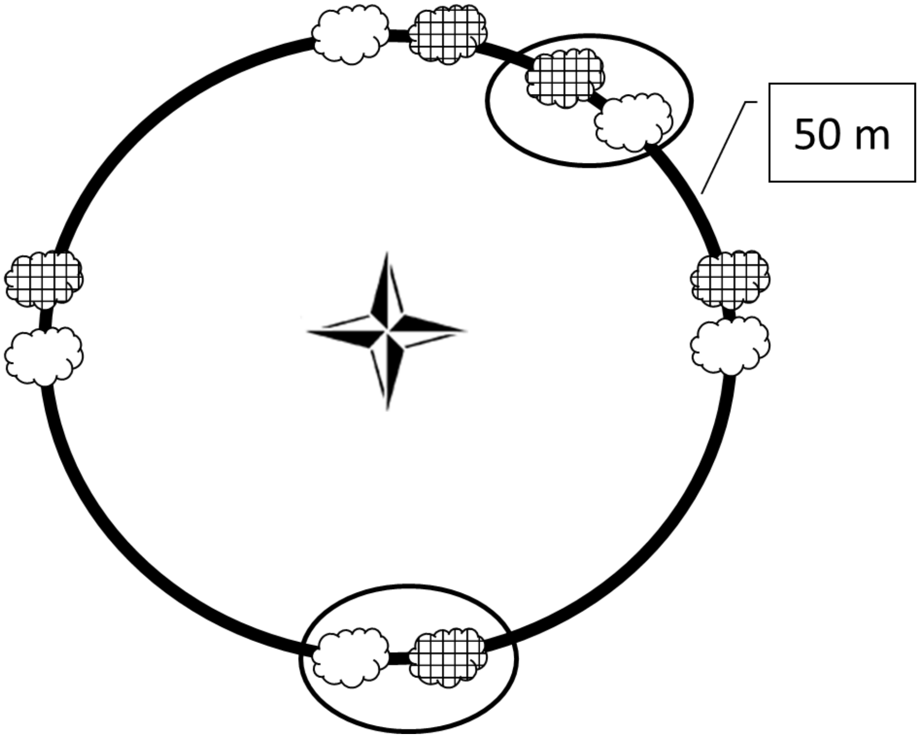

Figure 1: **Experimental set-up in the phantom gas field project. Four pairs of A. tridentata wyomingensis shrubs were selected at 50 m radius from speakers (noise) or dummy speakers (control); indicated by the compass rose. Four shrubs were covered with vertebrate exclusion netting (positive arthropod control) as indicated with checkered pattern. Four other shrubs were not covered with netting. Shrubs exposed to clipping treatments are marked with a black oval. The remaining six shrubs we wrapped with window screen around their base and secured with zip ties to collect litter.**

Figure 2: Design for positive arthropod control netted shrubs. Vertebrate exclusion netting (50.8 mm grid size) was stretched around four rebar posts and secured with zip ties.

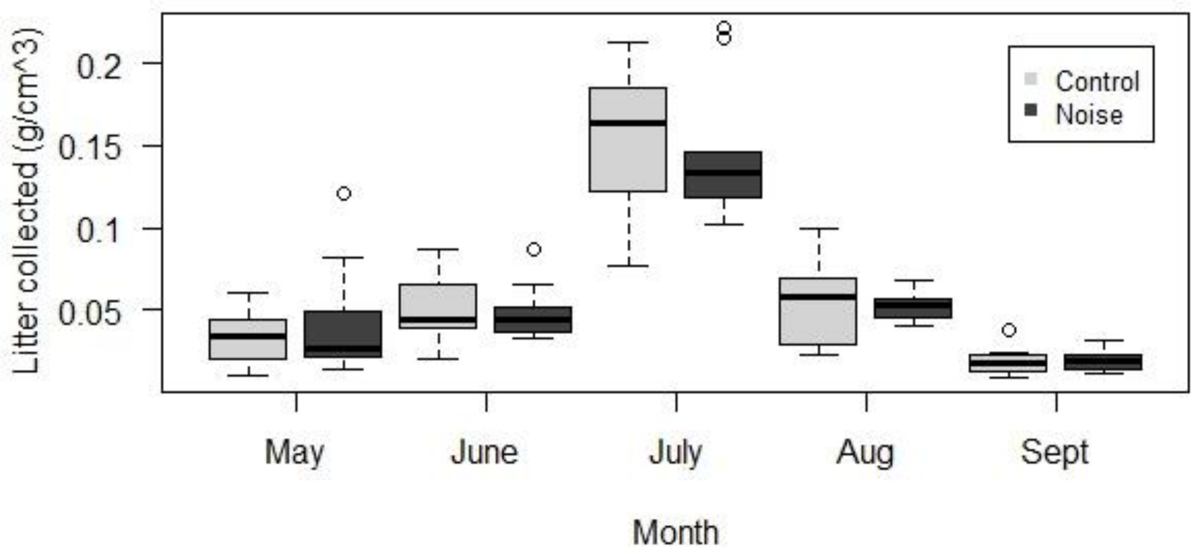

Figure 3: **Standardized amount of senesced litter (g/cm^3) collected from A. tridentata wyomingensis over five months from control and noise sites. Boxplots show means and SEM is represented by error bars. Noise treatments had no effect on amount of litter collected.**

