Fall 2014

The Effects of Simulated *Spermophilus Franklinii* Burrowing on Prairie Soil Invertebrate Communities

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By
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B.S. Governors State University, 2012

THESIS

Submitted in partial fulfillment of the requirements

For the degree of Master of Science,
With a Major in Environmental Biology

Governors State University
University Park, IL 60466

2014

Acknowledgments:

I would like to thank Dr. John Yunger, Dr. Mary Carrington, and Dr. Tim Gsell for all of their help and advice throughout the work of this study. Without their guidance and time this would have never been achieved. I would also like to thank the Illinois Department of Natural Resources for approving this research and Jim Edgar Panther Creek Site Superintendent Mike Wickens for his advice and flexibility in helping choose the most appropriate plot locations. I would also like to thank my brother, Neal Brown, for all of the sweat and hours put in helping me set up my plots in the extreme heat in addition to the hundreds of soil cores taken. A very special thanks goes to the memory of Jon Mendelsson for his guidance and input throughout this thesis, you will be missed.

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Introduction

While the definition of disturbance can be debated, any form of disturbance within an ecosystem can change the structural and functional properties within that system (Whicker and Detling 1988). Disturbances can range from discernible events such as fires and floods to inconspicuous occurrences demonstrated in the underground development of an ant colony. Biotic disturbances, such as subterranean burrowing by small mammals, can alter an ecosystem both perceptibly as well as imperceptibly (Whicker and Detling 1988, Rogers et al. 2001, Kalisz and Davis 1992). This type of burrowing can transform both the physical and chemical properties of the soil (Miedema and Van Vuure 1977, Carlson and White 1988) in addition to the density, species composition and productivity of vegetation (Koide et al. 1987, Gibson 1989). Burrows of small mammals can also impact a variety of soil processes including organic matter turnover, and inorganic material distribution, aeration, and mineralization rates (Laundre and Reynolds 1993). Many studies have shown the effects of small mammal burrowing on overlying vegetation characteristics and soil chemical composition (Whicker and Detling 1988, Kalisz and Davis 1992, Rogers et al. 2001, Coppock et al. 1983) however there have yet to be any studies undertaken on the effects of subterranean burrowing on soil invertebrate community structure.

Environmental Disturbance

Definitions of disturbance vary; however a major theme involved in environmental disturbance is the destruction of biomass (Grime et al. 1987) leading to the opening up of space and consequently resources that can be utilized by new individuals (Roxburgh et al. 2004). A disturbance is usually considered to be an event having both a positive and negative aspect. The negative aspect is the complete or partial destruction of populations, while the positive aspect is an increase in availability of resources (Sommer 1995). Disagreement in attempting to define disturbance is often a result of the degree and mechanism of the disturbance, which may differ with respect to the community being studied (Floder and Sommer 1999). The effect of the disturbance depends upon size, frequency, time of occurrence, and intensity (Gibson 1989). It can be difficult to study the impacts of environmental disturbances due to their spatial size and magnitude of destruction, making them challenging to duplicate using a well-replicated design (Eberhardt and Thomas 1991).

One study of environmental disturbance by LaJeunnesse et al (2010) observed the effects of global climate change on the symbiotic relationship between dinoflagellates and reef building corals. This relationship between these two organisms is especially sensitive to environmental stress (particularly temperature); however the ecosystems within which they live have undergone major oscillations in global climate change in the recent past. It has been found that prolonged environmental changes, such as an increase or decrease in temperature, can affect the symbiotic relationship between these dinoflagellates and the corals. It raises the question of how such sensitivity to environmental stress allowed for their persistence through major environmental changes and ultimately how they will respond to predicted environmental warming in the near future. This type of study can bring about concerns for environmental trending and how preventative measures may be taken for negative effects of certain disturbances in the future.

