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Camille Traylor
traylor.camille@gmail.com

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EFFECTS OF DISTURBANCE AND RESTORATION TREATMENT ON FERTILE ISLANDS IN LAKE MEAD NATIONAL RECREATION AREA

By

Camille A. Traylor

Bachelor of Science – Chemistry
University of San Francisco
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A thesis submitted in partial fulfillment
of the requirements for the

Master of Science – Biological Sciences

School of Life Sciences
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Camille A. Traylor

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School of Life Sciences

Scott Abella, Ph.D.
Examination Committee Chair

Stanley Smith, Ph.D.
Examination Committee Member

Philippos Tsourkas, Ph.D.
Examination Committee Member

Jacimaria Batista, Ph.D.
Graduate College Faculty Representative

Kathryn Hausbeck Korgan, Ph.D.
Graduate College Dean

Abstract

Disturbances by humans are one of the main drivers of change in contemporary desert ecosystems. Restoration treatments such as topsoil application and outplanting can be implemented in response to disturbances in order to maintain soil stability and a diverse plant community. Fertile islands - nutrient enriched areas beneath perennial shrubs - are fundamental features of deserts that can facilitate annual plant growth. A major uncertainty in desert ecology is how much time is required for fertile islands and nurse plant effects (the facilitation of one plant by another) to develop below maturing perennial plants. By studying naturally recruited perennial plants no older than age 10 years using a unique study design including sites where soils were severely disturbed, homogenized, and denuded of perennial plants 10 years earlier and comparing with undisturbed desert, this study assessed soil, annual plants, and soil seed banks beneath *Ambrosia dumosa* shrubs. Influences on fertile island development of the restoration treatments of applying salvaged topsoil and outplanting were also assessed. Plant cover and species richness of native plants tended to be higher in undisturbed areas, while exotic plants had higher cover in disturbed areas regardless of treatment type. The fertile island effect was prevalent below shrubs across all treatments including disturbed/unrestored, disturbed/restored, and undisturbed controls. Native and exotic plants also grew in association with the fertile island instead of in interspaces between shrubs. The soil seed bank was larger and more species-rich in fertile islands compared with interspaces. Additionally, areas that had topsoil applied contained larger soil seed banks than disturbed, unrestored sites. Topsoil reapplication may be beneficial to maintaining abundant seeds in the soil seedbank, but a whole plot analyses of vegetation cover and species richness should be conducted to determine differences in vegetation among treatment types.

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Chapter 1: Introduction

As deserts make up one-third of Earth and are inhabited by one-sixth of the human population, maintaining productivity in these areas with low precipitation and high variability is a challenge to desert land management. Preserving native plants and encouraging a diverse plant community can be even more difficult due to disturbances that have a large negative effect on deserts. The spread of invasive plants in deserts is often linked to disturbances and can potentially convert desert shrublands to grasslands, modifying ecosystem processes such as fire regimes and nutrient cycling (Brooks et al., 2004; Wilcox et al., 2011). Extreme environmental conditions, a lack of resources, and disturbances can affect vegetation dynamics, soil seed banks, and soil nutrients. Further research on effects of disturbances should be conducted as invasive plant species and what drives their abundance is an important goal for land management, especially in deserts.

Invasive species have the potential to dominate the plant flora in deserts, decreasing biodiversity and posing a threat to wild animals.(Gray and Steidl, 2015; Brooks, 2000) The desert tortoise is one species of the Mojave Desert that is listed as threatened on the federal endangered species list. This animal has particularly been negatively affected by the spread of invasive species because of invasive plants' ability to outcompete with native plants (Drake et al., 2016). Since animals the desert tortoise prefers more nutrient rich plant species, native species are more frequently foraged and invasive plants are usually avoided. Invasive species dominance can also contribute to an increase in fire fuel and a change to fire regimes (Brooks et al. 2004) making fires more severe and more frequent, a regime unfamiliar to native plants. The spatial distribution of invasive plant species in the desert has also been frequently studied. Many plant species prefer to inhabit areas underneath perennial shrubs due to shade provided by the shrub canopy and an accumulation of soil nutrients under the shrub (Holzapfel and Mahall, 1999; Schafer et al., 2012; Kleinhesselink et al., 2014). However, some species may avoid this microhabitat because of competition for resources. Vegetation dynamics also depend on soil seed banks that are generally contained in the upper layers of soil (Olano et al., 2005). When disturbances occur, the topsoil containing a large portion of the seed population and soil nutrients can be significantly altered.

Restoration methods are often employed in response to disturbances with the goal of supporting native plant species and mitigating the spread of invasives. Topsoil reapplication and outplanting treatments are two restoration methods that can be used to help maintain these natural components of the soil during disturbances. Topsoil reapplication ensures that some of the original soil components, including organic matter and the seed population, are preserved (Defalco & Esque, 2014; Scoles-Sciulla and DeFalco, 2009). Outplanting allows for important plants to develop strong root systems in a controlled nursery before transplanting to restoration sites. The long term effects of these treatments and their effects on soil nutrient distributions have not been frequently studied.

In Lake Mead National Recreation Area, roads have been constructed with the requirement to salvage topsoil and re-apply it onto nearby land in order to reduce the effect it would have on plants and animal communities. Plants that were removed to build the roads have also been salvaged and cared for at the Lake Mead nursery facility until they were transplanted back onto the topsoil when the roads were finished (Abella et al. 2015). The purpose of this research is to evaluate the effects of topsoil reapplication and outplanting treatments on fertile islands, seed banks, and vegetation. Questions to be answered are: (1) how does topsoil reapplication and outplanting treatment affect the soil nutrient distribution in the Mojave Desert?

(2) How is the abundance of winter annuals on disturbed soils affected by fertile islands? (3) Does seed bank emergence reflect species abundance in above ground vegetation?

Chapter 2: Literature Review

Introduction

Over a third of the human population lives in arid lands and along with population growth, clearing for renewable energy developments, road-building, invasion by flammable plants and fires, mining, off-road vehicle use, and other disturbances are increasingly damaging native desert vegetation and soils (Millenium Ecosystem Assessment (2005). Disturbances are frequently occurring and play a large role in clearing out vegetation. Learning more about how disturbances affect ecosystems will aid in finding restoration methods that better support wildlife habitats. When disturbances occur, land management goals often include preserving features of the land that support biological activity. Deserts are areas with low net primary productivity and should be studied in particular so that further degradation does not occur. Soil nutrients and soil seed banks are important in the distribution of plants in deserts and can be negatively affected by disturbances and slow to recover in due to the limited amount of resources. Studies have shown that in deserts, there are concentrated amounts of soil nutrients underneath shrubs rather than in interspaces between shrubs (Thompson et al., 2005; Titus et al., 2002; Schlesinger et al., 1996). This aggregate of soil nutrients is termed "fertile islands." This literature review is comprised of studies that emphasize the importance of fertile islands, soil seed banks, and their effect on plant community compositions.

Fertile Island Development

The fertile island microhabitat differs from that of the interspaces between shrubs. Romney et al. (1980) measured soil nutrients beneath shrub canopies and in bare interspaces in between shrubs. Under the shrub, soil properties that were higher underneath the shrub were the saturation extract conductivity, cation exchange capacity, potassium, organic carbon, organic nitrogen, and available phosphorus among others. Soil in the top 0-9 cm (A1 horizon) contained 0.211% nitrogen beneath shrubs. In the A2 horizon (9-13 cm depth) soil nitrogen content was 0.050 %, and 0.044% for the C1 horizon (13-36 cm depth). In the top 0-34 cm of bare spaces, there was 0.035 % organic nitrogen in the soil.

Walker et al. (2001) measured soil parameters on fertile islands under shrubs *Larrea tridentata*, *Ambrosia dumosa*, and *Coleogyne ramosissima* and in interspaces and found that pH, water, organic matter, and nitrogen are higher underneath the shrub canopy than in interspaces between shrubs. These data coincide with several other studies in the Mojave Desert, such as Thompson et al. 2005, Titus et al. (2002) and Schlesinger et al. (1996). The early study by Schlesinger et al. (1996) confirmed available nitrogen, phosphate, chloride, sulfate, and potassium were higher underneath shrubs than in interspaces in the Mojave Desert. Some of the main soil nutrients most limiting for plant growth – nitrogen, phosphorus, and potassium – and soil moisture are seen at locations closest to the shrub roots. Since the shrub canopy provides shade to the soil beneath the shrub, this may cause a lower evaporation rate allowing the soil to retain more water. Schlesinger et al. (1996) also provided findings that nutrients such as Rb, Ca, Mg, Na, Li, and Sr were either greater in interspaces, or equal under shrub canopies and interspaces. Kleinhesselink et al. (2014) also studied fertile islands and showed that soil parameters such as particle size and organic matter are greater on the fertile island and that wind speeds are reduced in the shrub canopy. Shade and reduced wind speeds can be sought out by animals in deserts, making the fertile island microhabitat a site they frequently visit. Titus et al. (2002) showed the effect of animals on fertile islands when sampling soil beneath canopies of shrubs including of *Larrea tridentata* and *Ambrosia dumosa* in the Mojave Desert. Results confirmed fertile island existence, but furthermore revealed a higher nitrogen, phosphorus, and potassium content under shrubs containing animal burrows. In addition to animal activity and nutrient uptake by roots, decomposition of plant matter also contributes to increased nitrogen content beneath shrubs. Garcia-Moya and McKell (1970) analyzed soil nitrogen in the Gold Valley of the Mojave Desert and found that soil nitrogen decreased with increasing distance away from the shrub and with increasing soil depth. Decomposition of plant matter leads to a slow release of nitrogen in the upper centimeters of the soil. Since there is an abundance of litter fall beneath the shrub, nitrogen content from decomposition should be higher in the fertile island than in interspaces.

Differences in fertile island development can depend on the species, size, and location of the shrub. Titus et al. (2002) showed that the nutrients present could depend on shrub species since, *Lycium* had more Na and Mg in the fertile island than did *Larrea tridentata* and *Ambrosia dumosa*. Thompson et al. (2005) also found difference in fertile island nutrients based on shrub species. *Ambrosia dumosa* has less soil organic matter than *Larrea tridentata* and *Coleogyne ramosissima. Ambrosia dumosa* also had a higher nitrogen mineralization content. However, the ratio of nutrients in the fertile island compared to the interspace was not significantly different across species. Since plant species differ in size, shading capacity, and root depth, there are many factors working together to drive the development and sustainment of the fertile island. Garcia-Moya and McKell (1970) studied the factors contributing to the overall nitrogen content in plants. They measured the nitrogen content of shrub leaves, stems, and roots of species that included *Acacia greggii, Cassia armata,* and *Larrea tridentata*. For all species, the mean nitrogen contained in stems did not vary significantly with its roots. However, the mean nitrogen content of leaves was significantly different than that of roots and stems. In addition, nitrogen content in leaves differed among species. Titus et al. (2002) discovered a positive correlation between shrub size and soil nutrients. This may be indicative of the increase in the amount of shade, which not only lowers soil temperatures but also creates a habitat that animals would frequently visit. As shrubs increase in size above ground, they are also increasing in root depth. This can lead to a greater ability to accumulate soil nutrients. Thompson et al. (2005) also looked at the fertile island across multiple elevations. Results showed that fertile islands have higher soil organic matter at middle elevations compared to low elevations. Although the fertile island effect is noted across different species and locations, the fertile islands may differ in their soil nutrient content as well as their effect on dynamics above ground. Mudrak et al. (2014) measured the fertile island produced by *Larrea tridentata* of different sizes in the Mojave and Sonoran deserts. Higher concentrations of soil nitrogen and potassium seemed to be associated with closer distances to the shrub stem. Phosphorus, calcium, and magnesium were less dependent on distance from the shrub center.

Few studies show the length of time needed for fertile islands to develop. One of these is a study by Rathore et al. (2015) in which fertile island development was examined for two shrubs, Haloxylon salicornicum and Calligonum polygonoides, in a semi-arid region in western Rajasthan, India. Soil properties were measured seven years after planting the two native shrub species. Results showed that, among other soil properties, soil nitrogen was 31-47% higher beneath the shrub canopy than in the interspaces, indicating the fertile island had formed within seven years since planting the shrub seedling.

Disturbance Effect on Fertile Island Development

Disturbances can affect the development of fertile islands and the types of disturbance can produce different effects. Bolling and Walker (2002) measured fertile island development of *Larrea tridentata* on abandoned roads in the Mojave Desert. Road disturbance was either intentional due to removal of topsoil or due to vehicles. All fertile islands on disturbed soil contained less nitrogen than those in undisturbed areas. In particular, the disturbances in which topsoil was removed were associated with a greater nitrogen deficit than disturbance caused by vehicles. Litter fall is concentrated in the upper few centimeters of the soil therefore nitrogen content in the topsoil can be partially attributed to decomposition. The disturbance caused by vehicles contained a center berm that contained all sampled *Larrea tridentata* shrubs. The center berm may have accumulated topsoil from nearby regions, facilitating a greater abundance of shrubs and nutrients. Craig et al. (2010) examined the fertile islands of *Larrea tridentata* and *Ambrosia dumosa* with regard to their distance from a nearby road. Exotic and native species richness was measured on fertile islands and interspaces at various distances from 5 m to 45 m from the road. Distance to the road did not affect exotic or native annual species richness and cover. However, shrub size was smaller at closer distances to the road. More studies are needed to determine the effect of disturbance on fertile island development.

Fertile Island Effect on Plant Community

Fertile islands can either have facilitative or competitive effects on other plant species. Kleinhesselink et al. (2014) measured the fertile island created by *Ericameria ericoides* and the annual plants associated with it in a coastal dune in northern California. Seedlings of the exotic species *Bromus diandrus* were grown in a greenhouse and transplanted onto fertile islands and interspaces. Both the soil on the fertile island and the shrub canopy proved to aid in facilitation a greater biomass of the annual plant. The benefit of the shrub canopy was also shown in a study taken place in the desert. Holzapfel and Mahall (1999) removed *Ambrosia dumosa* shrubs from fertile islands. Shrub removal resulted in a negative effect on annuals under the canopy. Experimentation with artificial structures was also used to mimic shrub canopies in interspaces. This also showed that the canopy had a positive effect on annual plant biomass, survival, and seed production emphasizing the importance of not only the aggregate of soil nutrients provided by the fertile islands but also the shrub canopy. However, some species may prefer the interspace due to less competition for water and nutrients. In a vegetation survey by Kleinhesselink et al. (2014), native annuals *Pterostegia drymariodies* and *Claytonia perfoliata* were more frequent in the fertile island. While other native annuals, *Chorizanthe cuspidata* and *Cryptantha leiocarpa,* were associated with interspaces. This may be due to the native species ability to compete for water and nutrients with the shrubs and other invasive species growing under the canopy. Schaefer et al. (2012) studied the effect of *Larrea tridentata* on the abundances of winter annuals in the Mojave and the Sonoran Deserts. Annuals were counted twice to measure seedling abundance and abundance during flowering. Annuals were also categorized into microhabitats of under the canopy, the canopy drip line, in the open near shrubs, and in the open far from shrubs. In the Mojave Desert, the microhabitat under the canopy contained more annuals on the north side of the shrubs compared to the south side, likely due to shading. However, direction did not affect the abundance of flowering annuals. Invasive annuals were most abundant in the open areas, while native annuals were most abundant on the canopy drip line and in the open near shrub microhabitat. *Larrea tridentata* had a net negative affect on annuals, more so for non-natives. Craig et al. (2010) examined the fertile islands of *Larrea tridentata* and *Ambrosia* *dumosa*. Total annual plant cover was higher on the fertile island compared to in interspaces. There was an increase in native species richness for species *Ambrosia dumosa* in particular. Exotic cover was higher in fertile islands of both shrub species compared to interspaces.