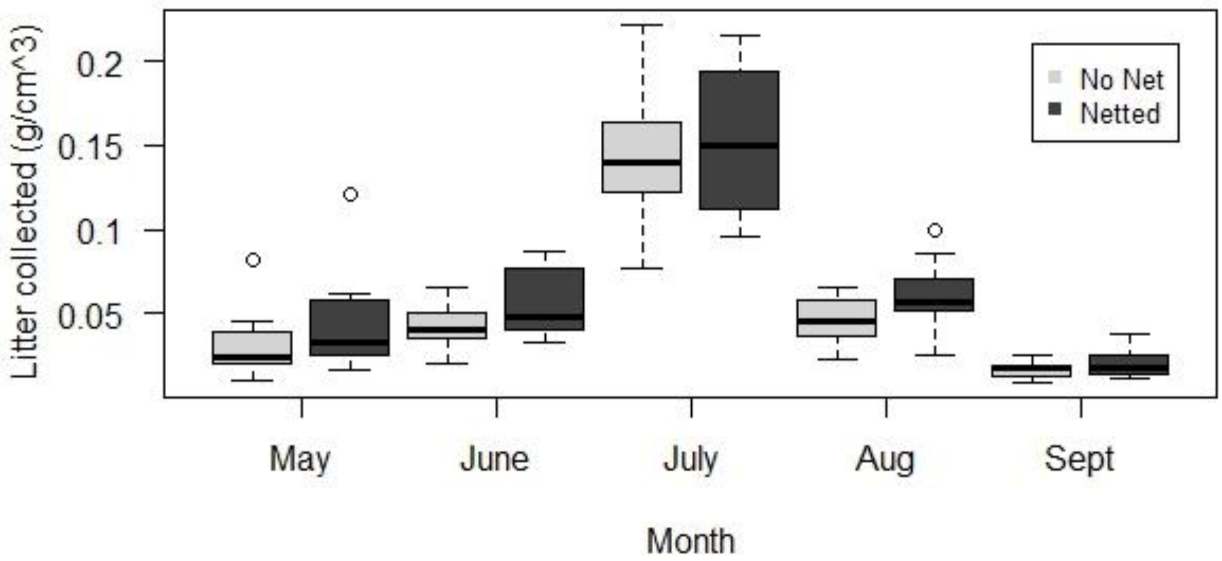

Figure 4: Standardized amount of senesced litter (g/cm^3) collected from A. tridentata wyomingensis over five months in Netted/No Net treatments. Boxplots show means and SEM is represented by error bars. Vertebrate exclusions had no effect on amount of litter collected.

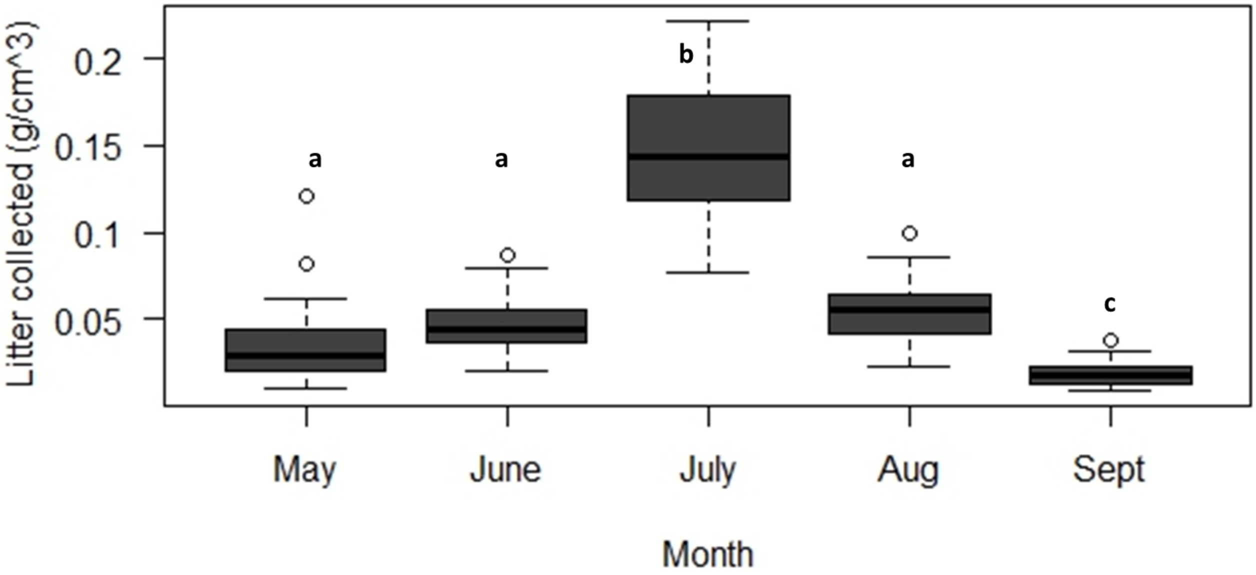

Figure 5: **Standardized amount of senesced litter (g/cm^3) collected from A. tridentata wyomingensis over five months. Boxplots show means and SEM is represented by error bars. Different letters indicate significant differences in litter collection amounts among months ($F_{(4,92)}$=168.7, p<0.001).**