Another study demonstrated small mammal regulation of vegetation structure in a temperate North American grassland savannah (Weltzin et al. 1997). They showed how black-tailed prairie dogs (*Cynomys ludovicianus*) can mediate the landscape of a natural area through suppression of certain woody species. What was found was that an increase in woody plant dominance in grasslands and savannahs could be explained by not only enrichment of atmospheric oxygen, changes in climate, livestock grazing and fire regimes but also corresponded to the elimination of black-tailed prairie dogs. They had showed that the prairie dog and the associated herbivores and granivores that coincide with their existence maintain grasslands and savannahs by preventing woody species from taking over native grasslands. Removal of prairie dogs from these areas generated woody species dominance as they were not suppressed by herbivory. This study showed how removal of a species (on purpose or incidentally) can have unintended effects on plant species composition and landscape structure.

Different forms of environmental disturbance can have major unintended effects on an ecosystem. They can destroy large communities of organisms which can have a chain reaction type effect, altering other characteristics of an ecosystem as well. Monitoring these types of ecological interactions can help manage environments for the future. It raises management concerns and hopefully aids in not only a reactive response to existing problems but also causes a proactive effort to prevent these types of issues in the future.

Effects on Plant Development

According to the gap dynamics theory (Smith and Huston 1989) and the regeneration niche concept (Grubb 1977), environmental disturbance such as the development of subterranean mounds and burrows should influence plant community structure by providing space for colonizer species to grow (Rogers et al. 2001). Initially, the formation of mounds inhibits live plants by suppressing their already established shoots (Huntly and Inouye 1988, Stromberg et al. 1996). However, the mounds eventually serve as gaps in vegetation sometimes enhancing germination in plant communities that are overcrowded and overgrown (Reichman and Seabloom 2002). It has also been found that the mortality of seedlings tends to be very high on mounds due to exposure to herbivores and dry soil conditions but if certain plants do survive there, they tend to be larger and produce more seeds than surrounding plants that are choked out in the overcrowded plant communities (Davis et al. 1995). Plant biomass is decreased dramatically directly over mounds and burrows, yet plants adjacent to the disturbances are found to benefit because of reduced competition for resources such as water, light and nutrients (Reichman and Seabloom 2002).

It is likely that gophers are important for maintaining and restoring the disturbance dependent aspects of native plant communities. In several studies it has been found that without the presence of pocket gophers, high soil fertility leads to increased plant biomass which ultimately reduces light availability at the surface. Pocket gophers have been found to uncouple this relationship by reducing biomass of plants through herbivory and production of mounds (Reichman and Seabloom 2002). This ultimately increases the heterogeneity of resources and results in a greater diversity of plant species (Huntly and Inouye 1988, Inouye et al. 1987). Rogers et al. (2001) found the effects of mounds and burrows on aboveground vegetation to be only temporary though, finding no statistical differences in variability in biomass after three growing seasons. Disturbances caused by burrowing have been found to significantly accelerate erosion and downslope soil movement on shallow slopes and inhibit them on steep slopes (Reichman and Seabloom 2002).

Intermediate Disturbance Hypothesis (IDH)

How species diversity is maintained in natural systems is one of the key questions in modern ecology. In 1960, Garrett Hardin proposed the competitive exclusion principle stating that coexistence of species cannot occur if they are competing for the same resource and all other ecological factors are held constant (in other words; complete competitors cannot coexist). The better competitor will eventually dominate long term, leading to the extinction of the other species or an ecological niche shift. Diversity maintenance is explained by factors such as niche differentiation or natural enemies, which reduce competition so exclusion does not occur (Floder and Sommer 1999). The intermediate disturbance hypothesis (IDH) states that the highest levels of organismal diversity are maintained at intermediate levels of disturbance (Paine and Vadas 1969, Connell 1978). The term has been used to predict that more species will result with an intermediate (rather than too frequent or rare) level of disturbance, regardless of whether or not this diversity can be maintained over the long term (Roxburgh et al. 2004). This hypothesis is based upon the idea that when disturbances are too rare, competitive species (k-selected) will dominate because they can typically outcompete other species for resources. If disturbances are too frequent, then opportunistic species (r-selected) will typically dominate and competitive species are at risk of going extinct due to faster recolonization by opportunistic specis. In either case, disturbances that are too frequent or too rare reduce species diversity by eliminating one or the other types of species. Species richness is maximized when disturbances are intermediate in frequency because intermittent disturbances suppress both opportunistic (high fecundity/early onset of reproduction/short generation time) and competitive (low fecundity/long life expectancy/larger body size) species, and allows for existence of both.