In addition to investigating the relationship between the fertile island and annual plants, studies have also measured the relationship between seedlings of perennial shrubs and an already established fertile island. Walker et al. (2001) used fertile islands under shrubs *Larrea tridentata*, *Ambrosia dumosa*, and *Coleogyne ramosissima* and interspaces to determine the effect on *Ambrosia dumosa* seedling survivorship. By planting seedlings in different habitats (e.g. interspaces, on fertile islands next to shrubs, and on fertile islands with removed shrubs) this study showed that the canopy has negative effects on survivorship with the best habitat being the fertile island with the above ground shrub removed and the next best habitat being in the interspace. This may indicate that sunlight may be more limiting for *Ambrosia dumosa* seedling survivorship than is nutrient acquisition. Jones el al. (2014) assessed the emergence, growth, and survivorship of *Coleogyne ramosissima* seedlings under nurse plants, *Larrea tridentata and Coleogyne ramosissima*, and in interspaces across different elevations. At low elevations *Larrea tridentata* positively affected seedling emergence compared to seeding in interspaces, but negatively affected growth, and had no effect on survival. At medium elevations, *Larrea* had no effect on seedling emergence and *Coleogyne* negatively affected seedling emergence. At higher elevations, *Coleogyne ramosissima* negatively influenced seedlings emerging without the protection of cages.

Studies have also shown the difference in fertile island development across elevations. Thompson et al. (2005) studied fertile islands of different species across multiple elevations and found that fertile islands have higher soil organic matter at middle elevations compared to low elevations.

Schenk and Mahall (2002) studied the interaction between two shrubs, *Ambrosia dumosa* and *Acamptopappus sphaerocephalus* to determine how they affect the plant community. A seedling experiment in the field revealed that *Ambrosia dumosa* seedling survival did not differ in the open interspaces, on the edge of mature *Ambrosia* shrub canopies, or *Acamptopappus* shrubs during the first 109 days after germination. Seedling survival was 90%. However, measurements after the growing season at 265 days after germination revealed that only 22% of *Ambrosia* seedlings were alive on the edge of the mature *Ambrosia* canopy, and only 45% were alive at the edge of the *Acamptopappus* shrub. In open areas, survivorship of seedlings was 95% at this time. At the end of the second growing season, 2% of seedlings survived at the edge of *Ambrosia,* 10% survived at the edge of *Acamptopappus,* and 42% survived in open areas. Seedlings of *Ambrosia* in open areas were larger, had more leaves, and had more potential for carbon accumulation. However, the seedlings that did survive near the *Ambrosia* shrub were taller than other seedlings. A greenhouse experiment showed that *Ambrosia* seedling grown in soil collected from interspaces did not differ in biomass compared to seedlings grown in soil collected from beneath *Ambrosia* shrubs. However, seedlings were twice as large as seedlings grown in soil collected from *Acamptopappus.* Results also showed that soil collected from shrubs had twice as much soil carbon than soil in open interspaces. Soil collected from shrubs also had 50% more soil nitrogen than soil from open interspaces.

Shmida and Whitaker (1981) measured plant cover in a *Larrea tridentata* plant community and characterized species distributions with respect to distance from the shrub stem to the open interspaces between shrubs. Shrubs used in this study were *Larrea tridentata,* *Ambrosia dumosa,* and *Lycium andersonii.* Species were analyzed in regard to which shrub species they prefer to grow in association with. Annual species *Cryptantha nevadensis, Phacelia ivesiana*, and *Mentzelia* were correlated with growing beneath the *Larrea* shrub rather than growing beneath *Ambrosia* or *Lycium*. *Cryptantha pterocarya* preferred to grow beneath *Lycium* and *Phacelia fremontii* grew beneath *Ambrosia*. Plants were also analyzed with respect to their preference towards growing beneath shrubs or in interspaces. Plants that preferred to grow in the interspaces included *Linanthus demissus, Nemacladus glanduliferus,* and *Chorizanthe rigida.* Species that grew in association with shrubs included *Mentzelia albicaulis, Cryptantha nevadensis,* and *Phacelia ivesiana.* Some plant species grew primarily in transition zones between the fertile island and the interspaces. These species included *Cryptantha circumscissa, Eriogonum rixfordii, Gilia cana* spp. *speciosa,* and *Phacelia fremontii.*

Brooks (1999) measured alien species invasibility and biomass in the Mojave Desert and their association with different levels of soil nutrients and disturbance. Analysis were performed in 1994, a year with low rainfall, and 1995, a year of high rainfall for this area. Results showed that alien species richness and biomass are lower in dry years than they are in wet years. However, they are proportionally higher in dry years, compared to native species richness, than they are in wet years where annuals tend to flourish. In 1994, alien species richness was 1.03 species/cm2 and in 1995 alien species richness was 1.92 cm2. in 1994 alien biomass was 12 kg/ha and in 1995 biomass was 89 kg/ha. Alien species richness did not seem to interact with disturbance however it was affected due to soil nutrient levels. in 1994, alien species richness grew primarily in interspaces. When rainfall was higher than average in 1995, alien species grew beneath *Larrea.* The disturbance variable did not have a significant effect on alien biomass across both years, however significantly effect alien species biomass in the year of low rainfall, where biomass was higher outside of the Desert Tortoise Research Natural Area (DTNA). Disturbance was high in this area, as opposed to inside the DTNA area. Similar to species richness, biomass of alien plants was also higher beneath *Larrea tridentata* shrubs than in interspaces during the high rainfall year, and this was reversed in the year of low rainfall.

A study in Joshua Tree National Park by Rodríguez Buriticá and Miriti (2009) evaluated species interaction of *Schismus barbatus* and *Ambrosia dumosa.* Results showed that individual *Schismus* plants have more biomass and are taller as distance to the *Ambrosia* shrub increase, indicating a positive effect of *Ambrosia* shrubs on *Schismus* individual performance. However, total density of *Schismus*, did not vary with distance to the shrub. An experimental study differed from this result, showing a negative association between *Schismus* density and the *Ambrosia* shrub when *Schismus* was seeded beneath *Ambrosia* canopies and in interspaces. The height and biomass of the *Schismus* plant in this experiment followed the pattern of natural *Schismus*, being larger at closer distances to the mature *Ambrosia.*

Vegetation Dynamics

Non-native species can lead to a decrease in biodiversity due to outcompeting with native species, an increase in fire fuel, and a decrease in available preferred forage for the desert tortoise making it important to understand vegetation dynamics and interactions that are support native and non-native species. Brooks and Berry (2006) analyzed the species richness and biomass of non-native annuals in the Mojave Desert and their dependence on disturbance types and severities, annual rainfall, elevation, soil nitrogen, and native plant diversity. Overall, invasive species composed 6% of the total species in a year with low rainfall (1994), and 27% of the total species in a year with high rainfall (1995). However, the total annual plant biomass was composed of 66% invasive species in 1994 and 91% of invasive plants in 1995. Invasive species only comprise a small amount of the species available but they are dominating in plant abundance, decreasing biodiversity. An increase in non-native biomass in 1995 also indicates that invasive grass biomass will be dominant when rainfall is limited. The invasive species that dominated was also different depending on rainfall. When rainfall was above average, *Bromus rubens* comprised most of the biomass. When rainfall was below average, *Schismus* spp. and *Erodium cicutarium* dominated. In addition, the fertile island harbored most of the *Bromus rubens* biomass and the interspaces most of the *Schismus* spp. and *Erodium cicutarium* biomass. Results also showed that during the year with high rainfall, invasive plant biomass was highest where the density of dirt roads was high. During the year with low rainfall, invasive biomass was highest where soil nitrogen was highest. This indicates that invasive plant biomass can depend on disturbance type and severity along with soil nitrogen, however the importance of each can depend on the amount of rainfall.

The distribution of annual plants can be affected by the soil nitrogen content. Brooks (2003) added nitrogen onto fertile islands beneath the shrub *Larrea tridentata* and in interspaces in the Mojave Desert. Similarly to previous studies, results showed that invasive species richness was low, where *Bromus rubens, Schismus* spp., and *Erodium cicutarium* composed 98% of the total invasive plant biomass. Nitrogen additions had no net effect on annual plant density, however this was because of an increase in invasive density and a decrease in native plant density. With nitrogen additions, invasive plant biomass increased by about 50% and total native plant biomass decreased by about 40%. Nitrogen addition also decreased native species richness one of the two years sampled. The increase in non-native plant biomass may allow it to better compete with natives for nutrients. This could contribute to the decrease in native plant biomass.

When comparing how nitrogen additions affected plant composition on the fertile island compared to the interspace, results showed that total plant density, biomass, and species richness did not differ. However, when looking specifically at invasive plant biomass, nitrogen addition in interspaces increased biomasses of species that tend to grow in interspaces (*Schismus* spp. and *Erodium cicutarium*) while nitrogen addition to the fertile island increased the biomass of *Bromus* rubens. This indicates that nitrogen addition benefits invasive species more so than for native species. Native species in the desert may be accustomed to growing with limited nitrogen. More studies should be done to determine if nitrogen deficit harms invasive species more so than it does for natives.

Soil Seed Banks

Soil seed banks can be important in determining the abundance of plants. Olano et al. (2005) measured a seed bank in gypsum soil of a semi-arid ecosystem in central Spain. The aim of this study was to determine if the September soil seed bank collected correlated with the annual vegetation survey collected in April. Results showed the September seed bank density and species composition was similar to annual cover. There was also a significant correlation between the seed bank density and annual community composition. Soil seed banks can be useful in land management efforts to predict future plant populations. Invasive species can be more easily mitigated when land managers can predict their distribution. They can prepare for changes in non-native plant biomass or may discover a habitat that facilitates rare and native species.

When disturbances occur the seed bank composition may change. Scoles-Sciulla and DeFalco (2009) examined seed bank germination in the eastern Mojave Desert after topsoil was salvaged, stockpiled, and reapplied to the land. The sampled topsoil layer included the upper 5-20 cm. The abundance of germinated seeds was compared to that of seed banks in undisturbed control plots. In the removed topsoil, there was an 88% loss in the density of the seeds able to germinate. This may be due to dilution of the seed bank. The majority of seeds are generally held in the upper few centimeters of soil. When the upper 20 centimeters of soil is gathered, much of the bare soil is mixed into the seed bank. DeFalco et. al (2009) examined seed banks on undisturbed and disturbed sites due to soil compaction or trenching. Annual seed density decreased on compacted soil compared to undisturbed soil. The trenched site however had a higher annual seed density than the undisturbed control. Annual species richness was the smallest at the compacted site and greatest at the trenched site. Perennial species were less abundant in both of the disturbed sites compared to undisturbed and did not differ significantly based on disturbance type. The large seed density in trenched sites may be due to a greater amount of litter.

Disturbance may also affect soil seed banks differently in the fertile island and in interspaces. Esque et. al (2010) studied differences in seed bank abundances in response to fire treatment in Mohave County, AZ. Before treatment was applied, seed bank density was higher beneath canopies than in interspaces. Seeds can accumulate beneath the shrub canopy by dropping from the shrub and by collecting seeds that are trapped in shrubs through wind dispersal. Animals that visit the fertile island may also bring seeds from nearby interspaces. In this study, the fertile island suffered a seed loss proportionally greater than in interspaces, indicating that fire negatively affects the fertile island seeds more than seeds in the interspaces.

Seeds of invasive species were more abundant both before and after fire treatment when compared to native species. Invasive seed density suffered a greater loss than did native species density indicating that native seeds are more resistant to damage after fire. Results also indicated species differences in response to fire. *Schismus* spp. seed density decreased after fire, but differences did not differ in the fertile island and the interspace. *Bromus* spp. seed density decreased after fire in the fertile island more so than in the interspaces. *Ambrosia dumosa* seeds were not affected in interspaces, but decreased in abundance under the canopies.

Seed bank recovery may be able to occur quickly in deserts. Olano et al. (2012) examined the ability of the seed bank to return to its original composition after disturbance in a semi-arid environment. By removing soil and replacing it with sterilized soil, they were able to evaluate seed bank recovery over a three-year period. Seed density in plots varied between season ranging from 4138 seeds/m^2 to 48301 seeds/m^2 in September. Over the course of three years, the September seed bank for a particular year was always more dense than the April seed bank. Results showed that the treatment did decrease seed bank density compared to controls. However after 18 months, seed banks were able to recover.

Price and Joyner (1997) measured the amount of seeds in the soil seed bank and seed rain to determine how granivory is spatially and temporally related to seed availability. Results showed that granivores are possibly primarily consuming seed rain as opposed to seeds in the soil seed bank. There were more seeds in the soil seed bank than there were in traps that collected seed rain. Seed abundance in the soil seed bank was also higher beneath the shrub canopies than in the interspaces between shrubs. However, the interspaces had more seeds from seed rain than the fertile island microhabitat. Certain seed species were more prevalent beneath shrubs than in interspaces. These species included shrubs *Larrea tridentata, Coleogyne* *ramosissima* and herbaceous species *Schismus barbatus, Amsinckia tessellata, Cryptantha pterocarya,* and *Bromus madritensis rubens*.

Conclusion

Disturbance of fertile islands and soil seed banks can play a large role in altering the distribution of annual plants, native and invasive. As the spatial distribution of soil nutrients decreases form beneath shrubs to interspaces, differences in preferred growth habitats of annual species have been noticed as well. Applying this knowledge, in addition to using soil seed banks to gain insight on the future plant community composition, can be helpful in restoring disturbed ecosystems. More research is needed to determine effective restoration treatments and to learn how to mitigate the negative effects brought on by disturbances.

Chapter 3: Manuscript

Introduction

Disturbances by humans are one of the main drivers of change in contemporary desert ecosystems. These disturbances can facilitate soil erosion, a loss in native species cover and biodiversity, and a loss of soil features diagnostic of deserts such as fertile islands (nutrient-enriched areas forming below perennial plants). Management plans have employed restoration efforts after disturbance in order to limit the effect of the disturbance onto the ecosystem (Lovich and Bainbridge 1999; Caldwell 2006). It is important to understand the efficacy of specific restoration methods on different types of soils and to assess the efficacy of these methods in contributing to rehabilitation to the ecosystem, including recovery of soil stability and diverse plant communities. Comprehensive knowledge of the relationship between vegetation, seed banks, and soil is required to adequately administer methods for restoration.

Topsoil in deserts consists of the upper few centimeters of soil and is usually high in fertility and organic matter. This layer of soil is beneficial to plants due to the seed banks and concentration of soil nutrients (Defalco 2014; Anderson 2002), and when the soil is removed or disturbed, a large amount of seeds and soil nutrients are depleted. The need to salvage the topsoil prior to mandated disturbances such as road construction should be studied in order to determine its effect on desert restoration, including in rare soils such as gypsum soils that harbor unique vegetation.Soil seed banks are an accumulation of seeds that are usually found in upper soil layers, and in deserts, especially in fertile islands associated with shrubs. This buildup of seeds can be caused by various factors such as wind dispersal and entrapment from shrubs (Defalco 2014; Guo et al. 1998). Seed banks are one of the key components responsible for above ground vegetation abundance. In some cases, seed banks can be used to predict above ground vegetation, which is a useful tool in land management (Olano et al. 2005). In other cases, there is little relationship between the seed bank and present aboveground vegetation, making understanding seedbank-vegetation relationships among ecosystems an ongoing priority in plant ecology.

An understanding of the distribution of desert soils is required in order to provide effective treatments for soil stability and plant recovery. Desert soils show concentrated amounts of soil nutrients underneath perennial shrubs rather than in the interspaces between shrubs. This aggregate of soil nutrients under shrubs is termed “fertile islands.” The fertile islands can either have facilitative or competitive effects on other organisms (Titus et al. 2002; Bolling and Walker 2002; Walker et al. 2001). The effects of fertile islands created by shrubs include: distribution of native and invasive annuals plants, protecting soil nutrients, protecting annuals from extreme climate conditions, and capturing seeds from wind and animals (Garcia-Moya and McKell 1970; DeFalco 2009). Invasive species are known to facilitate fires, decrease abundance of native plants of mature shrublands, and reduce native annual plant forage for the federally listed endangered species, desert tortoise (Brooks and Berry 2006; Brooks 1999a; Brooks and Esque 2002).