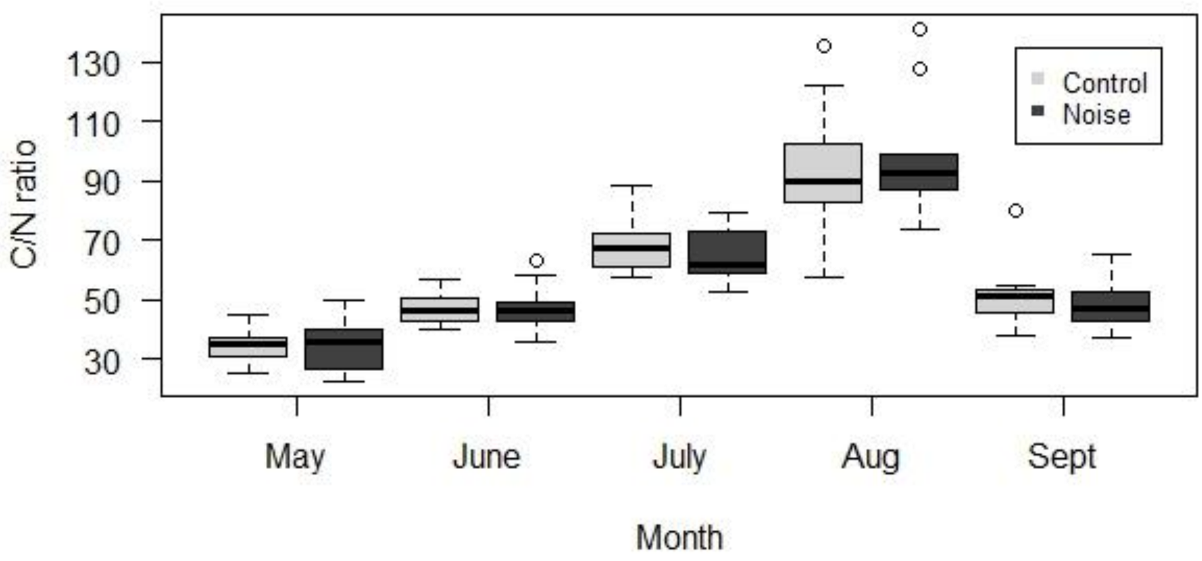

Figure 6: C/N ratio of litter collected from A. tridentata wyomingensis over five months from control and noise sites. Boxplots show means and SEM is represented by error bars. Noise treatments had no effect on C/N ratio.

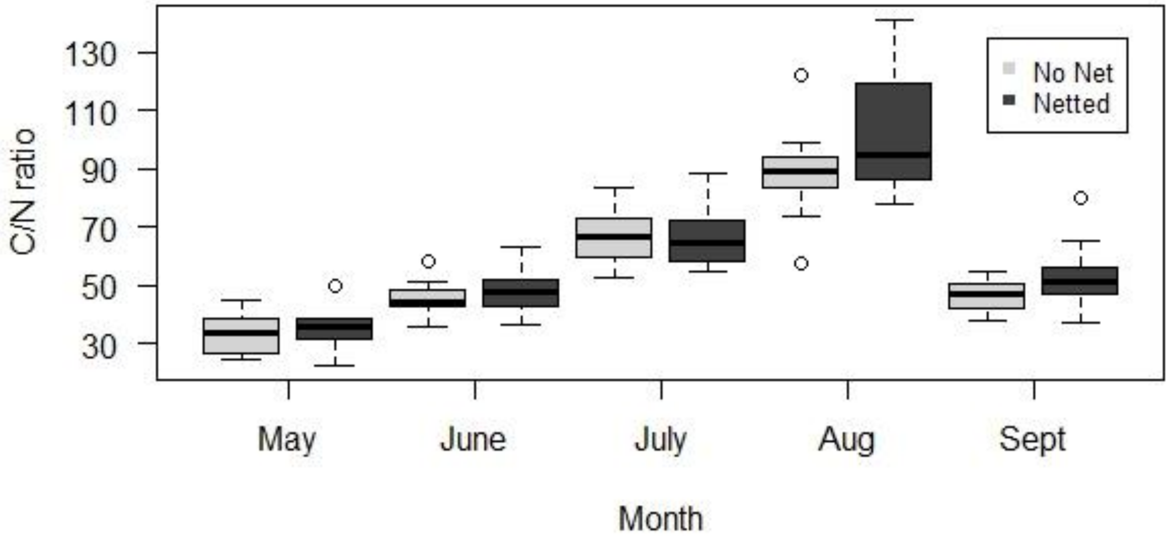

Figure 7: C/N ratio of litter collected from A. tridentata wyomingensis over five months from Netted/No net treatments. Boxplots show means and SEM is represented by error bars. Vertebrate exclusions had no effect on C/N ratio.