In Sommer's (1995) diagrammatical representation of the intermediate disturbance hypothesis (Fig. 1) he shows that a combination of frequent but weak disturbances (upper left corner of the diagram) is similar to an undisturbed steady state where small scale disturbances will lead to fluctuations that can be integrated into the lifespan of an organism. The combination of rare but strong disturbances (lower right corner) will lead to extinction of populations that cannot recover within the interval between disturbances. Sommer goes on to say if it is a combination of strong and frequent disturbances (upper right corner), no population will be able to survive and rare and weak disturbances (lower left corner) will be inconsequential and similar to an undisturbed steady state. This creates a diagonal angular section moving across the graph from frequent and weak to rare and strong in which you have opposing spectrums ranging from competitive exclusion to extinction and middle diagonal in between.

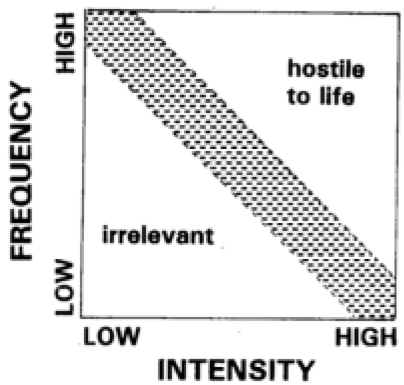

Fig. 1. Diagrammatical representation of the Intermediate Disturbance Hypothesis

However, it is debated whether or not the intermediate disturbance hypothesis results from a single mechanism or group of mechanisms that leads to stable coexistence of species. Some researchers suggest that the IDH is an oversimplified representation of a far more complex set of events that can enhance and erode diversity through various linked processes at a variety of scales (Sheil and Burslem 2003). Based upon the IDH theory, coexistence is promoted when disturbances recur through time at intermediate frequencies. Although "intermediate" can be defined based upon different temporal scales, the most important is the scale relevant to the generation times of different organisms (Padisak 1994, Wilson 1994). Roxburgh et al. (2004) states that in order for an inferior competitor to coexist with a superior competitor, there must be differences between the species in responses to disturbances.

Subterranean Burrowing

Soil is the major raw material used for burrow construction in most terrestrial habitats. Soil provides effective physical protection and also supports many plants and animals, primarily insects, that a variety of fossorial animals use (Reichman and Smith 1990). Mielke (1977) states "the activities of fossorial rodents may provide an explanation for the genesis of North American prairie soils." Certain burrowing animals have been labeled as ecosystem engineers because their physical activities modify or create certain habitats and alter resource availability for other organisms (Jones et al. 1994, Reichman and Seabloom 2002). Development of certain morphological, physiological, and behavioral traits such as powerful muscles for digging, tolerance of low oxygen and high carbon dioxide levels, and great sensitivity to soil vibrations helps these subterranean animals survive in this ecological niche (Nevo 1979, Narins et al. 1992). Evolutionarily, there are many advantages to developing the ability to burrow including shelter, maintaining a homeostatic environment, food storage and avoidance of desiccation (amphipods/amphibians) and predators (Reichman and Smith 1990, Holsinger and Dickson 1977). Some burrowing animals will build very extensive networks of connecting underground burrows and leave behind "tailings" in the form of mounds at the entrances and exits of their burrows (Anderson 1987, Reichman and Smith 1990, Benedix 1993). Mounds are believed to have an effect on the diversity of plants by having the ability to act as a catchment for seeds (Laycock 1958, McDonough 1974, Hobbs and Mooney 1995) and providing available space and resources for less competitive, colonizing species to establish themselves (Schall and Leverich 1982, Hobbs and Hobbs 1987, Goldberg and Gross 1988, Reader and Buck 1991, Davis et al. 1995). Burrow construction and soil displacement have been documented in some studies to alter plant species composition and community development (Davis and Kalisz 1992, Platt 1975) and in other studies to have a very minimal effect, if any on vegetation characteristics (Rogers et al. 2001).