It is beneficial to study the effects of these fertile islands on specific species to better understand vegetation dynamics in relation to fertile islands. The distribution of resources plays a significant role in the vegetation abundance and species prevalent in an area (Ott et al. 2011). Fertile island development and its influence on seed banks and annual vegetation are some of the driving forces of desert plant ecology.

In Lake Mead National Recreation Area, Northshore Road was reconstructed and realigned beginning in 1993. Salvaging soil, stockpiling, and reapplying topsoil were requirements put in place during road construction to limit the impact of the disturbance on to wildlife and plant communities. Although Scoles-Sculla and DeFalco (2009) found that reapplication of topsoil will cause the seed bank to be diluted, it is expected that outplanting perennials in addition to this method will contribute to the seed bank if the outplants survive long enough to be transplanted onto the reapplied soil. In a later phase of the construction during a 2009-2014 study, Abella et al. (2015) propagated and transplanted plants to assess the effect if would have on vegetation. Areas where topsoil was applied without any outplanting treatment applied showed rates of lower revegetation even seven years after topsoil reapplication. Lower perennial plant cover was also observed compared to the undisturbed sites. The most recent phase of the Northshore Rd. realignment (2008-2010) spans sensitive biocrust and desert pavement communities in association with Gypsids and Calcids soils. Topsoil was stockpiled and the first large-scale plant salvage was conducted in gypsiferous and surrounding soil types in Lake Mead National Recreation Area. Biocrust samples were also collected from the path of destruction along the new Northshore Rd designated route and stored. Once road construction was completed, specific topsoil and planting treatment were established to test outplanting methods and biocrust restoration methods. The purposes of the project by Abella et al. (2015) were to test salvage and outplanting techniques for vegetative specie and biocrusts restoration techniques in gypsiferous soil and surrounding soil habitats in LMNRA.

This study will determine if fertile islands produced by *Ambrosia dumosa* can appear after disturbances and restoration treatments. This will also show how well the fertile island facilitates annual plant species and provide insight into how native and non-native species interact beneath the fertile islands as opposed to in interspaces between shrubs.The purpose of this research is to evaluate the effects of topsoil reapplication and outplanting treatments on fertile islands, seed banks, and vegetation. Questions to be answered are:

1. How does topsoil reapplication and outplanting treatments affect formation of fertile islands, seed banks, and vegetation of winter annuals?
2. How is the abundance of winter annuals on disturbed soils affected by fertile islands?
3. Does seed bank emergence reflect species abundance in above ground vegetation?

Methods

Study Site

The study was conducted along roadsides in Lake Mead National Recreation Area in the southern Nevada portion of the eastern Mojave Desert. Mean rainfall in this area for the past decade is just over 16 cm/yr, most of which occurs in the winter or during the monsoon rain season between July and September. Temperatures in winter range from a high of 16°C in January during the day to 2°C at night. In July, temperatures reach of 42°C during the day and 23°C at night. Soil samples used for analyses were collected in January 2018 and January 2019. Vegetation sampling took place in April 2018 and March 2019.

This area is a desert shrubland characterized by the perennial shrubs *Larrea tridentata* and *Ambrosia dumosa*. Invasive annual species are also a high concern in the Mojave Desert. The soils in this area often contain gypsum and calcium carbonate. Common animals in this area include bighorn sheep, jackrabbits, and the federally threatened desert tortoise.

Site History

Disturbance

The study area encompasses the corridor of Northshore Road between mileposts 27 to 48. Most of the construction occurred in previously disturbed areas and the existing roadbed which resulted in minimal disturbance to the surrounding undisturbed lands with limited new disturbance. However, approximately 2.5 km of non-continuous road segments were built into previously undisturbed soils, and approximately 2.6 km non-continuous existing roadbed segments were obliterated.

The project was part of ongoing, multi-year Federal Highway Administration (FWHA) , Federal Lands Division work and NPS cyclic road maintenance (Dey 2006). The purposes of the FHWA project were to rehabilitate and reconstruct segments of road to improve pavement conditions and rehabilitate deteriorated and inadequate drainage (United States 2003).

The reconstruction and realignment of Lakeshore Rd and Northshore Rd in Lake Mead National Recreation Area (LMNRA) began in 1993. Specific actions were required during road reconstruction to reduce the overall impact to wildlife and plant communities, including salvaging, stockpiling and reapplying topsoil. Anecdotally, this process is believed to not disrupt the soil seed bank dramatically. However, research has shown dilution of the native seed bank during this process (Scoles- Scuilla and DeFalco 2009). For Phase I along Lakeshore Road, plants were propagated and transplanted, which, if plants survived, provide additional seed sources throughout the recovery process. For the rest of the road construction only topsoil was salvaged and reapplied and no seeding or planting treatments were implemented. At these sites, lower revegetation rates were observed even after seven years following completion of construction and reapplication of topsoil and lower perennial plant cover was observed compared to surrounding undisturbed areas (Scoles-Sciulla and DeFalco 2009). The most recent phase of the Northshore Road realignment (2008-2010) spans sensitive biocrust and desert pavement communities in association with Gypsids and Calcids soils. Topsoil was stockpiled and the first large-scale plant salvage was conducted in gypsiferous and surrounding soil types in LMNRA. Biocrust samples were also collected from the path of destruction along the new Northshore Rd designated route and stored. Once road construction was completed, specific topsoil and outplanting treatments were established to test outplanting methods and biocrust restoration methods. The purposes of these projects were to test salvage and outplanting techniques for vegetative species in gypsiferous soil and surrounding soil habitats in Lake Mead National Recreation Area (LMNRA).

In October 2008, LMNRA salvaged small to medium native perennial plants, including the common perennials *Ambrosia dumosa*, *Baileya multiradiata*, *Eriogonum inflatum, Psorothamnus fremontii*, *Sphaeralcea ambigua*, and, although not commonly found in gypsiferous soils, *Larrea tridentata* (DC.) Coville. Plants were cared for at the LMNRA nursery facility until transplanted within reconstructed roadside segments after construction was complete in January 2010.

The road reconstruction contractor was required to salvage the top layer of desert soils (topsoil) from any of the potential impact areas and stockpile topsoil as close to salvage sites to retain native biota and seed banks.Topsoil removal depth varies from the top 5-30 cm due to the equipment and landscape. Stockpiled surface soil was returned by the contractor to locations as close as possible to salvage sites after completion of construction (United States 2003). Due to the removal of segments of the old road, not all areas received topsoil; subsurface soil was used for filling and landscape contouring.

In 2011, 20 transects were installed as a part of the outplanting study. In 2017 twelve of these transects were relocated and undisturbed pairs were also established. In these areas, soil nutrients, vegetation cover, and soil seed banks were analyzed in interspaces and beneath fertile islands produced by new recruits of the shrub *Ambrosia dumosa*. All shrubs used in this study occurred naturally within the past decade, making the maximum age of all fertile islands a known factor.

Experimental Design

In October 2017, twelve roadside segments were identified along Northshore Rd. that had been disturbed due to construction and restoration treatments in 2008. Sites received either topsoil application, topsoil application with outplanting, or no treatment. Three sites were chosen that had received no treatment, four sites received topsoil reapplication only, and five sites received topsoil reapplication and outplanting treatment. Twelve undisturbed segments were also identified in areas adjacent to the disturbances to be used as controls. Within each segment, six 1 m × 1 m microsites were located for analyses. Three microsites were centered on the shrub species *Ambrosia dumosa* and three were centered on interspaces between shrubs. To evaluate the long-term effects of two restoration methods, topsoil reapplication and outplanting treatments, I measured soil nutrients, perform seed bank assays, and measure annual vegetation beneath fertile islands and in interspaces on roadside segments that received either:

1. Topsoil with outplanting
2. Topsoil without outplanting
3. No topsoil and no outplanting

Soil Analysis

Within each segment, a 50m soil transect was placed approximately in the center region. To analyze the soil in fertile islands and in interspaces, a 150-mL sample at 0-5 cm depth was taken from microsites closest to the transect at 0 m, 25 m, and 50 m within 10 cm of the transect line along either side. The minimum size of each shrub was 0.5 m. Each set of three samples was composited into one 450-mL sample. Soil analysis samples were dried and sieved through a 2-mm sieve and analyzed for texture using the hydrometer method. Since high gypsum content occurs in these soils, the hydrometer method can result in a miscalculation of sand content so sample measurement units were relative to one another. Organic C was tested using the Loss on Ignition method. In 10 mL crucibles, 5-10 g of soil were used and placed in a oven at 500°C for 4 hours. Total Nitrogen, total Carbon using a C/N analyzer,, and pH tests using a 1:1 soil:water ratio. were analyzed by Oklahoma State University. Samples for soil analysis and soil seed bank analysis were collected in January of 2018.

Soil Seed Bank Assay

A soil seed bank emergence assay was performed on samples to measure the persistent seed bank. Soil samples were collected in January 2018 using the same collection methods described in the soil analysis, and immediately potted in 15-cm diameter pots with 2 cm thickness on top of a 1:3 soil mixture of organic mulch to sand at UNLV greenhouse facilities. Pots were placed under an automatic watering system and watered two times daily with environmental conditions set at a springtime day/night time temperature range of 15/25°C. Due to the development of physical crust in these soils, the soil surface was roughened every few days to disrupt the physical crust layer. At two months, a 150-ml solution of 1000 ppm of gibberellic acid was added to pots to induce germination. As species were identified, they were tallied and removed from pots. Pots were observed for approximately 6 months. Unidentified individuals were classified into growth habits (e.g., forb, graminoid), if they did not survive to maturity.

Vegetation Analysis

A vegetation census was taken in March of 2018 and 2019 while winter annuals were in the flowering stage of their life cycle. Along the disturbed and undisturbed transects, quadrats 1 m x 1 m in size were used and centered on the perennial shrubs or in interspaces between shrubs. Aerial cover of plants was recorded visually using Peet et al. (1998) cover classes. The cover of the perennial shrub itself was not included in the analysis. The microhabitats analyzed were underneath the shrub and in the interspaces between shrubs. Perennial shrubs were typically 0.5-1.0 m wide. Plants were identified by their species name, nativity, lifeform, and longevity following the USDA Plants Database.

Statistical Analysis

Univariate

Separately for each year data were collected (2018 and 2019) vegetation and soil data were analyzed using a three-factor mixed-model analysis of variance including disturbance status (disturbed, not disturbed), restoration treatment (topsoil applied, topsoil + outplanting applied, and no treatment), microsite type (below *Ambrosia* or interspace) and all interactions. The individual microsites were averaged per transect. Microsite was nested within site and was a random variable. We implemented the analysis using PROC MIXED in SAS 9.4. Where assumptions were not met for normality of data residuals, residual distributions were examined and distribution of residuals (cover, lognormal; richness, poisson) was assigned in the model statement. For soils, total nitrogen and total carbon were log10+1 transformed before analysis. To compare treatment plots to paired reference sites, a similar model was used as above.

Microsite and disturbed treatments were assigned as fixed effect and compared to reference site microsites. Plots were nested within site to ensure pairing of disturbed plot and paired reference site.

Multivariate

A bivariate Pearson correlation analysis was performed to identify soil variables highly correlated with each other ($r > |0.90|$). Using a set of three variables (pH, total N, and total C), the full data set and partial data sets were ordinated (only disturbed and only undisturbed areas) using principal components analysis. Correlation was used as the distance measure to account for differences in measurement scales of the variables, and performed analyses in PC-ORD version 7.07 (McCune and Mefford 1999). Permutational multivariate analysis of variance (Anderson 2001) was then used, using Euclidean distance and with the three variables each relativized by their maximum value, at three different levels in PC-ORD. First, all sample units were included to test variation across a four-level classification of disturbance (disturbed, undisturbed) and microsite (*Ambrosia* or interspace) with sites serving as blocks. Second and third, we performed analyses separately within disturbed and undisturbed areas to isolate the effect of microsite, with sites serving as blocks.

Separate matrices of relative cover (cover of species/∑ cover of all species in a sample unit) were computed for each study year (2018 and 2019) and for annual and perennial species data sets. We performed three permutational multivariate analyses of variance (Sørensen distance) on each of the matrices including all sample units to test variation across a four-level classification of disturbance (disturbed, undisturbed) and microsite (*Ambrosia* or interspace), and within disturbed and undisturbed areas to isolate microsite effects. Sites served as blocks for all analyses. To identify species significantly associated with disturbance-microsite combinations, we conducted blocked indicator species analyses (with sites serving as blocks) separately on these matrices for all sample units (across four disturbance-microsite categorical combinations) and within disturbed and undisturbed areas to isolate microsite effects. Indicator values range from zero (no association of a species with a group) to 100 (full association), with P values estimated through randomization tests (Dufrêne and Legendre 1997) as implemented in PC-ORD.

Results

Climate

In the two years studied, sites received a substantially different amount of rainfall during the hydrological years of October 2017-March 2018 and October 2018-March 2019. In the first year, the study area received 62mm of rainfall. In the following year, sites received 130mm of rainfall. The average fall-winter rainfall in the desert since 1992 is 80mm. The 2018 hydrologic year received the second highest amount of rain in the last 10 years and February of this hydrologic year received the most rainfall than any other February in the last 10 years. The previous year sampled in 2017 received the second lowest amount of rainfall in the last decade. This study is able to show the different ways in which desert plants respond to variation in the availability of water, one of the most limiting resources.

Soil Nitrogen in the Fertile Islands and Interspaces in Disturbed and Undisturbed Soils

Soil nitrogen in fertile islands developed in the disturbed areas had higher total nitrogen than in their interspaces (FI = 0.06%, INT = 0.02%). The same differences are seen in the microsites of undisturbed soil (Figure 4). Fertile island soil in undisturbed areas have a nitrogen content of 0.09% and soil in interspaces contains 0.03% nitrogen. When comparing the disturbed with the undisturbed soils, the soil nitrogen content in interspaces do not differ greatly from each other. The disturbed fertile island however, only has 2/3 the amount of soil nitrogen than that of fertile islands in undisturbed soil. Principal component analysis also showed that there is differences in soil nitrogen between the fertile island and interspaces were stronger in undisturbed soils than for disturbed soil (Figure 4A-C). Differences in soil pH and soil carbon were not statistically significant.

Plant Cover in Disturbed vs Undisturbed Soils

Total native plant cover and total forb cover differed in disturbed and undisturbed soils. Native plant cover was low in disturbed soils (0.6%) compared to undisturbed areas (2.4%) in 2018. Plant species that occured in disturbed areas were *Plantago ovata* and *Chorizanthe rigida*, *Enceliopsis argophylla, Tequila latidor,* and *Sphaeralcea ambigua.* Plant species that occured only in undisturbed areas were *Mentzelia albalcus, Gilia* species, and *Lepidium lasiocarpum, Lesquerella tenella,* and *Monoptilon beloides.* This same trend was seen in 2019 (Disturbed = 0.4%/m^2, Undisturbed = 1.5%/m^2) (Figure 5A-B). In 2018 total forb cover was also higher (2.4%) in undisturbed areas than in disturbed areas (0.7%) (Figure 7A).