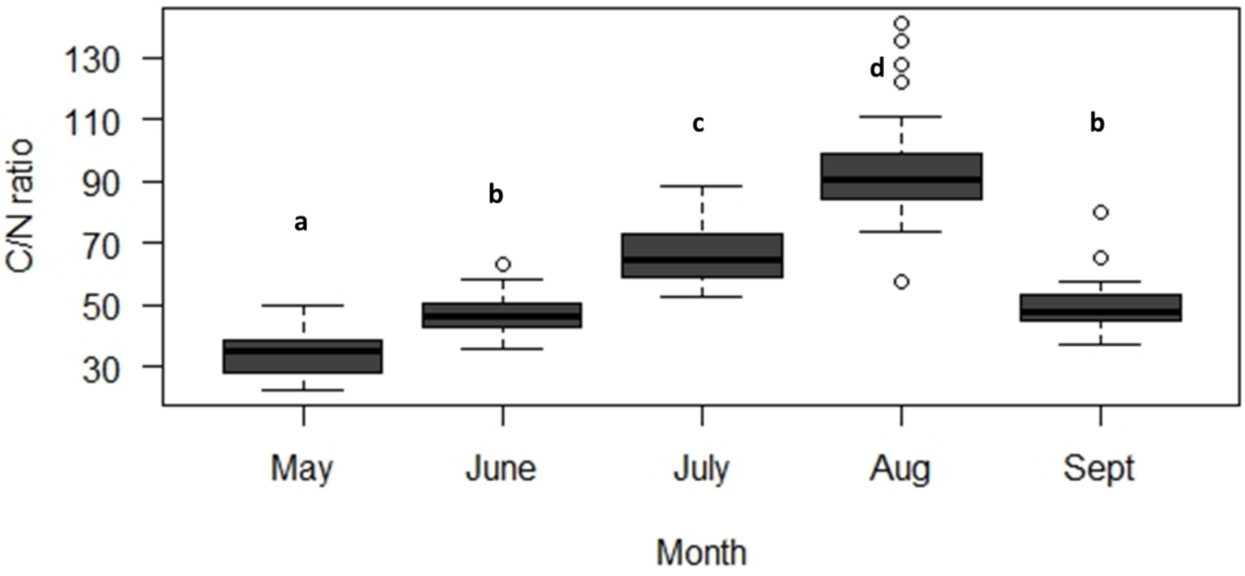

Figure 8: C/N ratio of senesced litter of A. tridentata wyomingensis over five months. Boxplots represent means and SEM are error bars. Different letters indicate significant differences in C/N ratio among months ($F_{(4,92)}$=196.4, p<0.001).

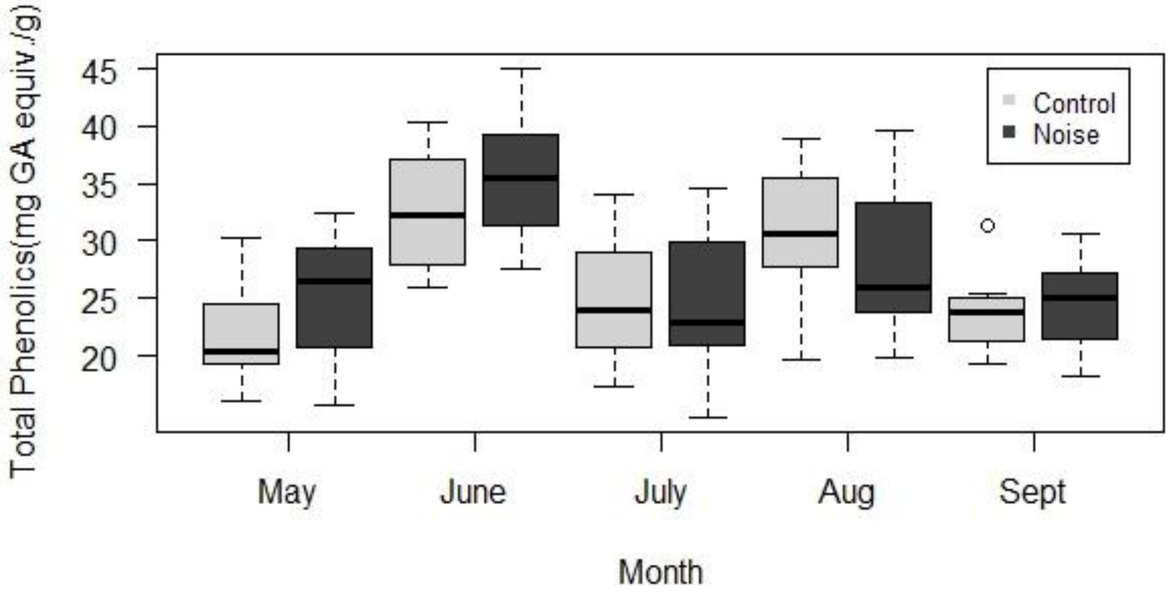

Figure 9: Total phenolics (mg GA equiv. / g dry wt of sample) for senesced litter of A. tridentata wyomingensis over five months from control and noise sites. Boxplots represent means and SEM indicated by error bars. Noise had no effect on total phenolic concentrations.