The most prevalent effects of subterranean burrowing are the aboveground mounds produced while excavating and maintaining tunneling systems. Burrowing animals can displace massive amounts of soil every year thus altering both the soil structure as well as the biotic life associated with it. The tunneling activity, consumption and remains of plants and production of excrement all have direct and indirect, long and short term effects on other ecosystem components (Huntly and Inouye 1988). Subterranean burrowing has been shown to influence the physical environment by altering patterns and rates of soil development and nutrient availability, the geography of the landscape and the consequential abiotic environment (Huntly and Inouye 1988). The most significant effects observed over burrows results from the consumption of belowground plant parts (Anderson 1987, Reichman and Smith 1990, Benedix 1993). In some studies the flora recorded on gopher mounds typically differed from the surrounding vegetation (Hobbs and

Mooney 1985, Inouye et al. 1987, McDonough 1974) whereas in others the species were a subset of the dominant species in the undisturbed surrounding community (Rogers et al. 2001). It has been shown that more frequently forbs or annuals are more abundant on mounds (Inouye et al. 1987).

Energetic Costs to Burrowing

There are however energetic costs to burrowing that depend upon soil type, burrow structure, length of burrow segments, angle of ascent, depth of tunnels, and burrow diameter (Vleck 1981). Burrowing diameter and cost of burrowing increases with body size, while the benefits do not, so burrowing becomes less beneficial as body size increases. The maximum possible body size of fossorial mammals depends on habitat productivity and energy cost of burrowing in local soils (Vleck 1981). It costs from 360 to 3400 times as much energy to dig 1 meter as it does to walk 1 meter on the surface (Vleck 1979). Varying architectural characteristics of burrows such as depth, length, and complexity can also influence how much impact burrows have on soil processes; while soil properties are thought to affect burrow structure (Laundre and Reynolds 1993). In a study by Laundre and Reynolds (1993) *Spermophilus townsendii* were found to construct larger burrows in firmer, loamy soils. By increasing the depth, size, and complexity of burrows the size of the disturbance increases and thus the impact on soil processes increases as well. Ultimately, factors that influence burrow structure could determine the impact a burrow has on certain soil processes in that area.

Burrow Structure

The structure of burrow systems varies significantly among species (Reynolds and Wakkinen 1987, Reichman and Smith 1990). The spacing between adjacent burrows is very technically organized, producing an accurate buffering area in between created burrows (Reichman et al 1982). Ground squirrels are known to construct both “shallow” and “deep” burrows; shallow burrows of *Spermophilus townsendii* are classified as being less than 60 cm deep and *Spermophilus elegans* as being less than 90 cm deep (Reynolds and Wakkinen 1987). One study by Laundre and Reynolds (1993) looked at the effects of soil structure on burrow characteristics of five small mammal species: Townsend’s ground squirrel (*Spermophilus townsendii),* Wyoming ground squirrel (*Spermophilus elegans*), deer mouse (*Peromyscus maniculatus*), Ord’s kangaroo rat (*Dipodomys ordii*), and montane vole *(Microtus montanus*). They found characteristics affecting burrow structure included bulk density of soil (g/cm^3) and soil texture (percent silt, sand and clay) which had significant effects on burrow depth, volume, length, soil displaced and complexity. Their data supported the prediction that burrow characteristics are affected by soil properties with the greatest influence being seen on the Wyoming ground squirrel. They also concluded other factors influencing burrow components included length of occupancy as well as age and sex of burrow occupant (Laundre and Reynolds 1993). Their final conclusions indicated soil components do have an effect on burrow characteristics which in turn could affect soil processes.