Species Richness in Disturbed vs Undisturbed Soils

Native species richness and forb species richness also differed in disturbed and undisturbed areas. There were less native annual plant species in disturbed areas (2.0 species/m^2) than in undisturbed areas (3.2 species/m^2) in 2018 (Figure 5B). In 2018, there were also more forb species in undisturbed areas (3.6 species/m^2) than in disturbed areas (2.2 species/m^2)

(Figure 7B) including species *Malcolmia africana*, *Langloisia setosissima*, *Cryptantha nevadensis*, *Pectocarya recurvata,* and *Erodium cicutarium*. Native annual forb species were more abundant in undisturbed areas in particular (3.4 species/m^2) in 2018 (Figure 8B). Shrub seedlings species was also greater in undisturbed areas than in disturbed areas in 2019 (Disturbed = 0.01 species/m^2; Undisturbed =0.4 species/m^2) (Figure 10C). Some of these species included *Atriplex hymenelytra*, *Ambrosia dumosa*, and *Psorothamnus fremontii*. In 2019, opposing previous trends, native perennial plant species richness was greater in disturbed areas (1.4 species/m^2) than in undisturbed areas (0.6 species/m^2) (Figure 5D). Native perennial plant species that occurred in disturbed areas were *Ambrosia dumosa* and *Enceliopsis argophylla*.

In 2018 and in 2019 exotic annual forbs also had many species growing in disturbed areas (2018: Disturbed = 0.85 species/m^2, Undisturbed = 0.18 species/m^2; 2019: Disturbed = 1.1 species/m^2; Undisturbed = 0.45 species/m^2). These exotic annual forbs included *Malcolmia africana*, *Salsola tragus*, and *Brassica tournefortii*.

Plant Cover Beneath the Fertile Island vs Interspace

In 2019, the fertile island microsites had higher native perennial plant cover (0.6%/m^2) than in the interspaces (0.01%/m^2)(Figure 6C). Exotic annual forb cover was also greater beneath the fertile island (1.2%) than in the interspaces (0.2%) (Figure 8D).

Plant Species Richness Beneath the Fertile Island vs Interspace

In 2019, total plant species richness was higher in the fertile island than in the interspace (FI=10.6 species/m^2, INT=6.2) (Figure 14A). Both the native and exotic plant community had enhanced species richness beneath the fertile island compared to interspaces (Figure 14B-C).

Native annual and perennial forbs had a greater species richness in the fertile island than in the interspaces (Figure 6B, 6D). Native annual species richness was 5.4 species/m^2 in the fertile island and 3.1 species/m^2in interspaces. Native perennial forb species occurred at 0.01 species/m^2 in interspaces and 0.35 species/m^2 beneath fertile islands (Figure 6D). Native annual species that tend to grow in the fertile island included *Plantago ovata*, *Chylismia brevipes*, and *Cryptantha nevadensis*, and the native perennial species included *Stephanomeria pauciflora, Acacia greggii,* and *Larrea tridentata* seedlings. In 2019 Exotic plant species also grow in association with the *Ambrosia* fertile island (FI=2.9 species/m^2, INT=2.1 species/m^2) (Figure 14C). These species included *Bromus rubens, Schismus* species, and *Malcolmia africana.* Exotic plant species richness in 2018 was also greater in the fertile island (2.4 species/m^2) than in the interspace (1.4 species/m^2) (Figure 9A). In particular, exotic annual gramminoids had a higher species richness beneath the fertile island (1.7 species/m^2) than in interspaces (0.79 species/m^2)(Figure 9B). These species included *Bromus* species and *Schismus* species. More species of shrub seedlings were found beneath the fertile island in 2018 and in 2019 (Figure 10A-B) including *Ambrosia dumosa* and *Psorothamnus fremontii* seedlings. In 2018, shrub seedling species richness was 0.44 species/m^2 beneath the fertile islands and 0.07 species/m^2 in the interspaces. In 2019, shrub seedling species richness was 0.32 species/m^2 in the interspaces and 0.98 species/m^2.

Plant Cover and Species Richness Among Treatment Types

Although analysis of shrub seedling cover showed high cover in areas that had been restored with topsoil compared to areas that received outplanting and no treatment (Figure 11), parsing out the disturbed and undisturbed values showed that this difference may be attributed to spatial variance in the site locations. In 2018, total exotic plant species richness was greater in sites that had received topsoil reapplication (3.6 species/m^2) than areas that received no treatment (1.2 species/m^2). Areas that received topsoil and outplanting did not differ significantly from other treatment types (2.9 species/m^2) (Figure 12A-B). In 2019, exotic gramminoid plants were also more species rich in areas that received topsoil (1.7 species/m^2) (Figure 12C-D). Areas that did not receive treatment had less species richness (0.25 species/m^2). Native perennial plant species richness did not differ between treatment types, however, areas that received topsoil had a significantly greater amount of perennial species (1.3 species/m^2) than in it's undisturbed pair (0.01 species/m^2) (Figure 13).

Soil Seed Bank Emergence

Soil seed bank emergence showed that most seedlings germinated in fertile islands that had received either only topsoil (58.8 seedlings/m^2) or topsoil and outplatning treatment (40.5 seedlings/m^2) (Figure 15A). Fertile islands in areas that received no treatment had low seedling emergence (17.4 seedlings/m^2) and this microsite did not differ significantly from interspaces (9.3 seedlings/m^2). Native plant seedlings were more abundant in fertile island soil from areas that received topsoil treatment (Figure 15C) compared to all other interspaces. Native annual plant sleedings in particular germinated more in soils collected from fertile islands in either restoration treatment compared to fertile islands in unrestored soils (TS=47.4 seedlings/m^2, TSOP=33.5 seedlings/m^2, NONE=7.1 seedlings/m^2) (Figure 15B) . Exotic plant seedlings were also most abundant in soil collected beneath fertile islands in areas that received topsoil and outplanting (32.0 seedlings/m^2), or topsoil reapplication only (44.8 seedlings/m^2) compared to the number of seedlings that emerged from fertile islands in untreated sites (6.8 seedlings/m^2) (Figure 15C).

Forb seedlings were more abundant beneath fertile islands of areas that received topsoil only (26.2 seedlings/m^2), and were lowest in interspaces from the same restoration treatment(6.5 seedlings/m^2) (Figure 16A). Fertile island soil from topsoil only areas had greater forb seedlings than fertile islands from unrestored areas (7.6 seedlings/m^2). Shrub seedlings were also most abundant in fertile islands that received topsoil only (16.7 seedlings/m^2). These areas produced more seedlings than fertile islands from the disturbed and unrestored sites (3.9 seedlings/m^2). The lowest amount of shrub seedlings occurred however in the undisturbed interspaces paired with those that received topsoil and outplanting treatment (3.6 seedlings/m^2). Fertile islands from topsoil areas produced the most shrub seedlings (Figure 16B).

Fertile island soil from areas that only received topsoil had greater native perennial seedling emergence than all interspaces across treatments and undisturbed areas (TS FI = 38.4 seedlings/m^2; TS INT = 0 seedlings/m^2). The fertile island in this topsoil area also produced more seedlings than fertile islands in areas that received no treatment(NONE FI = 10.7 seedlings/m^2) (Figure 17).

Discussion

Soil Analysis

Soil nitrogen and water are some of the most limiting resources for plant growth in deserts. Nutrient availability for plants can be reduced due to extreme conditions such as dry periods and high solar radiation. Perennial shrubs have been found to harbor soil nutrients in the fertile island even years after the shrub is dead, potentially increasing nutrient availability for other plants to take advantage. High soil nitrogen content in the fertile island can facilitate other perennial shrubs to grow in these areas, which can in return provide shade to plants, reducing solar radiation and evaporation rates.

In all disturbed and undisturbed sites, soil nitrogen was significantly higher underneath the perennial shrub *Ambrosia dumosa,* than in the interspaces between shrubs (Figure 1A). This finding is consistent with previous studies that have demonstrated the fertile island effect (Romney et al., 1980; Walker et al., 2019; Schlesinger et al., 1996; Garcia-Moya and Mckell, 1970; Mudrak et al., 2014). Fertile islands in undisturbed areas had more soil nitrogen than those of disturbed areas, similar to results found by Bolling and Walker (2002), indicating that although the fertile island effect is present, it has not yet reached the same magnitude as undisturbed soil nitrogen. This can occur particularly in disturbances that have caused removal of topsoil. Disturbances in deserts can cause instability in the soil through erosion, reducing native biota, and depleting nutrients which can alter the soil nutrient cycles. Using treatments that help stabilize the soil and maintain nutrients can put the land on the trajectory towards recovery. Fertile islands in previous studies have shown that shrubs of *Larrea tridentata* have a nitrogen content of 0.12% beneath the shrub and 0.03% in interspaces (Brooks 1999).

Soil nitrogen was doubled in the fertile island than in interspaces in disturbed areas, and soil nitrogen was tripled in the fertile island than in interspaces in undisturbed areas. A study by Rathore et al. (2015) measured soil properties of shrubs that were seven years old and found that soil nitrogen increased 31-47% beneath the shrub canopy than in interspaces. Available soil nitrogen in these areas was 36.7 mg/kg ± 3.4 in the interspaces and 53.8 mg/kg ± 4.4 (0.0367% and 0.0538% respectively). Differences in shrub species used may account for slight differences in soil nitrogen content beneath the fertile island. Fertile islands in my study may be a maximum of 10 years, as opposed to 7 years in the Rathore et al., (2015) study, giving potentially 42.8% more time for potential nitrogen to accumulate beneath the shrub, although the exact shrub age is unknown and some may even be less than a couple of years old.

Vegetation Analysis - Disturbed vs Undisturbed

Most of the forbs observed in this study serve as forage for wild animals in this area. Forbs in the the undisturbed areas are more prevalent, so the disturbances seem to have a negative effect on forb cover 10 years after the disturbance took place. Low plant cover in disturbed areas may be due to soil erosion and soil compaction, reducing nutrient availability for plants. Forb cover may have an association with more abundant soil nutrients such as nitrogen. The diversity of forbs and native plants was also low in disturbed areas. Native annual species were more abundant in undisturbed areas, however, native perennial plants were more diverse in disturbed areas than in undisturbed areas in 2019. In 2019, a wet year, the perennial plants in the disturbed areas had experienced one of, if not the most wet year in its' life time (Figure 3). Perennial shrubs in these areas may have been attempting to optimize their reproductive success more so relative to perennial plants in undisturbed areas whose maximum ages are unknown. Although native perennial plants were higher in disturbed areas, shrub seedling richness was higher in undisturbed areas.

Vegetation Analysis - Fertile Island vs Interspace

In the fertile island plant cover was high specifically for all native perennial plants and exotic annual forbs. Studies have previously shown that the shrub canopy can facilitate greater biomass of annual plants (Kleinhesselink et al., 2014; Schaefer et al., 2012; Craig et al., 2010). This is to be expected because soil nitrogen is higher in the fertile island, and shade is provided by the *Ambrosia dumosa* shrub. Restoring native plant cover without also increasing exotic plant cover can be difficult when no additional treatment is applied because exotic plants have a generalist resource requirement, so they are expected to take advantage of any resources that are facilitating natives. Although higher annual exotic cover can lead to increases in fire fuel (Brooks et al., 2004), the benefits of high native perennial cover can make it difficult to determine whether the net effect of fertile islands are positive or negative. Native perennial plants have the advantage of being able to optimize reproductive success by reproducing in a later year when conditions are more ideal. In dry years, the native perennial plants have potential to reallocate energy that they would use for reproduction and spend it on growth and maintenance. This could potentially help maintain native plant communities and reduce competition in areas that also have exotic annual plants.

Total species richness was also higher beneath the fertile island. Native species richness in particular was higher and this was seen specifically for both native annual forbs and native perennial forbs. Exotic species richness was also higher, and particularly had a higher diversity of exotic annual graminoids such as *Bromus* spp. and *Schismus* spp. Previous studies by Brooks (1999) have showed that exotic species richness is higher beneath *Larrea* shrubs in a year of high rainfall, but higher in interspaces in a year with low rainfall. Maintaining biodiversity of native plants is one of the highest priorities in many restoration projects, making understanding dynamics between native and exotic plants an important aspect of restoration ecology. There were also more species of shrub seedling beneath the fertile island than in the interspaces in both years. This differs from previous experimental studies that showed perennial shrubs such as *Ambrosia dumosa* prefer to grow in interspaces rather than beneath a developed perennial shrub (Walker et al., 2001; Schenk and Mahall, 2002;). However, the species of major perennial shrub in the fertile island can greatly facilitate or compete with other species attempting to develop beneath the fertile island (Ott et al. 2011; Schaefer et al. 2012). Species that can facilitate another shrub have the potential to enhance the fertile island effect. Different shrub species can also produce fertile islands of differing qualities. Native plants such as *Pterostegia drymariiodies* and *Claytonia perfoliata* prefer to grow beneath some fertile islands and *Chorizanthe cuspidata* and *Cryptantha leiocarpa* prefer to grow in interspaces (Kleinhesselink et al. 2014). Some shrubs such as *Larrea tridentata* have a negative effect on annual plant growth in the fertile island (Schaefer et al., 2012). Having both plants on the fertile island may diversify the plant community beneath the fertile island.

Vegetation Analysis - Treatment Type

Native perennial plant species richness did not differ between treatment types. However, in 2018 there were more native perennial species in topsoil areas than in their undisturbed pairs. These plants are all natural recruits that have developed within the past 10 years. The topsoil areas may have provided nutrient rich soil that supports these native perennial plants. Exotic species richness was also higher in areas that only received topsoil than areas that received no treatment. However, neither of these areas differed significantly from the undisturbed pairs.The topsoil may have contained exotic seeds in it, or may be an overall more hospitable place for plant growth compared to that of soils that have been disturbed and unrestored.

Soil Seed Bank

In areas that received treatment, more seedlings germinated from soil collected from fertile islands. Interspaces had a low amount of seedlings. Seedlings germinated most from fertile island soil collected from areas that had only received topsoil. Soil seed bank composition could be diluted due to disturbance (Scoles-Sciulla and DeFalco, 2009; DeFalco et al., 2009;

Esque et al., 2010), however studies have shown that the soil seedbank is quick to recover and can happen in as little as 18 months (Olano et al., 2012). The shrub above the fertile island has the potential to drop seeds to contribute to the soil seed bank. Seed abundance in the fertile island can also be due to entrapment of seeds by wind. Animals may also move seeds from interspaces into fertile islands when seeking shade. The topsoil that was salvaged and stored could have maintained a lot of the native seed and biota prior to disturbance. Areas that had no treatment applied did not have many seeds that germinated in their fertile islands. The amount of seedlings in these fertile islands did not differ from that in interspaces in areas that did not receive treatment, signifying that the fertile island effect was most prevalent in areas that received treatment. Native plant seedlings also did the best in areas that had only received topsoil. Exotic plant seedlings also also germinated more from fertile islands of areas that received treatment, showing again that exotic plants will succeed in environments where natives also succeed. Forb and shrub seedlings were also more abundant in areas that received topsoil only. Lower values in areas that received topsoil and outplanting treatment may be due to competition with the outplants. The outplants are older and may have potential to take greater advantage of resources. However, results did not show statistical differences between the two topsoil treatments.

Conclusion

The goal of this project was to understand how topsoil reapplication and outplanting treatments affect the seed banks, soil compositions, and vegetation cover of the Mojave Desert in Lake Mead National Recreation Area. Seed population in the seed bank can vary between disturbed and undisturbed areas. This should be understood because seed banks are useful in being able to monitor species abundance. The depletion of seed banks due to disturbance must also be evaluated because selective and rare species that are not favored in certain climates may produce seeds that have remained dormant over time. Removal of these may ultimately lead to a less abundant species. Difference in species interactions must also be studied because it can account for the wide variety of species composition of the desert. Invasive species abundance is one aspect of the desert that land managers must learn how to limit. The relationship between species abundance and soil composition will be helpful in understanding how to employ management plans.