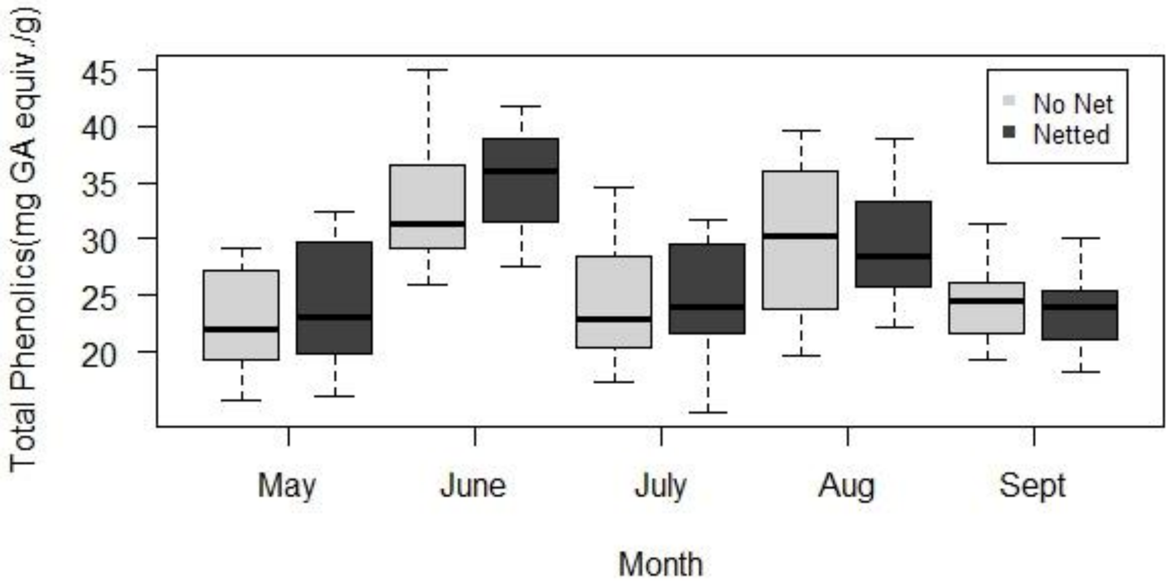

Figure 10: **Total phenolics (mg GA equiv. / g dry wt of sample) for senesced litter of A. tridentata wyomingensis over five months from Netted/No Net treatments. Boxplots represent means and SEM indicated by error bars. Vertebrate exclusions had no effect on total phenolic concentrations.**

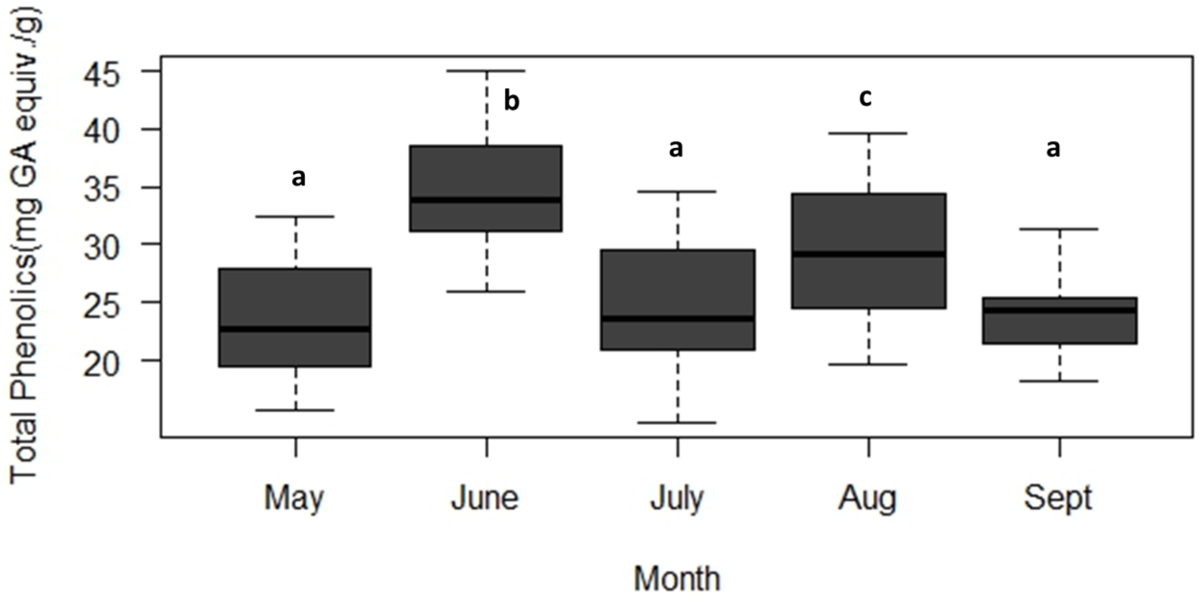

Figure 11: **Total phenolics (mg GA equiv. / g dry wt of sample) for senesced litter of A. tridentata wyomingensis over five months. Boxplots represent means and SEM indicated by error bars. Different letters indicate significant differences in total phenolic concentrations among months ($F_{(4,92)}$=31.7, p<0.001).**

Table 1: N, C, C/N ratio (%) and Total phenolics (mg GA equiv. g $^{-1}$ dry wt) of senesced A. tridentata wyomingensis litter by month. All values are means ±SEM.