Soil

Soil acts as the interface between the atmosphere, biosphere, and lithosphere (Jobaggy and Jackson 2001). It undergoes intense vertical exchange of physical and chemical materials through weathering, atmospheric deposition, leaching and biological cycling (Trudgill 1988) resulting in unique stratified gradients. Globally, the vertical ranking distribution among soil nutrients from shallowest to deepest is phosphorus, potassium, calcium, magnesium, sodium and chlorine (Jobaggy and Jackson 2001). Jobaggy and Jackson (2001) found that nutrients most strongly cycled by plants (phosphorus and potassium) were more concentrated in the topsoil than were nutrients that are less limiting to plants (such as sodium and chlorine). What they discovered was that plant cycling was the dominant factor influencing the vertical distribution of nutrients in soil. Leaching and biological cycling alter the vertical stratification of soil nutrients in opposite ways; leaching usually moves nutrients downward and biological cycling transports them in an upward direction towards the surface. Some processes contributing to nutrient cycling include uptake of nutrients by plants, litterfall and throughfall, and ecological disturbances such as subterranean burrowing.

Soil particles vary in size, aggregation and nature throughout the horizontal and vertical strata of the soil (Bongers and Ferris 1999). The heterogeneous nature of the soil allows for the existence of many different types of organisms filling different niches. Typically larger organisms create their own burrows whereas smaller organisms are generally aquatic and live in the water films between soil particles (Bongers and Ferris 1999). Gopher mound soil has been found to differ in soil characteristics such as texture and water-holding characteristics than that of surrounding undisturbed soil (Andersen 1987). Levels of various soil nutrients, including nitrogen, phosphorus, and potassium may be significantly higher (Koide et al. 1987) or lower (Inouye et al. 1987, Koide et al. 1987, McDonough 1974) in gopher mounds than in undisturbed soil. Soil nitrogen content varies with depth, with highest values near the soil surface, and content decreasing with increasing depth (Inouye et al. 1987). By constructing foraging tunnels, gophers displace nitrogen-poor subsurface soil on the ground surface in the form of mounds. This results in soil being redistributed and mixed thus creating patches of surface soil with lower than average nitrogen content and mounds with differing nutrient contents, moisture, water holding capacities and organic matter than areas between mounds (Litaor et al. 1996, Sherrod and Seastedt 2001). In addition to displacing soils, burrowing animals alter soil nutrient levels by leaving scraps of food in the burrows as well as excreting waste. Zinnel (1988) sampled soil above dens and food storages and found that total nitrogen in the top 60 cm of soil was significantly higher in the areas surrounding dens. Elevated soil nutrient levels near dens may result in increased levels of certain elements (e.g., nitrogen, sodium) in plant tissues and may also contribute to the different communities of soil invertebrates found around burrows. The movement of soil by erosion also has the potential to lower cation exchange capacity, pH buffering and pH levels (Sherrod and Seastedt 2001).

Temporal/Spatial Scales

At different temporal and spatial scales, burrows can have a variety of effects. Plant biomass overlying abandoned burrows can remain lower than undisturbed areas for several years due to impeded root regrowth and lower nutrient and water availability (Reichman and Smith 1985, Reichman 1988). Huntly and Inouye (1988) denoted the effects pocket gophers have on ecosystem processes at a variety of temporal and spatial scales. At about 1 week and 1 m^2, pocket gopher activity resulted in increased light penetration, soil resource alteration, decreased plant biomass, increased available resources, and new plant colonization sites. At around 1 year and 100 m^2 there was an increase in resource and topographic heterogeneity, plant species richness, variability in plant biomass, as well as an increase in microhabitats for consumers. Over the long term temporal scale (around 50 years) they found effects of altered soil fertility, altered rates and paths of succession, in addition to altered topography.