Restoration methods are needed in order to rehabilitate disturbed areas of the desert. However the efficacy of these methods must be evaluated, especially on a long term scale. A unique feature of this project is that owing to the availability of supporting long-term data from the research sites, the maximum ages of fertile islands are known. This information is often missing from other studies, making the age of a fertile island and its possible influence on ecosystem properties a significant unknown. In this study, the fertile islands are no more than 10 years old, and soil properties after treatment in the treatment areas were quite uniform, enabling evaluating the early development of fertile islands in a restoration setting.

Fertile islands can be characterized by soil nutrients, vegetation cover, and the composition of the soil seedbank. Differences in soil nitrogen content show that In all disturbed areas, a fertile island was identified in regard to vegetation cover. Although an increase in vegetation cover in the restoration sites included exotic species cover and richness, the alternative of not treating disturbed sites has detrimental effects decreasing overall native plant cover and biodiversity, which limits the amount of forage available for wild animals. Limiting growth of exotic species such as *Bromus* and *Schismus* can be challenging without the use of treatments such as herbicides. Planting native perennial plant species may be a way to help maintain diverse plant community in disturbed soil. More research could be developed to determine which perennial shrub species can have mutually beneficial relationships in a fertile island and determining how these fertile islands differ from those with shrubs that stand alone. In future studies, one might take into account the size of the perennial shrub. *Ambrosia* shrubs in the unrestored areas appeared to be smaller and have less foliage than shrubs in other areas. Studies may also benefit from a plot scaled account of vegetation cover as opposed to individual microsites. Topsoil application and outplanting treatments proved to be effective in facilitating a more productive plant community.Areas that received no treatment had little cover and the perennial shrubs were much smaller and had less foliage than plants shrubs in the restored areas. Native perennial plants may be more resilient on disturbed soil than native annuals plants, especially in a wet year. More soil analysis of phosphorus, potassium, and available nitrogen to determine more characteristics of the fertile island effect. Fertile Island development should be measured at five years and possibly one year to determine exactly how long it takes for a perennial shrub to form the fertile island.

The unbalanced amount of sample sizes at the three different locations is one of the limitations to this study. Future studies could take into account microhabitats beneath the fertile island such as areas close to the stem, and areas on the canopy drip line to further categorize spatial distributions in the plant community. Disturbances were positively associated with exotic plant abundance and native perennial plants in one year indicating that native perennials may be more resilient than native annuals on disturbed soils, especially in a wet year. More soil analysis of phosphorus, potassium, and available nitrogen, in addition to total nitrogen is recommended to get an accurate account of useable resources. Taking multiple measurements at different times of the year would also help gather a more comprehensive account on the availability of soil nutrients.

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Figure 1: Map of Lake Mead National Recreation Area

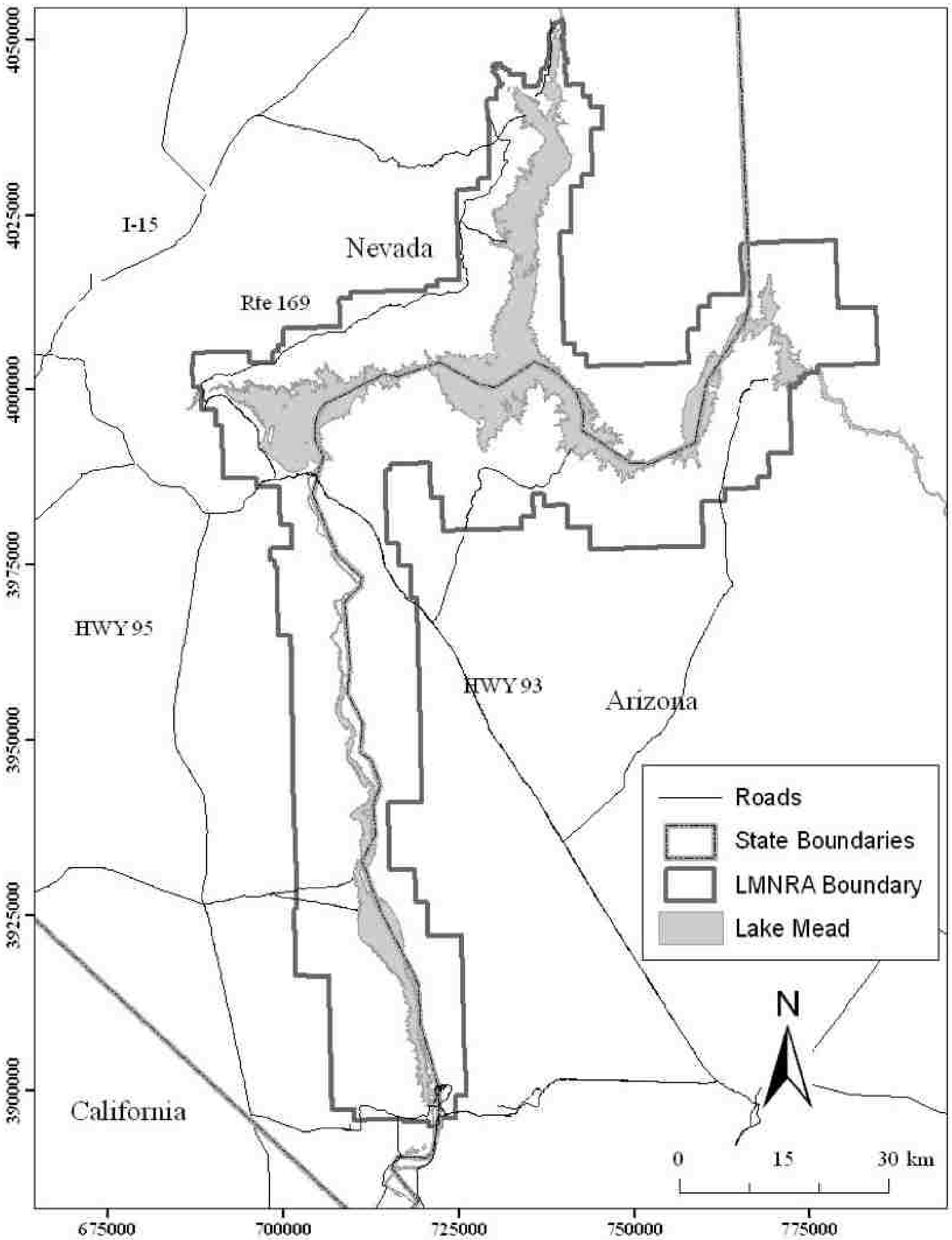


Figure 2: Pre-Existing Road Condition in 2009 After Disturbance and Before Restoration Treatments Were Applied

Photo by Lindsay Chiquoine

Figure 3: Total Fall and Winter (October-March) Precipitation for the Start of Each Hydrological Year from 2008-2018

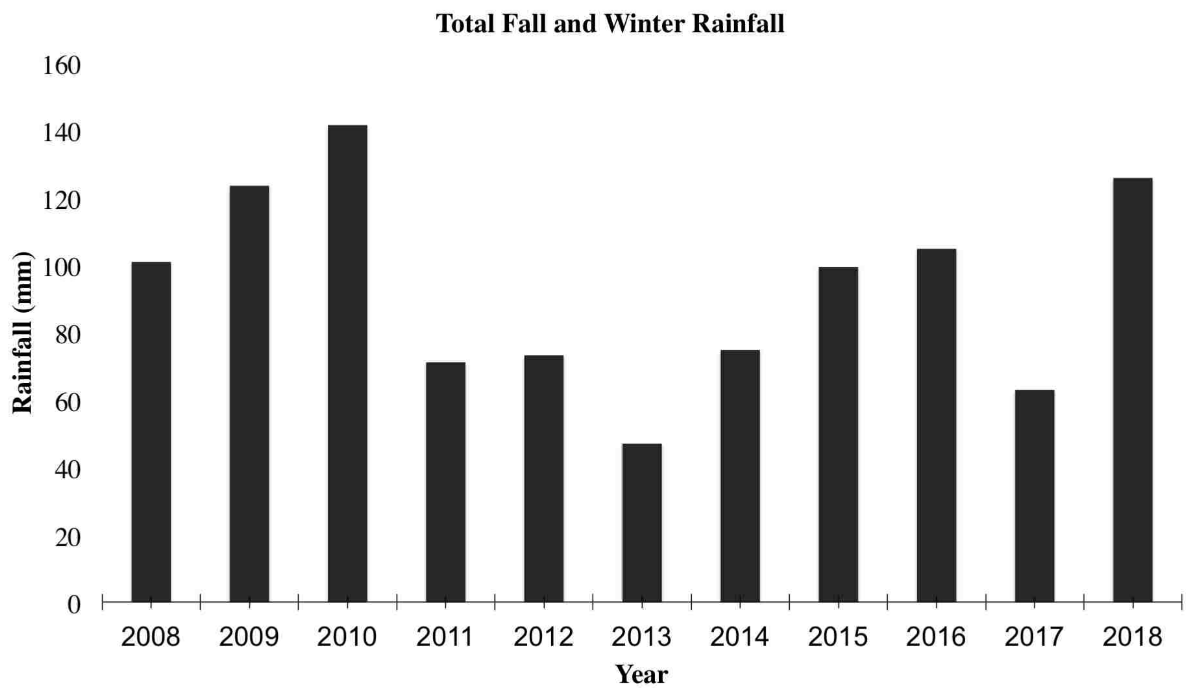
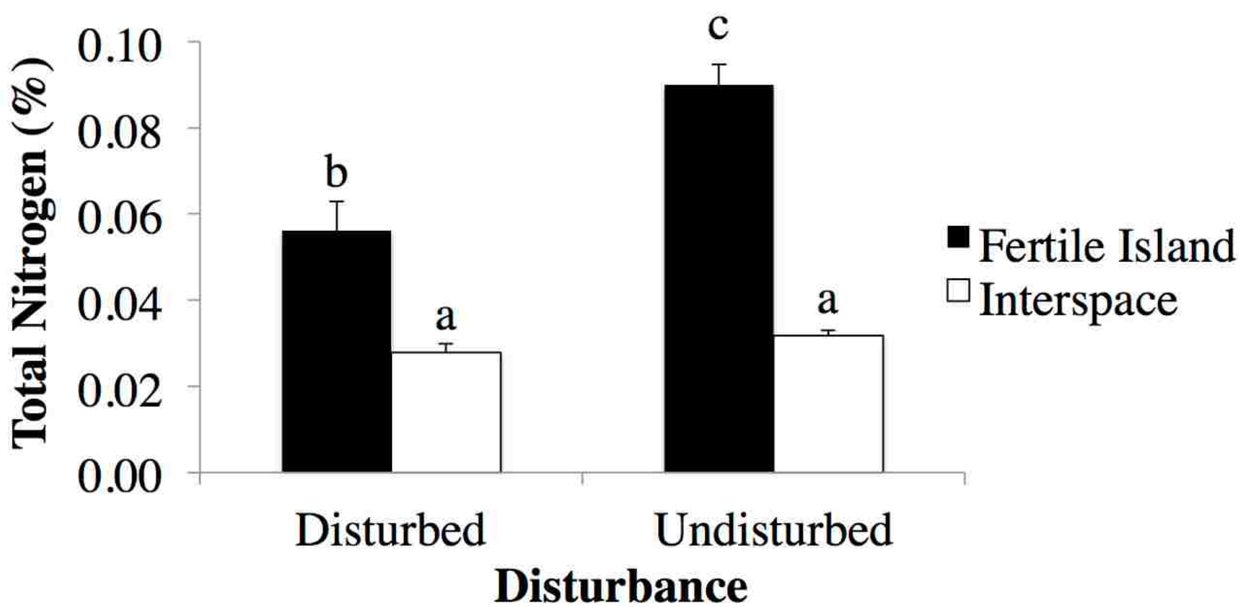


Figure 4A: Total Soil Nitrogen Content in Disturbed and Undisturbed Soils in Fertile Islands and in Interspaces.



Means without shared letters differ at $p<0.05$. Error bars are one standard error of means.

Figure 4B: Principal Component Analysis Plot Showing Variation in Soil Parameters Among Microsites in Disturbed Soils

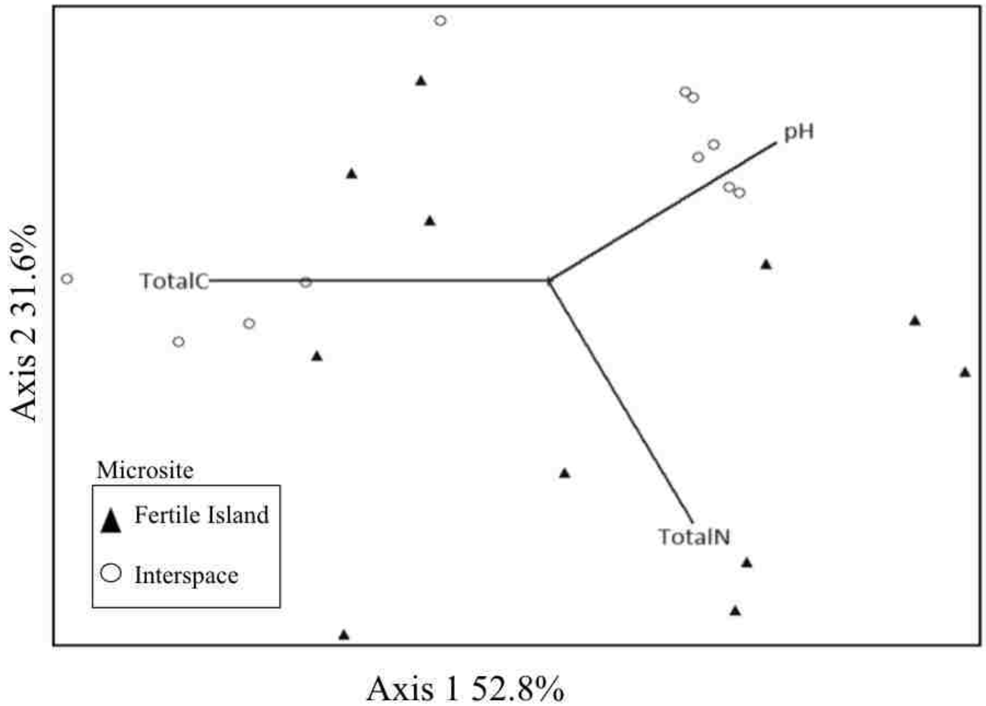


Figure 4C: Principal Component Analysis Plot Showing Variation in Soil Parameters Among Microsites in Undisturbed Soils