Month	%N	%C	C/N	Total Phenolics
May	1.44 ± 0.060	47.66 ± 0.134	34.37 ± 1.340	23.45 ± 0.991
June	1.01 ± 0.136	46.76 ± 0.099	47.00 ± 1.344	34.19 ± 1.037
July	0.70 ± 0.019	46.00 ± 0.088	66.87 ± 1.914	24.74 ± 1.109
August	0.50 ± 0.020	46.10 ± 0.080	95.40 ± 3.993	29.65 ± 1.252
September	0.98 ± 0.032	47.65 ± 0.295	49.94 ± 1.874	24.08 ± 0.727

Table 2: Percent change in monoterpene concentrations in Control/Noise and Netted/Un-netted treatments for A. tridentata wyomingensis foliage. Samples were collected at the beginning of the growing season (April) and at the end (October). All values are means ±SEM.

	Control / netted shrub	**Control / un-netted shrub**	**Noise / netted shrub**	**Noise / un-netted shrub**
Beta-pinene	43.66 ± 20.22	-16.46 ± 30.64	0.15 ± 25.30	22.52 ± 26.49
Alpha-phelendrine	26.20 ± 16.31	43.32 ± 10.41	3.50 ± 21.55	43.30 ± 7.58
p-cymeme	49.13 ± 22.12	-93.23 ± 73.49	18.52 ± 42.16	49.46 ± 12.56
Thujone	40.25 ± 6.92	34.25 ± 5.25	34.97 ± 8.91	35.60 ± 6.87
Terpinolene	40.19 ± 16.68	46.12 ± 9.81	29.80 ± 12.28	43.57 ± 10.01
Monoterpene 1	-4.53 ± 14.82	16.48 ± 5.30	6.54 ± 16.82	25.75 ± 4.37
Monoterpene 2	-539.24 ± 354.64	-454.20 ± 230.09	-571.01 ± 246.84	646.32 ± 225.27
Monoterpene 3	-42.99 ± 46.46	-66.79 ± 92.11	-36.40 ± 52.06	-24.96 ± 33.20