Soil Invertebrate Importance

Soil invertebrates are an extremely important and commonly overlooked component of natural ecosystems. Not only are they typically the most abundant (possessing the greatest biomass) in an ecosystem but they also form the base of the food chain; function in nutrient cycling; act as aerators, decomposers, and pollinators; provide tunnels for water movement; fertilize soil; mineralize nutrients; degrade toxicants; and function as indicator species through their presence or absence. Invertebrates are an ideal focus for studying disturbance effects because they are an important component of native ecosystems, are sensitive to environmental change, and are easily sampled in large numbers (Bromham et al. 1999). Environmental disturbances can cause changes in structure and composition of invertebrate communities (Majer 1983). Changes in soil structure can have effects on the properties of the soil including deterioration of soil structure, decreasing infiltration capacity (Abbot 1989), increasing runoff (Laycock 1989) and promoting soil erosion (Bromham et al. 1999). Modifying soil composition can result in changes in the flora and fauna of an environment and have true ecological consequences. Soil invertebrate communities are dependent upon each other for carbon as well as energy (Bongers and Ferris 1999). The structure of below-ground food webs is disrupted by environmental disturbances and changes in soil composition such as pollution, heavy metal contamination, mineral fertilizers and pesticides, and physical disturbance (Bongers and Ferris 1999). The consequences of these environmental disturbances however are unpredictable because they are dependent upon other factors as well such as the heterogeneous nature of the soil, fluctuations in abiotic conditions, chemical and physical capacities, and other biotic and abiotic interactions (Bongers and Ferris 1999).

Burrowing Effects on Other Organisms

Burrowing animals can also have effects on other organisms. Huntly and Inouye (1988) found that gophers have a positive effect on grasshopper abundance. They found that gopher mounds benefit grasshoppers because most grasshoppers oviposit in open soil with increased nitrogen levels where the probability of survival of eggs and young are the highest (Dempster 1963, Goldburg 1986). Abandoned burrows have also been shown to be used by other burrowing animals as well as amphibians and reptiles. Soil invertebrates have a major role in many ecological processes. In a study by Laundre (1993) the hypothesis that water infiltration into the soil can be increased with the presence of small mammal burrows was confirmed. Water recharge amounts in the soil were significantly higher in areas with burrows than adjacent areas without burrows.

One study by Regosin et al. (2003) compared population densities of spotted salamanders in areas containing small mammal burrows and areas without them. They found that these salamanders may be dependent upon the burrows for safety as the salamanders are unable to burrow themselves. Salamanders were more likely to abandon an area from which burrows had been removed, thus affecting overall salamander density and reproduction.

Soil Invertebrate Effects

Soil invertebrates can also have very noticeable effects on ecological succession within plant communities. Not only do vertebrate and herbivore interactions aboveground have effects on community structure but interactions belowground can also play a major role. One study had shown that soil fauna dramatically decreased root biomass, indicating major root herbivory occurring with effects increasing over time (De Deyn et al. 2003). In the same study, addition of soil fauna resulted in an increase in plant species diversity and a decrease in the total biomass of the dominant plant species. De Deyn et al. suggests that soil invertebrate root herbivores were selectively feeding on roots of dominant plants, helping to control the abundance of dominant plant species and increasing plant species evenness. Reduction in root biomass of dominant plants provided an indirect advantage for subdominant plant species to obtain more nutrients and have a better chance to grow and survive. Selective suppression of dominant plants can possibly be attributed to higher root quality and accessibility or to a lower tolerance to herbivory. Invertebrate communities change over time along with the succession of plant communities from early to mid and late successional stages.

Diversity Indices

A diversity index typically reflects how many different types (in this case, orders) there are in a certain dataset. It also takes into account how evenly the individuals are distributed among those order types. Diversity indices typically take the form of ratios, represented by the diversity present to the maximum possible diversity (occurring when each individual belongs to a different order). The values of the index increase both when the number of species increases as well as when the evenness increases. There are many types of diversity indices found in ecological literature including Simpson (1949), Shannon- Weiner (1949), Brillouin (1956), McIntosh (1967), and Hurlbert (1971), with the most widely used combining species richness with evenness (Peet 1975). Diversity indices are also frequently used because they stabilize mathematically after the most abundant species are included.