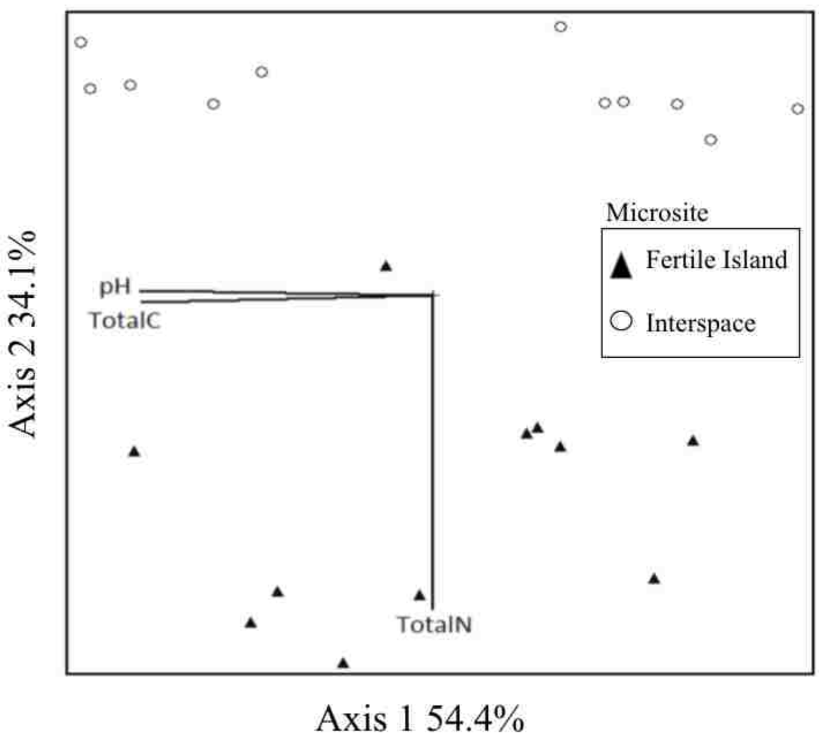
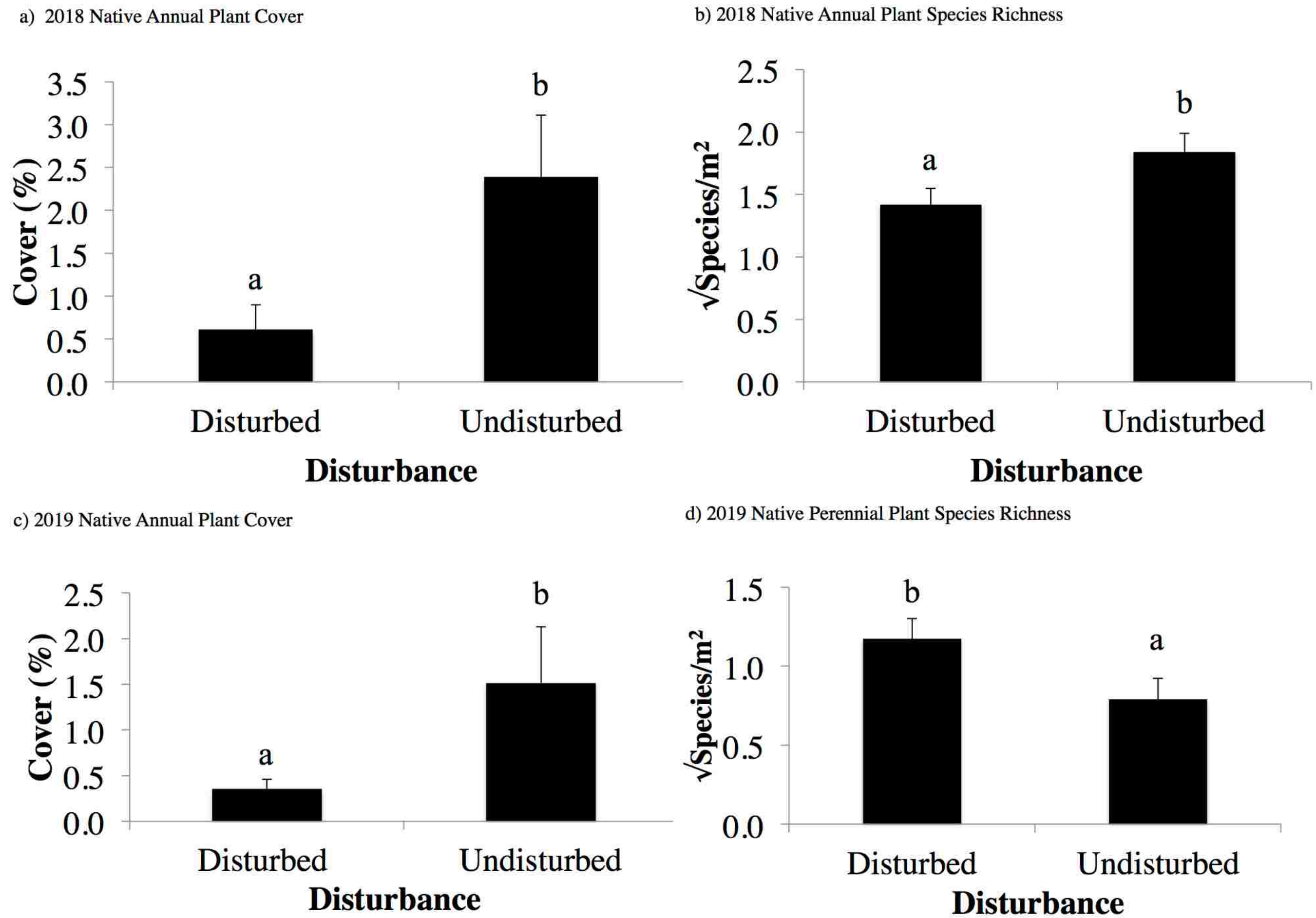
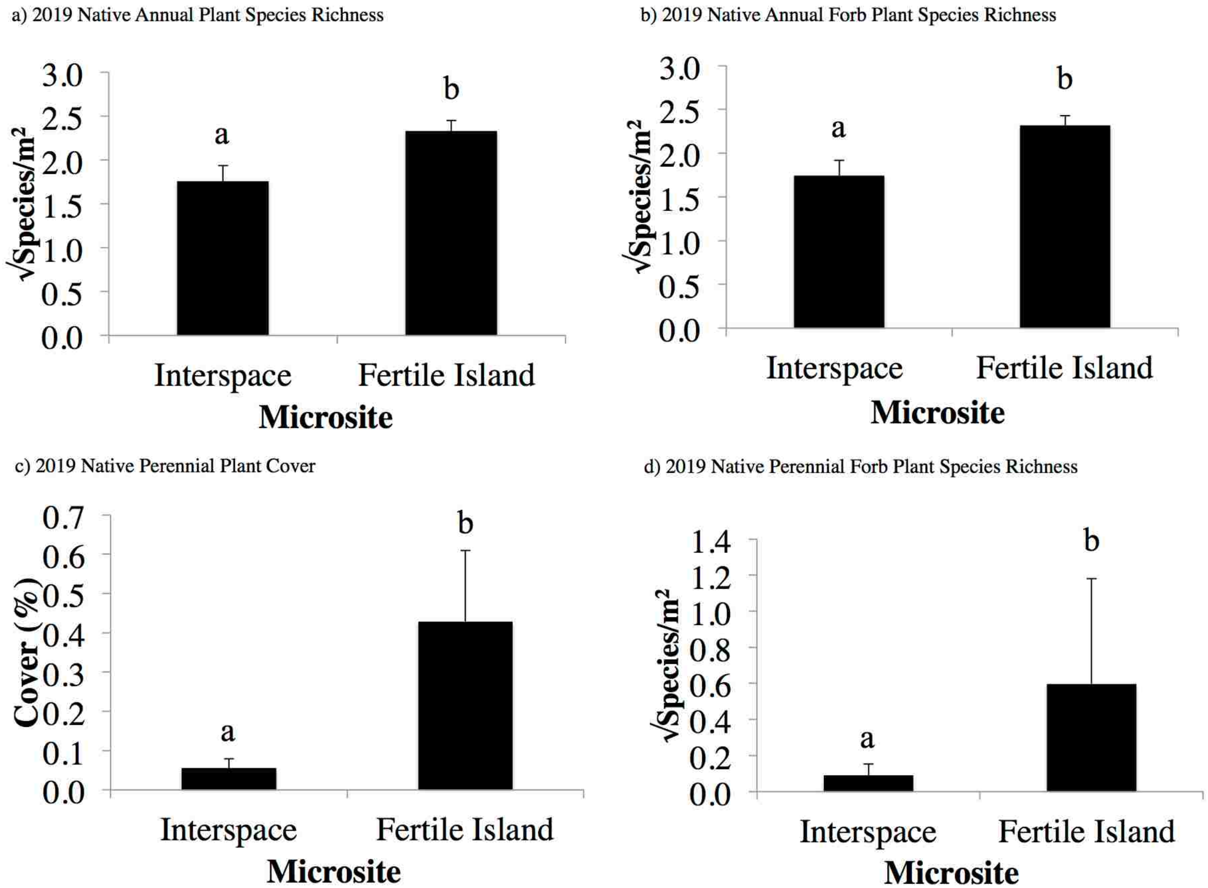


Figure 5: Native Plant Cover and Species Richness in 2018 and 2019.



Means without shared letters differ at $p<0.05$. Error bars are one standard error of means. Species count was transformed to the square root of the number of species found per m^2.

Figure 6: 2019 Native Plant Cover and Species Richness Among Microsites

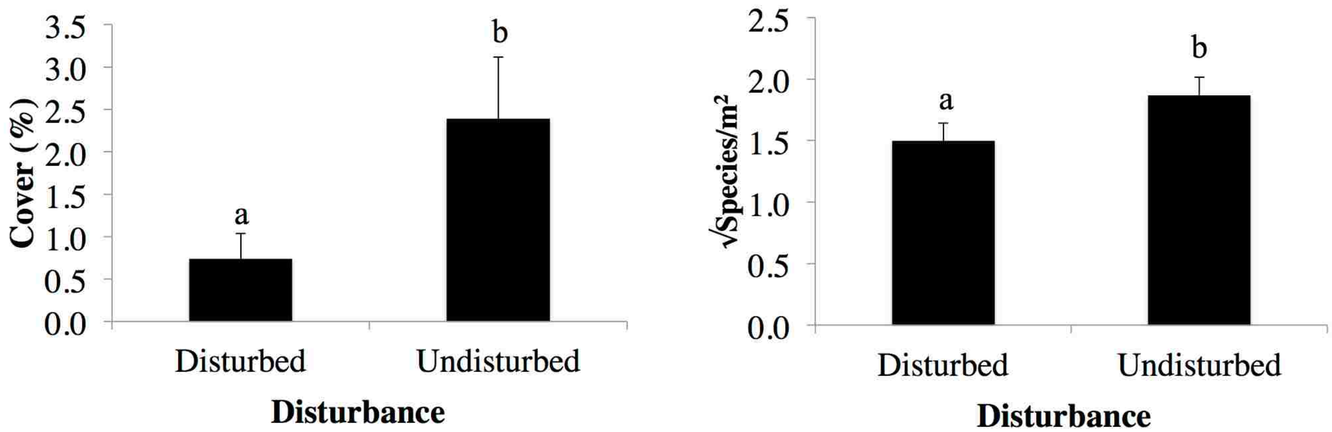


Means without shared letters differ at $p<0.05$. Error bars are one standard error of means. Species count was transformed to the square root of the number of species found per m^2.

Figure 7: 2018 Forb Cover and Species Richness

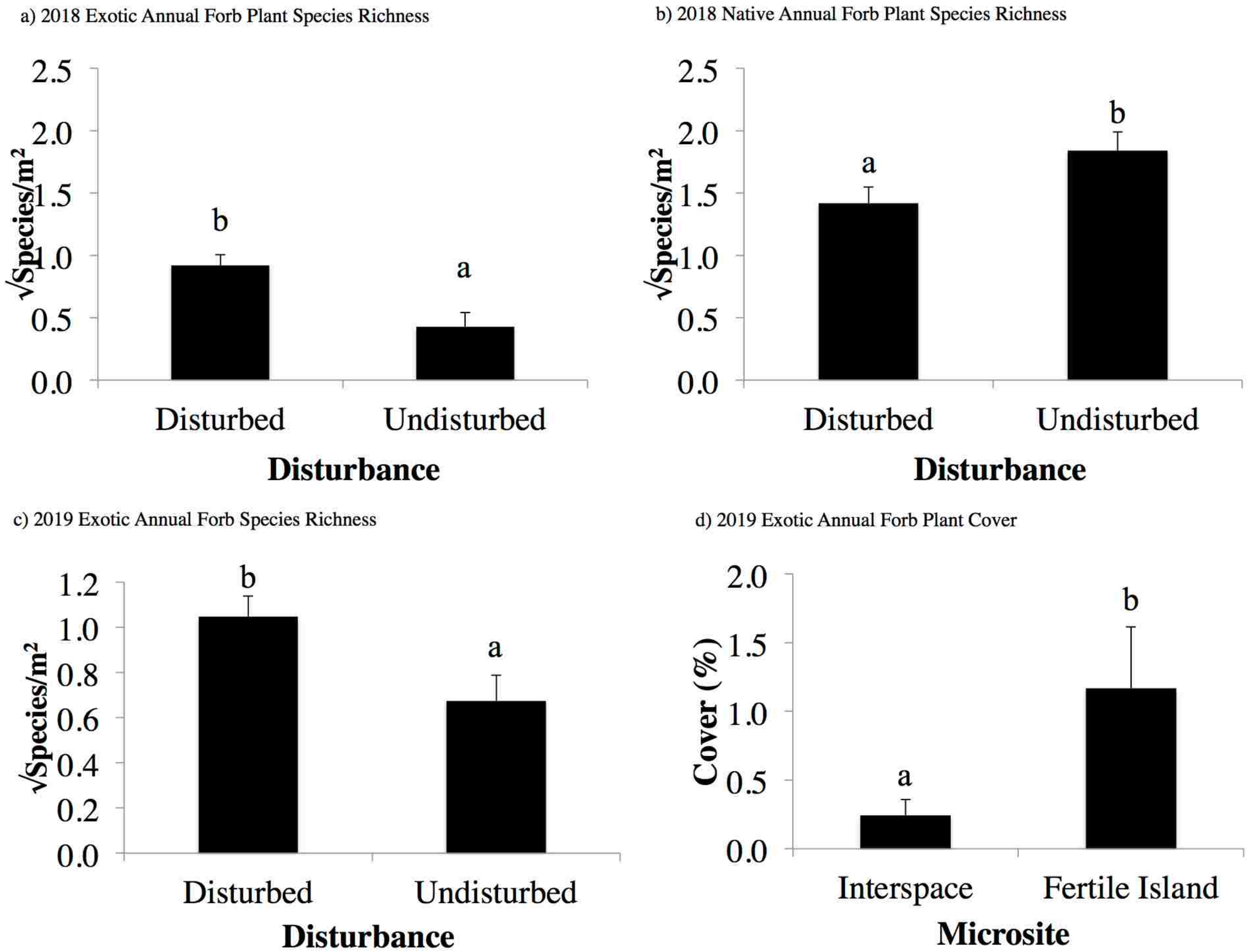
a) 2018 Total Forb Plant Cover

b) 2018 Total Forb Plant Species Richness



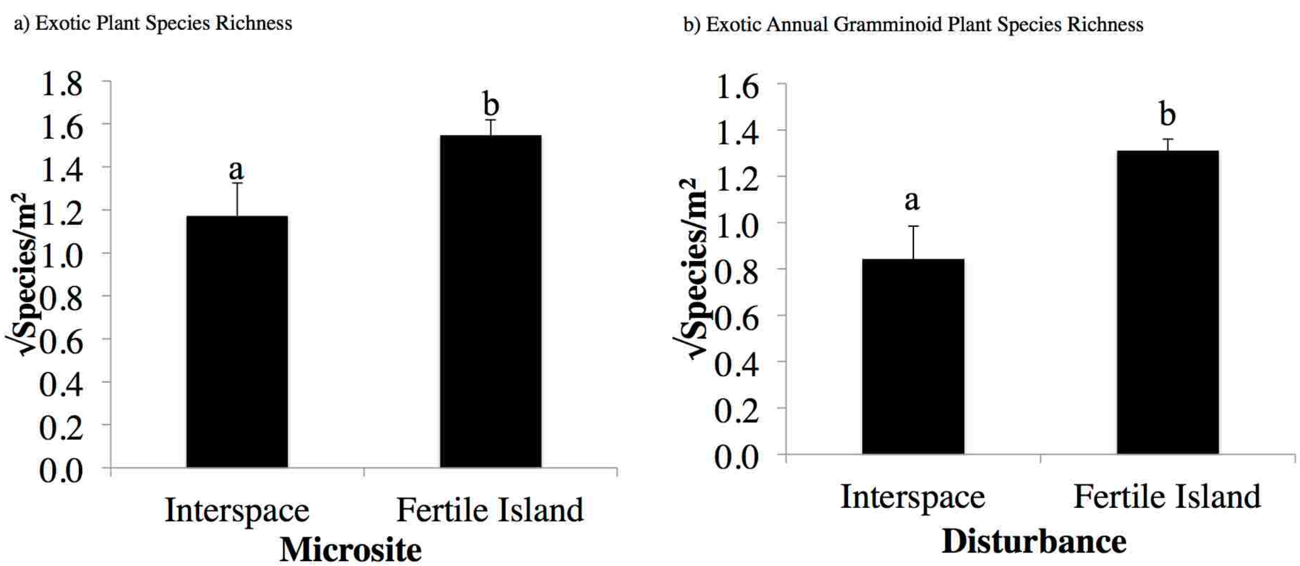
Means without shared letters differ at $p<0.05$. Error bars are one standard error of means. Species count was transformed to the square root of the number of species found per m^2.