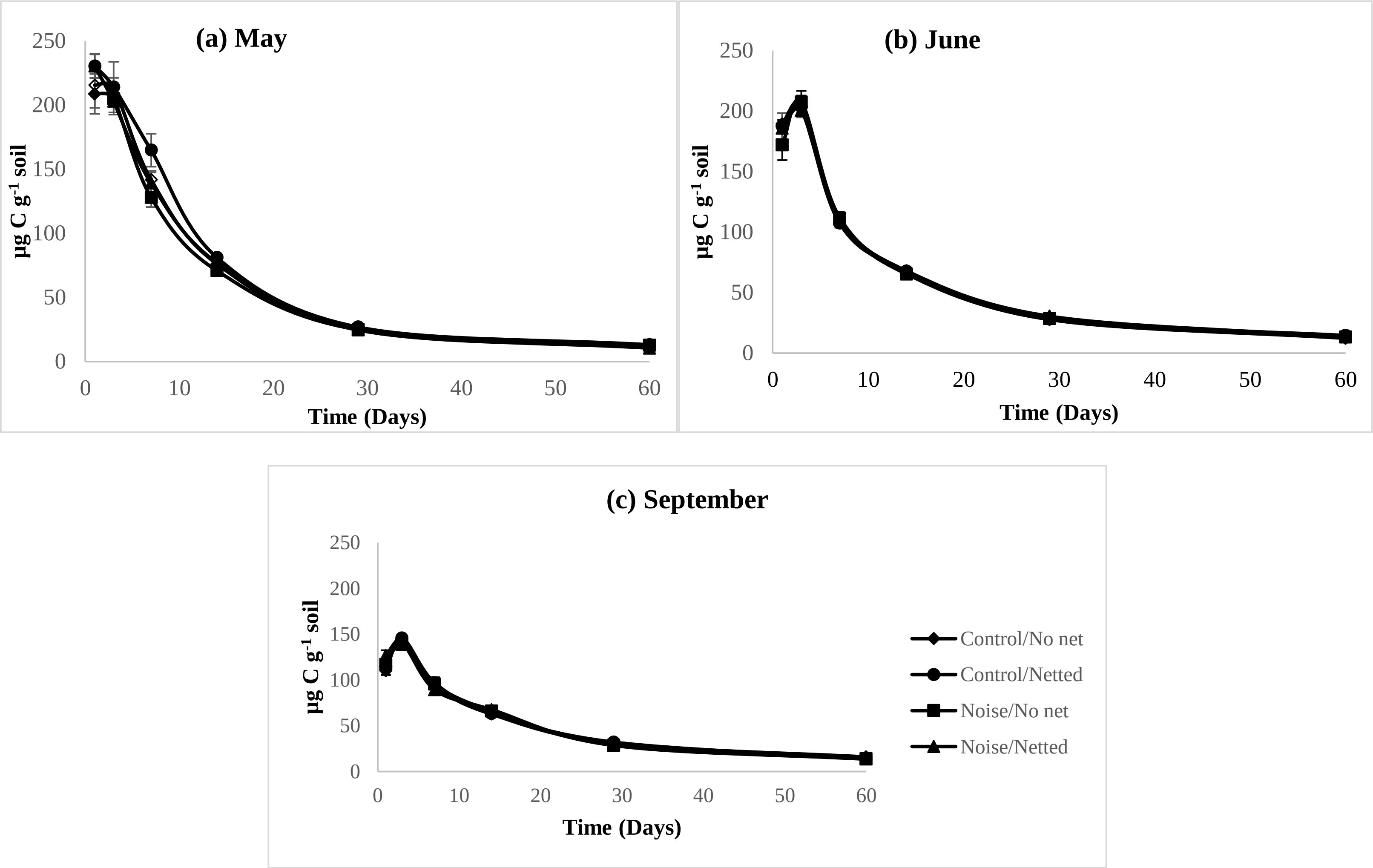

Figure 12 (a-c): **Rate of C respired from A. tridentata wyomingensis senesced litter during 60 day potential decomposition experiment. Plants were exposed to gas compressor station noise and vertebrate exclosure treatments. Values are means with SEM represented with error bars. Treatments (Noise and/or Net) had no effect on C respired.**

Table 3: Number of parameters (k), Akaike's Information Criterion value adjusted for small sample size (AIC_c), the difference between a given model and the model with the lowest AIC value (ΔAIC), and the AIC weight of models for the rate of C efflux during 60 day incubation experiment (μg C g^{-1} soil).

Model	*k*	AIC_c	ΔAIC	wi
Carbon respired (μg C g^{-1} soil)				
Month+Day+Day*Month	8	4310.18	0.00	1
Month+Day	6	4341.58	31.40	0
Month+Day+Net+dB	8	4344.62	34.44	0
Month+Day+Net+dB+Net*dB	9	4346.67	36.48	0
Null	5	4774.94	464.76	0

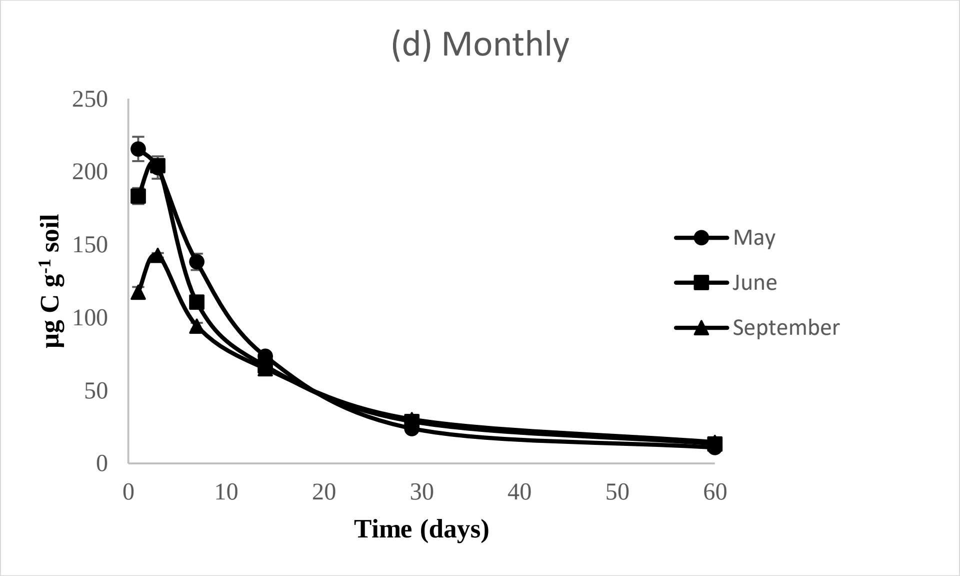

Figure 13 (d): Monthly rate of C respired from A. tridentata wyomingensis litter incorporated in a common soil during 60 day potential decomposition experiment. Values are means with SEM indicated by error bars. Top model indicates C respired is best predicted by day sample was taken (i.e. 1, 3, 7, 14, 29, 60) and month litter was collected in ($F_{(2,42)}$=101.7, p<0.001).