Natural History of Spermophilus franklinii

Franklin's ground squirrel (order Rodentia, suborder Sciurognathi, family Sciuridae, subgenus Poliocitellus, genus *Spermophilus,* species *franklinii*) is a subterranean mammal once found commonly throughout midwestern North America (Lewis and Rongstad 1992). Superficially, they resemble the eastern gray squirrel; however they have a shorter, less bushy tail and shorter rounder ears (Ostroff and Finck 2003). *S. franklinii* has a brownish gray coat speckled with pale and dark flecks. Franklins ground squirrels (*Spermophilus franklinii*) inhabit shrubby areas and woodland-field transition zones in central and north central United States and the prairie provinces of Canada (Murie 1973). They are found in Kansas, Missouri, northern and central Illinois, northwestern Indiana, Nebraska, Iowa, Minnesota, North Dakota, South Dakota, and southern Wisconsin (Lewis and Rongstad 1992). Their eastern range limit in the United States extends into northwest Indiana yet is dramatically declining (Johnson and Choromanski-Norris 1992). Their populations throughout this range are relatively discontinuous and sparse but high concentrations of animals have been reported (Sowls 1948). Franklin's ground squirrel is now rare over much of its range. One of the main reasons speculated for their declining numbers is the destruction of their preferred tallgrass prairie habitats due to urbanization and agricultural practices (Heske et al. 2001). Franklin's ground squirrel is a relatively large (475-568 mm length, 400-950 g weight) rodent that builds intricate tunneling systems and spends most of its time underground. A study by Martin and Heske (2005) observed the dispersal ability of Franklin's ground squirrels in a tallgrass prairie in Urbana, Illinois. In 2002 they trapped a small, isolated population of Franklin's ground squirrel in a 12 ha tallgrass prairie "island" surrounded by agricultural crop rows. Radiotracking of 14 juveniles showed that males dispersed farther than females, and all individuals moved farther than 1 km from the study site. Dispersal began around 9-11 weeks of age and occurred typically in late July and August.

Hibernation

From late June until the onset of hibernation, *S. franklinii* builds up a thick layer of fat (Choromanski-Norris and Fritzell 1986). Hibernation typically lasts 7-8 months (Kurta 1995) from August through April and during the 4-5 months of activity individuals reproduce and gain enough fat to survive the winter (Iverson and Turner 1992). Several individuals may hibernate together in the same burrow (Ostroff and Finck 2003). Males typically become inactive sooner than females because they do not have the energy expenses of gestation and lactation; females require more time to build up fat storages for hibernation (Iverson and Turner 1972). Juveniles gain mass faster than adults and usually weigh enough to enter hibernation by mid-September or early October (Sowls 1948, Iverson and Turner 1972, Murie 1973) but are typically later than adults to do so. Mating occurs from the time of emergence in spring until early June (Chomanski-Norris and Fritzell 1986, Iverson and Turner 1992). Photoperiod has been suggested to cue emergence from the burrows (Iverson and Turner 1972), males are typically the first from mid-April (Chomanski-Norris and Fritzell 1986) to early May (Reichart and Galloway 1994) coinciding with the establishment of dominance hierarchies (Kivett et al. 1976). Females typically emerge from the burrows 1-2 weeks after the males (Chomanski-Norris and Fritzell 1986).

Diet

Spermophilus franklinii is omnivorous and typically changes its diet based upon season. Diets comprise primarily vegetation, animal products, and seeds and fruit during spring, summer, and late summer, respectively (Jones et al. 1983). During the spring season, vegetable matter consumed mainly consists of succulent roots, herbaceous shoots, and grasses (Sowls 1948). The squirrels typically do not drink water because most of their water is derived from succulent plants (Sowls 1948). As the growing season proceeds they begin to feed on the shoots, leaves and buds of different plants: dandelion, sow thistle, stinging nettle, white clover, chokecherry, cultivated grains, red-berried elder, berries, fruit and stones (Sowls 1948). They will also feed on garden vegetables such as carrots, garden peas, potatoes, string beans and tomatoes and when animal products are available they will feed on insects, frogs, toads, fish, bird eggs, young birds, mice, rabbits, ants caterpillars, crickets, and grasshoppers (Fitzgerald et al. 1994, Jones et al. 1983, Kurta1995, Schwartz and Schwartz 1981).