Figure 8: Forb Cover and Species Richness



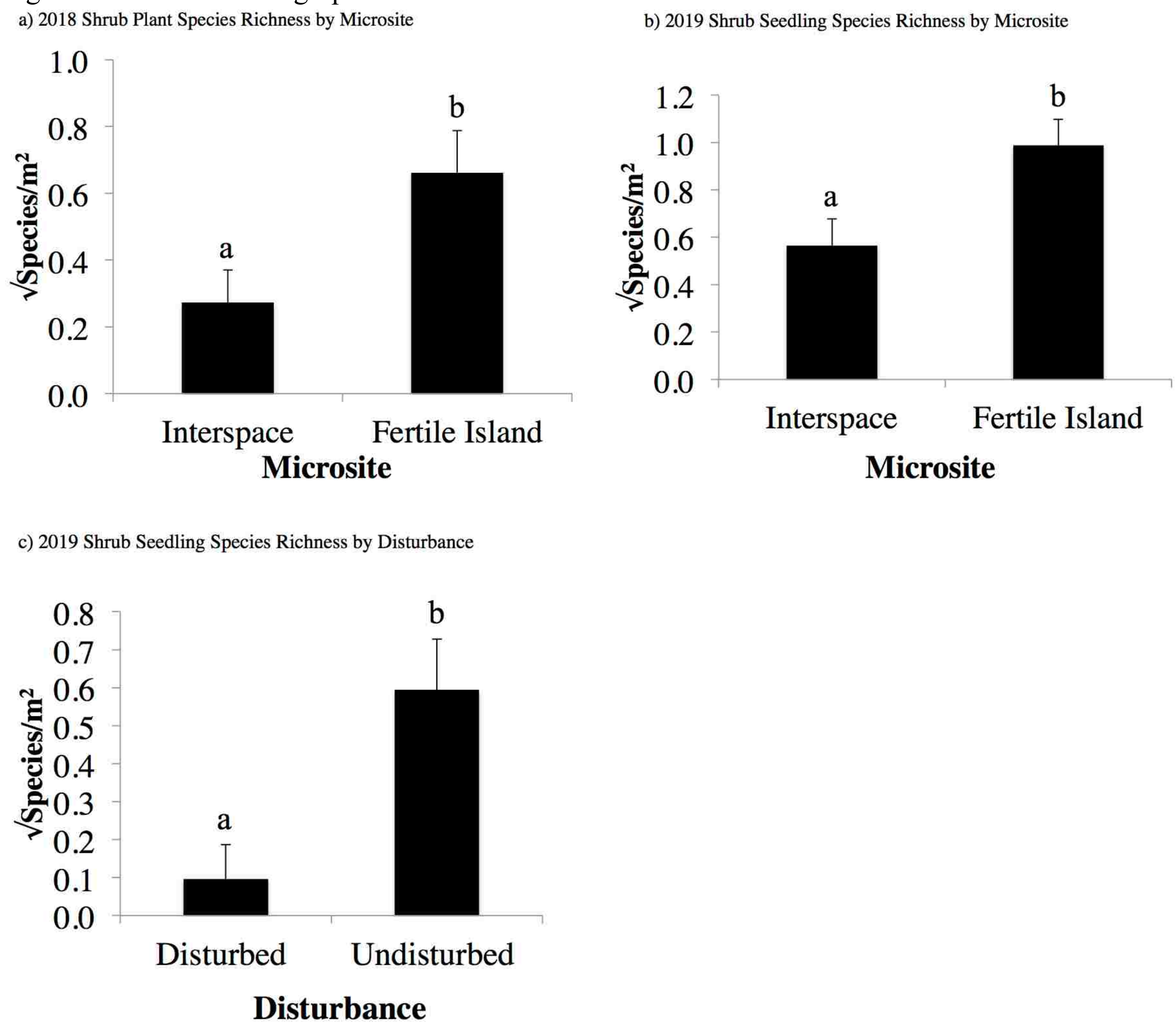
Means without shared letters differ at $p<0.05$. Error bars are one standard error of means. Species count was transformed to the square root of the number of species found per m^2.

Figure 9: 2018 Exotic Plant Species Richness



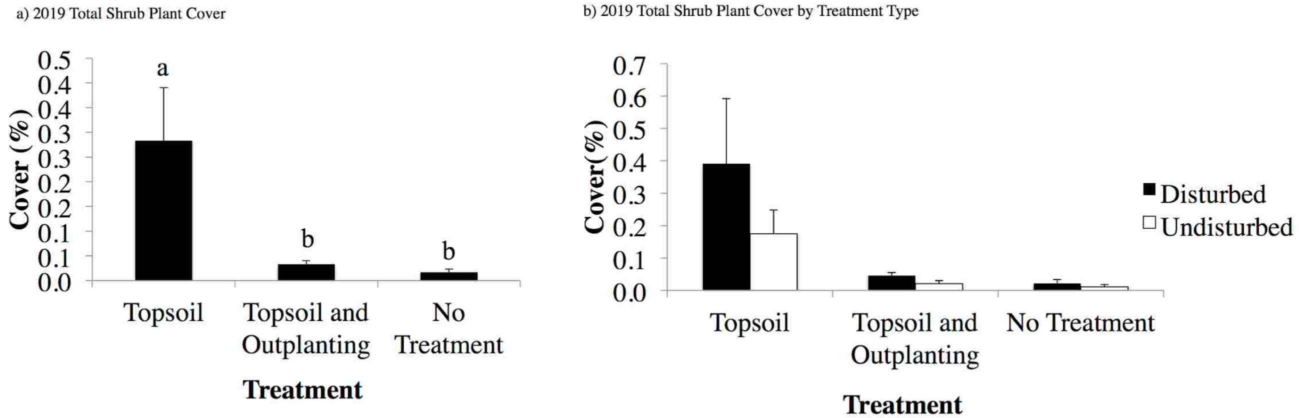
Means without shared letters differ at $p<0.05$. Error bars are one standard error of means. Species count was transformed to the square root of the number of species found per m^2.

Figure 10: Shrub Seedling Species Richness



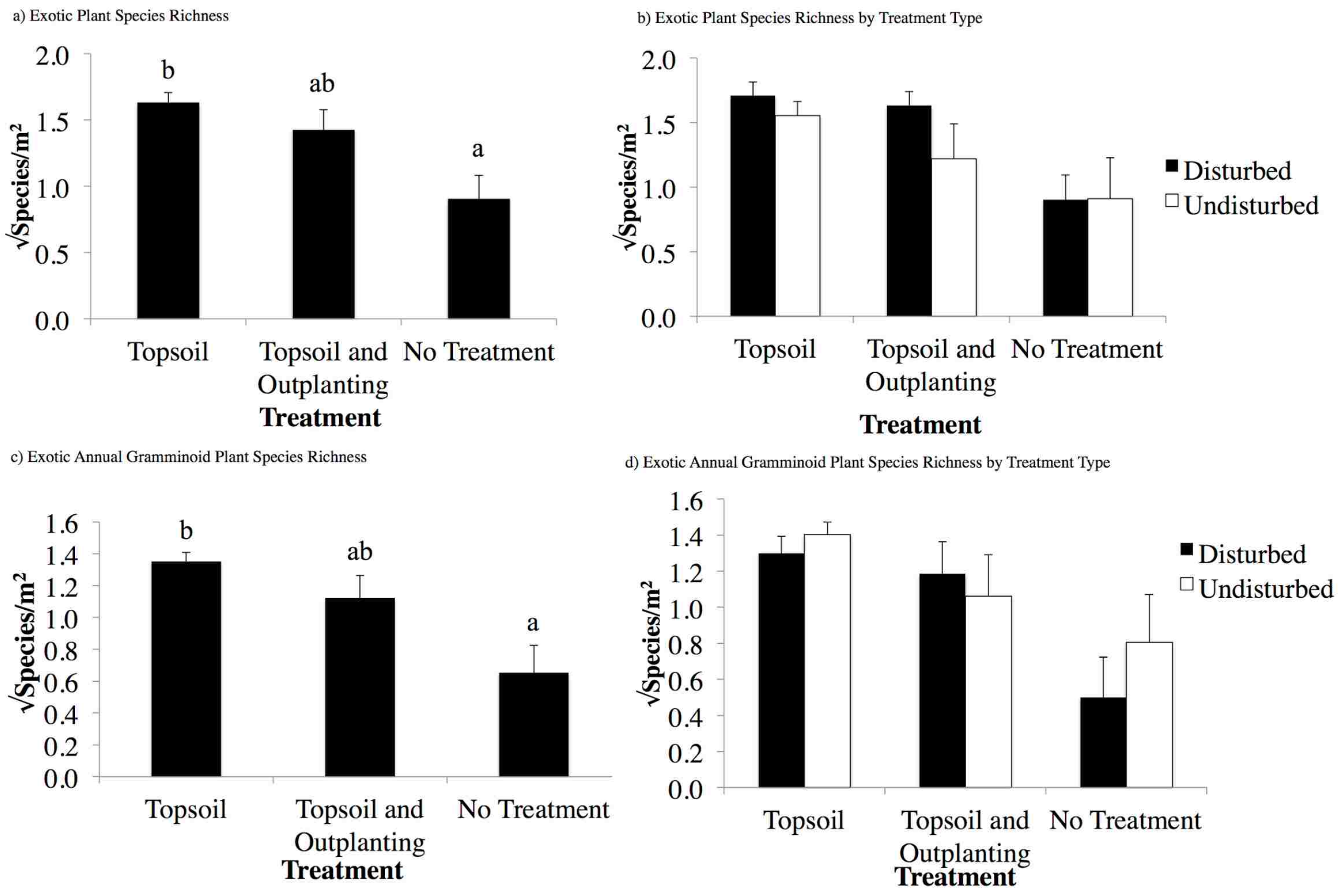
Means without shared letters differ at $p<0.05$. Error bars are one standard error of means. Species count was transformed to the square root of the number of species found per m^2.

Figure 11: Shrub Seedling Cover.



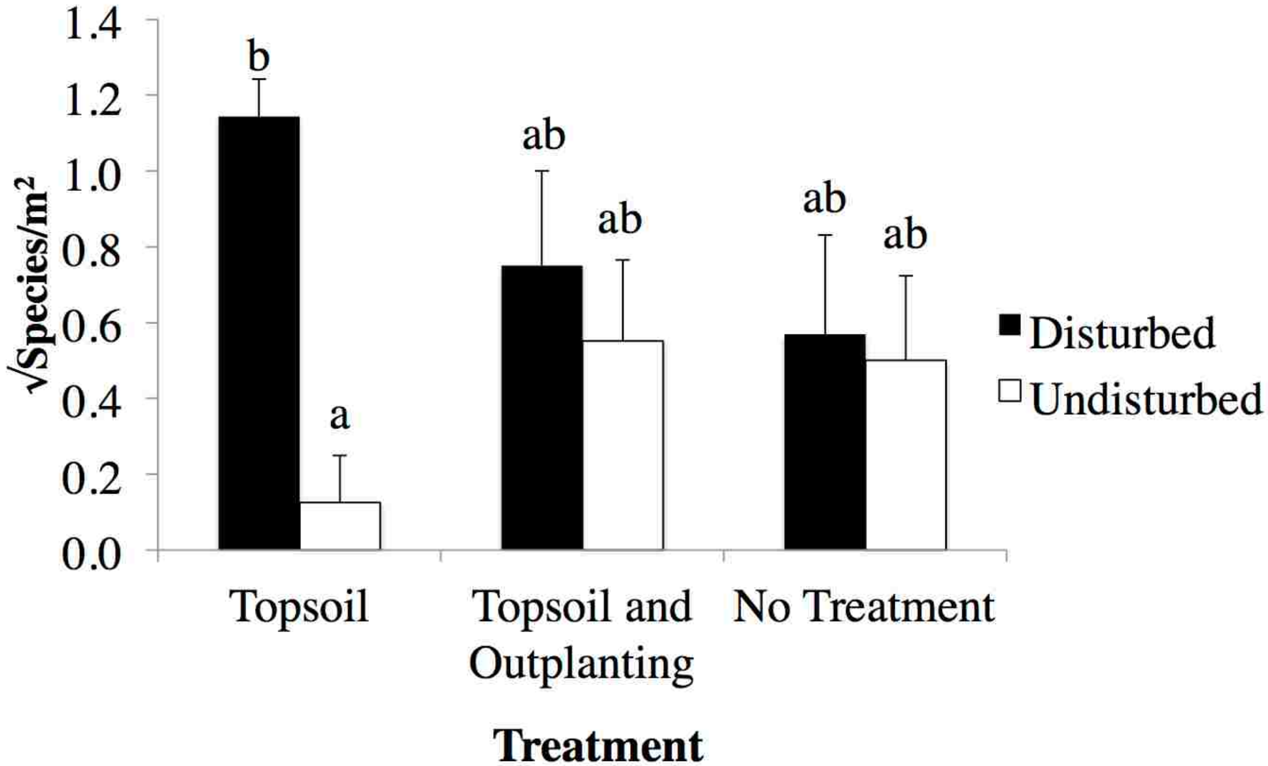
Means without shared letters differ at p<0.05. Error bars are one standard error of means.