Table 4: **Pairwise comparisons using Bonferroni correction of C efflux for month and day sample was taken. Asterisks (*) indicate level of significance, n.s. indicates no significant difference for that comparison.**

Month	Day 1	Day 3	Day 7	Day 14	Day 29	Day 60
May-June	p<0.05 *	n.s	p<0.01 **	n.s	p<0.01 **	p<0.05 *
May-September	p<0.001 ***	p<0.001 ***	p<0.001 ***	p<0.05 *	p<0.001 ***	p<0.01 *
June-September	p<0.001 ***	p<0.001 ***	p<0.001 ***	n.s.	n.s.	n.s

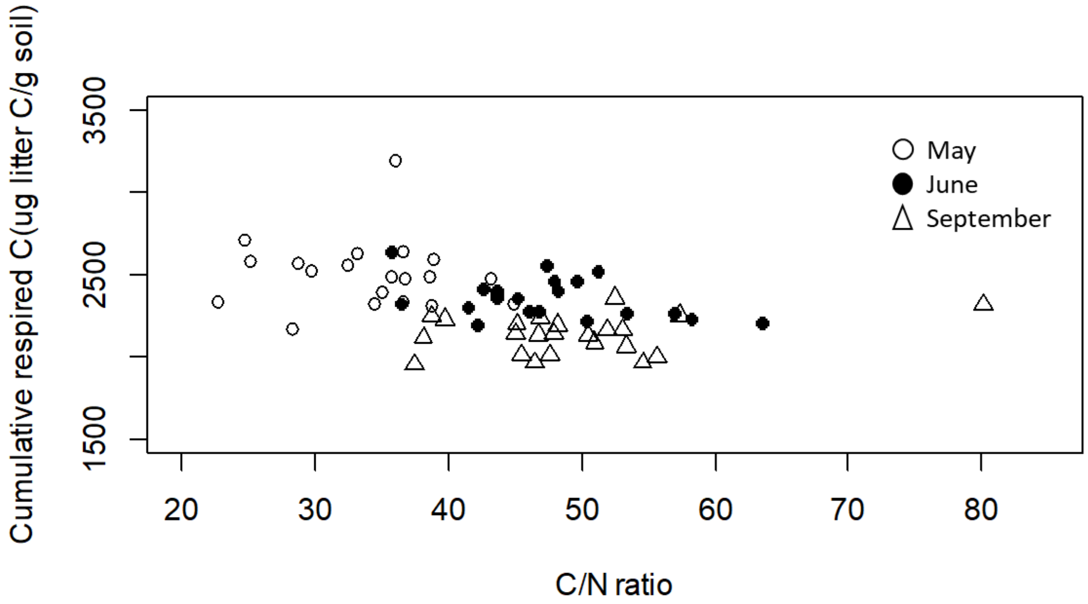

Figure 14: Cumulative C respired during potential decomposition experiment for May, June and September as a function of C/N ratio. The lower the C/N ratio, the greater the C efflux ($F_{(3,60)}$=20.99, p<0.001, R^2=0.51).

Table 5: Percent change of arthropods as a function of decibel levels (i.e. compressor station noise). Arthropods are grouped by adult feeding strategies. (Cinto-Mejia, 2017)

Broadband-2015		**week**	**dB**	**%change/~12dB**	**95 C.I.**
Detritivore	β	-0.374	-0.359	-30%	0.7783-0.6273
	s.e.	0.005	0.055		
Grazer	β	-0.010	0.291	+33.7%	1.4325-1.2489
	s.e	0.003	0.035		
Omnivore	β	-0.092	0.268	+30%	1.6536-1.0332
	s.e	0.027	0.120		
Parasite	β	0.033	0.173	+18.8%	1.2733-1.1098
	s.e	0.004	0.035		
Pollinator	β	-0.011	-0.133	-12.40%	0.9691-0.7909
	s.e	0.006	0.052		
Predator	β	0.070	0.152	+16.4%	1.2380-1.0949
	s.e	0.004	0.031		
Sap Feeder	β	-0.227	0.254	+30%	1.4799-1.1240
	s.e	0.007	0.070		
Scavenger	β	-0.104	-0.155	-14.3%	0.9699-0.7560
	s.e	0.006	0.064		

Table 6: **Maximum and minimum temperature (°C), maximum and average precipitation (mm), and standardized quantity of litter collected (g/cm^3) from A. tridentata wyomingensis by month in 2015. Quantity values (g/cm^3) and total phenolics (mg GA equiv. g $^{-1}$ dry wt) are means ±SEM.**

Month	Max temp (°C)	Min temp (°C)	Max precip. (mm)	Avg precip. (mm)	Quantity (g/cm^3)	Total Phenolics (mg GA equiv. /g dry wt)
May	34.4	10.5	9.1	1.5	0.0366 ± 0.005	23.45 ± 0.991
June	43.3	23.8	3.6	0.25	0.0484 ± 0.004	34.19 ± 1.037
July	40.0	23.8	31.0	1.27	0.1484 ± 0.008	24.74 ± 1.109
August	41.1	26.6	2.54	0.25	0.0533 ± 0.004	29.65 ± 1.252
September	35.5	17.2	6.35	0.51	0.0184 ± 0.001	24.08 ± 0.727