Figure 12: 2018 Exotic Plant Species Richness and 2019 Exotic Annual Graminoid Species Richness Among Treatment Types



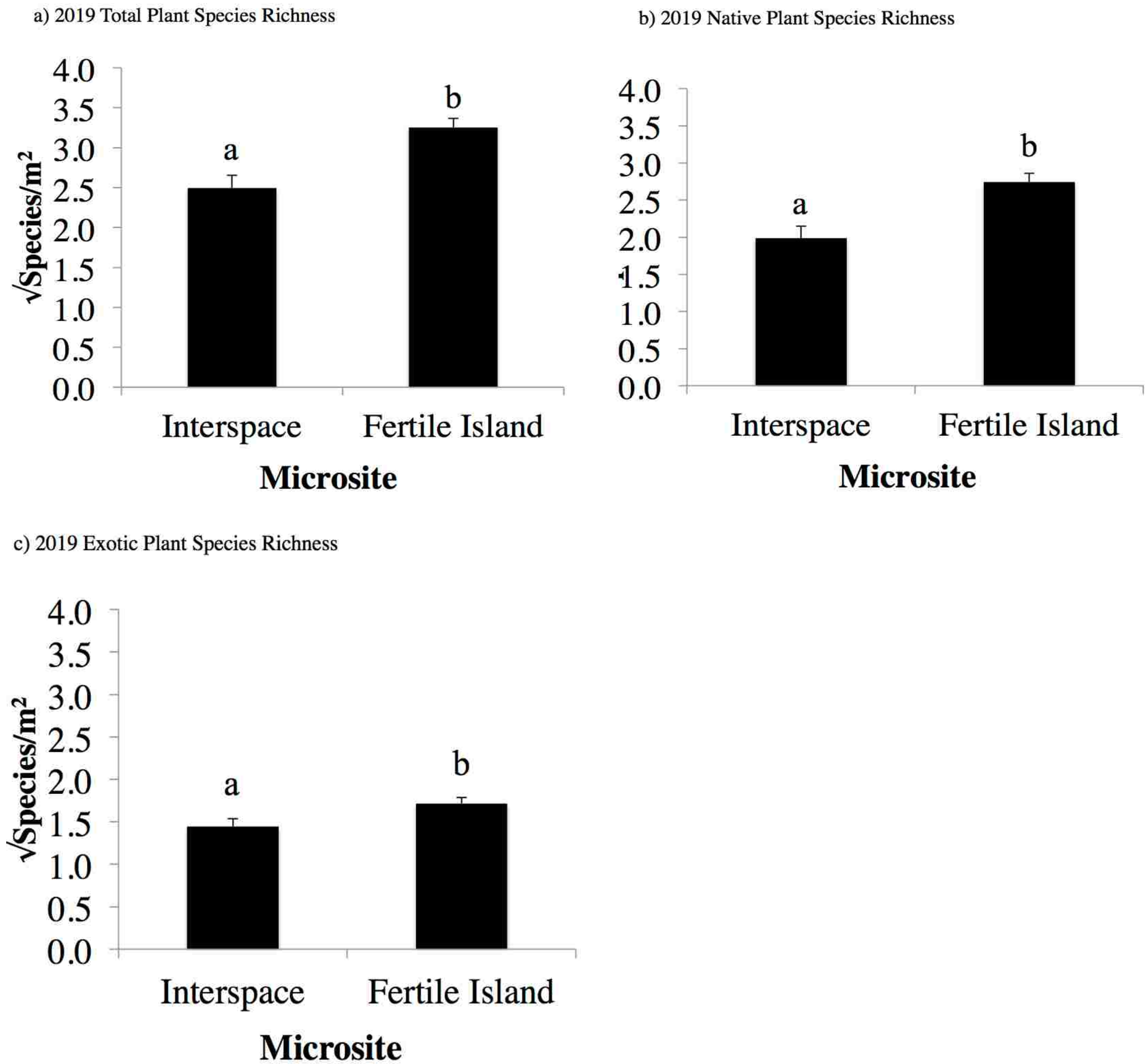
Means without shared letters differ at $p<0.05$. Error bars are one standard error of means. Species count was transformed to the square root of the number of species found per m^2.

Figure 13: Native Perennial Plant Species Richness.



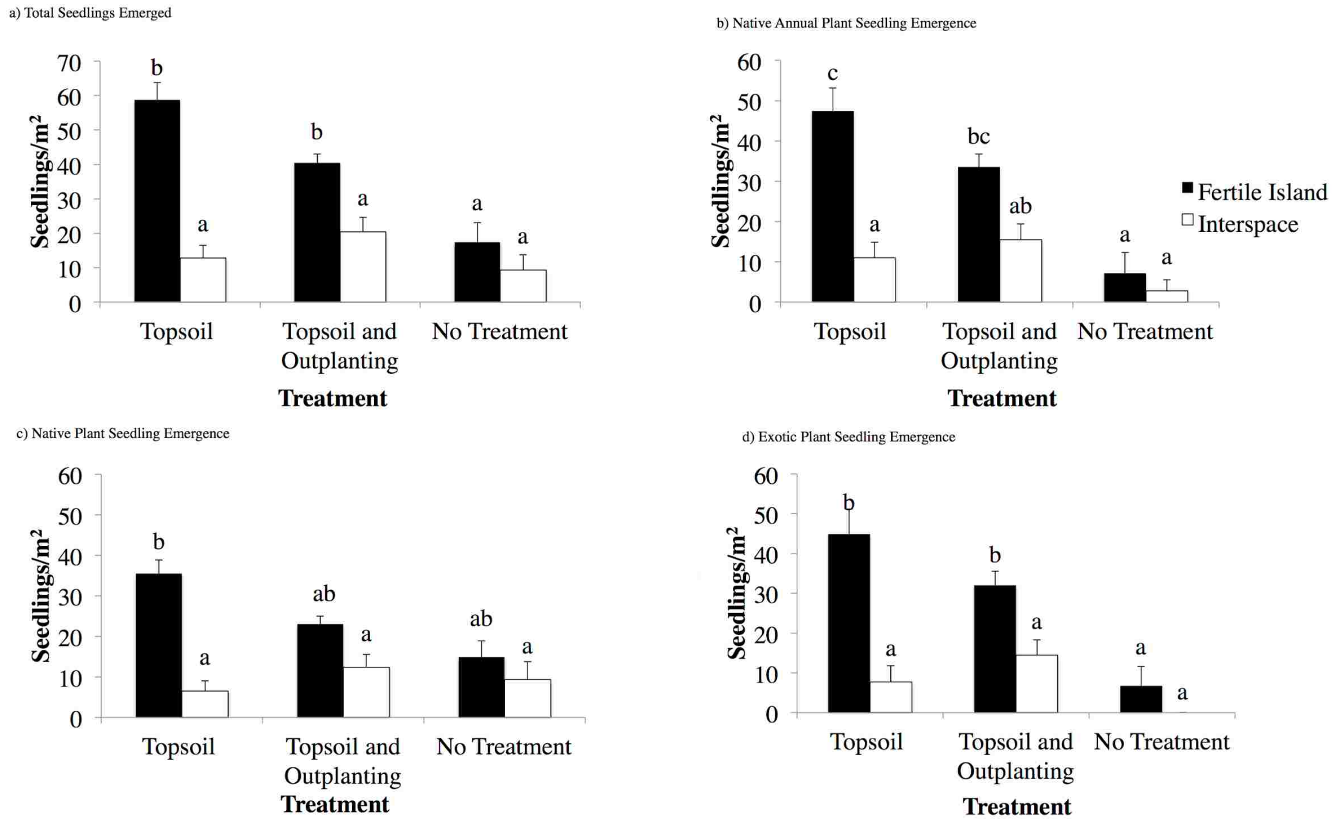
Means without shared letters differ at $p<0.05$. Error bars are one standard error of means. Species count was transformed to the square root of the number of species found per m^2.

Figure 14: 2019 Plant Species Richness.



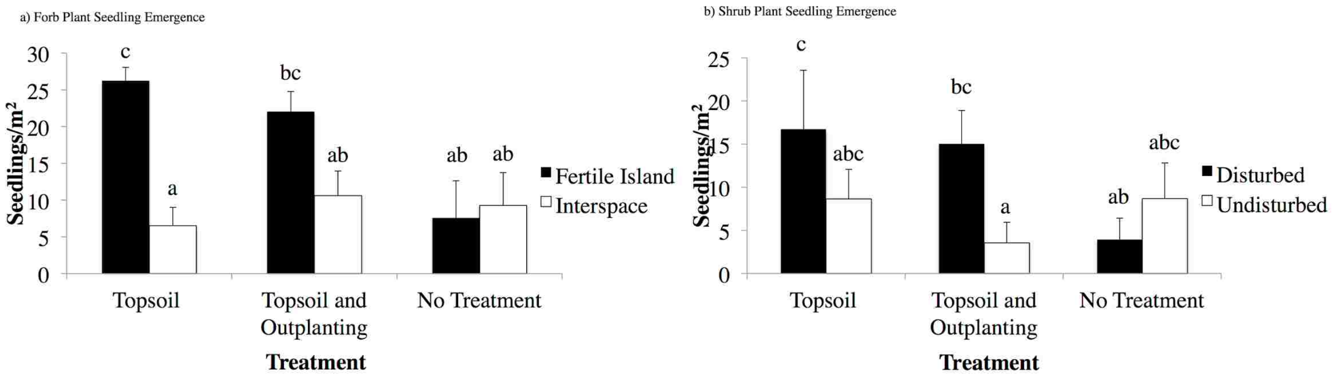
Means without shared letters differ at $p<0.05$. Error bars are one standard error of means. Species count was transformed to the square root of the number of species found per m^2.

Figure 15: Seed Bank Emergence.



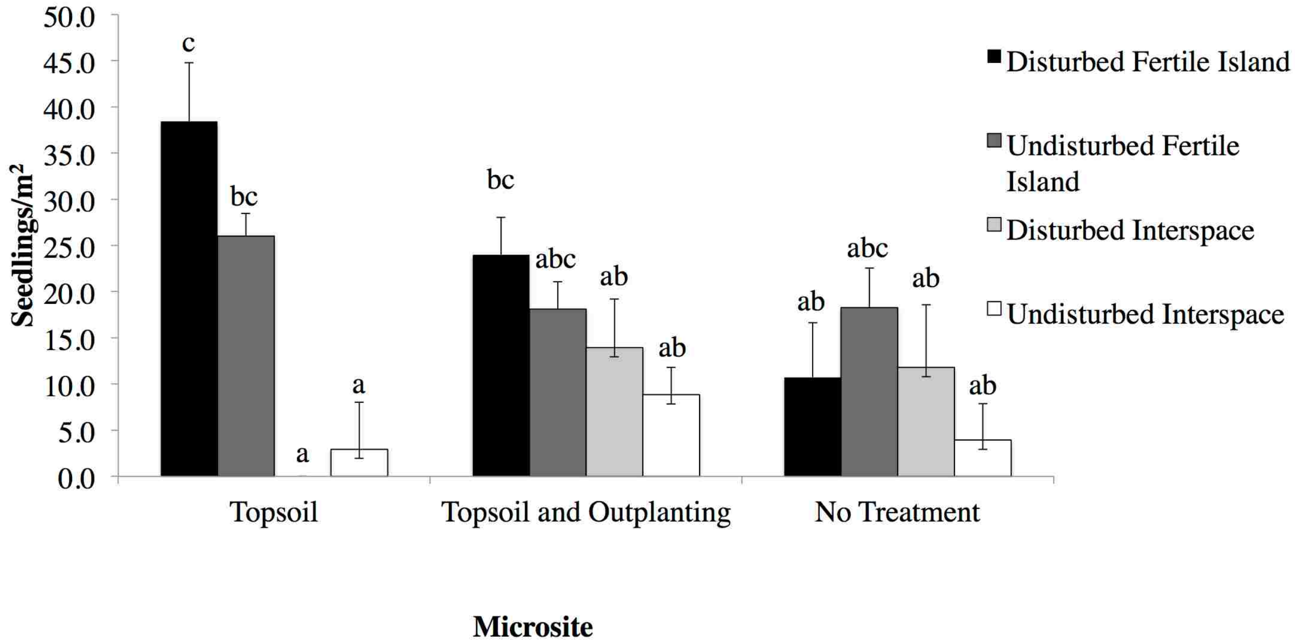
Means without shared letters differ at $p<0.05$. Error bars are one standard error of means.

Figure 16: Forb and Shrub Seedling Emergence



Means without shared letters differ at p<0.05. Error bars are one standard error of means.

Figure 17: Native Perennial Plant Seed Bank Emergence



Means without shared letters differ at $p<0.05$. Error bars are one standard error of means.

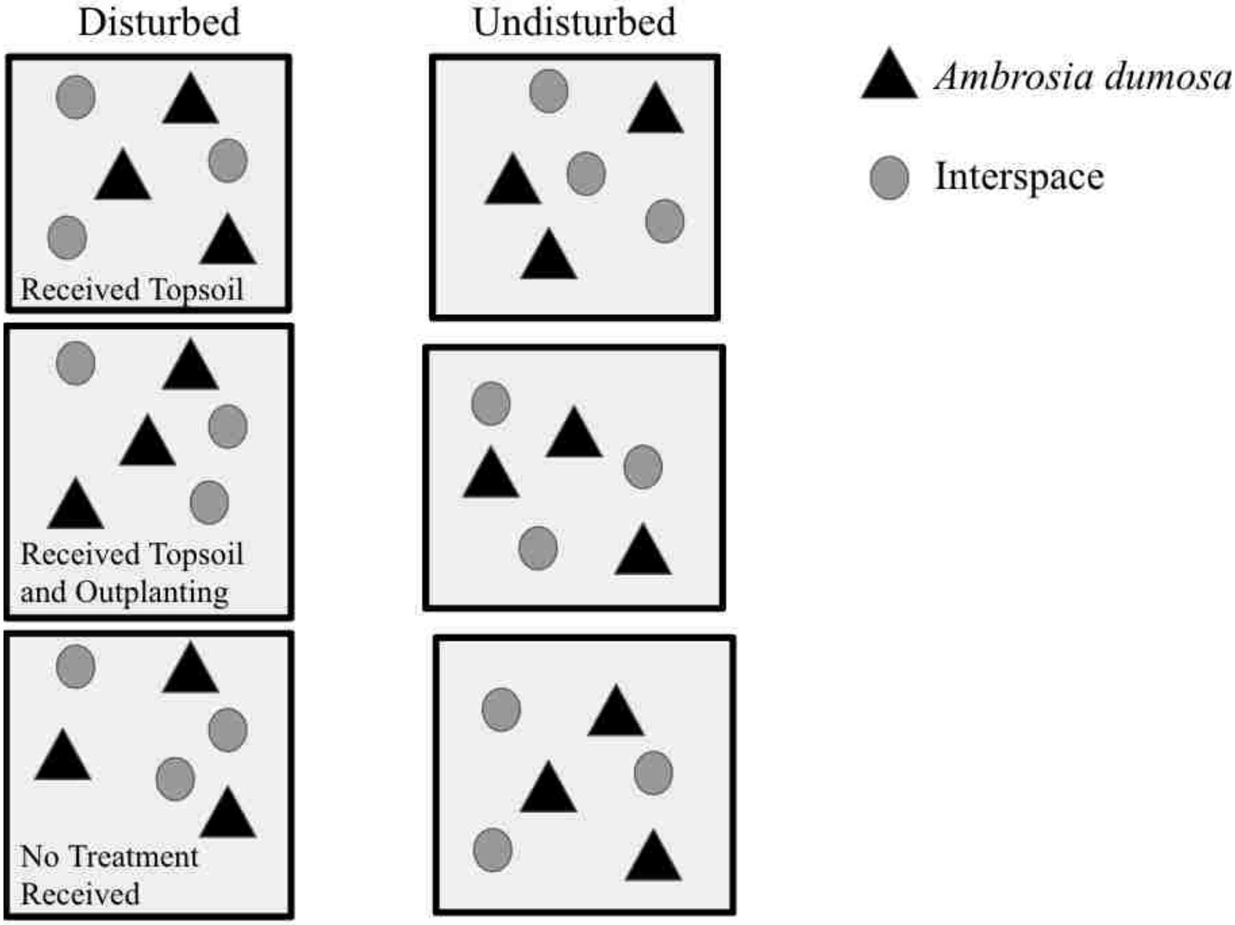
Figure 18: *Ambrosia dumosa* Shrubs Used for Fertile Island Measurement from Different Treatment Types

a) Topsoil Only

b) Topsoil and Outplanting

c) No Treatment

Figure 19: Experimental Design of the Types of Sites



This is a 3 factor nested design including disturbance status (2 levels: disturbed or undisturbed), restoration treatment (3 levels: received topsoil, received topsoil and outplanting, did not receive treatment), and microsite (2 levels: fertile island or interspace). This was applied to 11 sites where each site contained a disturbed/undisturbed pair. Each disturbed area had a restoration treatment (four sites received topsoil, four sites received topsoil and outplanting, and three sites received no treatment). While each undisturbed area did not receive a restoration treatment, the undisturbed area was paired with a disturbed area that had restoration treatment. In each area, as shown in diagram, there were three *Ambrosia dumosa* shrubs sampled to represent the fertile island, and three interspaces were sampled. The three values were then averaged together per site to have one value for each of these microsites (fertile island or interspace).

Curriculum Vitae

Camille Traylor

4505 S. Maryland Parkway
School of Life Science
University of Nevada Las Vegas
Las Vegas, NV 89118
Email address: traylor.camille@gmail.com

Education

University of San Francisco
B.S., Chemistry, May 2017

University of Nevada, Las Vegas
M.S., Biological Science, May 2019