Survivorship

The survivorship curve of Franklin's ground squirrel is representative of a type II curve, meaning survival rates are independent of age (Erlien and Tester 1984). Typical life expectancy of females is 4-5 years whereas that of males is only 1-2 years (Erlien and Tester 1984). The main predators of *S. franklinii* are badgers (*Taxidea taxus*), coyotes (*Canis latrans*), hawks, long-tailed weasels (*Mustela frenata*), mink (*Mustela vison*), red foxes (*Vulpes vulpes*), short-tailed weasels (*Mustela erminia*), snakes, and striped-skunks (Haberman and Fleharty 1972, Jones et al. 1983, Kurta 1995). *S. franklinii* live in burrows with complex branching tunnels typically about 8 cm in diameter that extend about 45 cm belowground (Haberman and Fleharty 1972). One branch consists of a nesting area approximately 30 x 25 x 20 cm that is padded with dried plant material (Haberman and Fleharty 1972), whereas other tunnel branches have dead ends and may usually include storage areas for food (Jones et al. 1983) or feces (Schwartz and Schwartz 1981). Burrows are usually built on steep slopes for drainage and typically have two to three entrances to allow escape from predators (Haberman and Fleharty 1972). *S. franklinii* is strictly diurnal (Chomanski-Norris et al. 1989, Sowls 1948); in North Dakota the squirrels become active between 0750 and 0900 hours and reenter burrows between 1900 and 2100 hours (Chomanski-Norris et al. 1989). *S. franklinii* lives alone or in pairs and is highly secretive (Jones and Birney 1988).

Conclusion

As demonstrated in this literature review, the effects of environmental disturbance on natural processes in ecosystems are extremely important to understand. From the smallest disturbances such as subterranean burrowing to the largest wildfires, understating how disturbances are affecting our remaining ecosystems will help to preserve them. Franklin's ground squirrel is only one example of the many animals that are disappearing due to urbanization. All over the world destruction of natural habitat is occurring and if something is not done to combat this problem the effects can be irreversible. Habitat destruction, invasive species, population growth, pollution and overexploitation are all major contributors to the environmental problems occurring today. Studying these issues will help us understand what effects they are having on the environment and what we can do to prevent their destructive consequences. Although each independent study may only tell a little bit of the entire story, every piece of information contributes to the overall wealth of knowledge that continues to grow with every experiment performed.

SYNTHESIS OF RESEARCH

Abstract. Burrowing of subterranean mammals can have ecological effects on overlying vegetation, invertebrate communities, and surrounding soil characteristics. Franklin's ground squirrel (*Spermophilus franklinii*) is a declining, tunneling mammal species previously found throughout Central Illinois. Preference for natural tallgrass prairie habitat with loose soil marks Illinois as the southern extreme of their range. Through urbanization and agricultural practices this species' population numbers have declined dramatically in southern and central Illinois. This study looks at the effects simulated Franklin's ground squirrel burrows have on soil invertebrate composition, abundance, and diversity by comparing effects of the presence/exclusion of burrows, animals, and their interactions. Through experimental plot manipulation we discovered that simulated burrowing has limited effects on soil invertebrate abundance. However, it's most pronounced effects were found at the entrance of the burrow where abundances were 33% to 50% lower than all other sampling locations. Interactive effects of burrow and animal also had an effect on Homoptera and Coleoptera abundance, only when burrow and animal were present simultaneously. The independent presence of an animal was also shown to have an overall effect on soil invertebrate diversity. Future research is recommended to look at the effects of simulated burrowing on plant community composition as well as soil characteristics and attempt to unite all three factors.

Key words: soil invertebrates; disturbance; subterranean burrowing; hymenoptera; soil cores.

INTRODUCTION

Environmental disturbance is any form of natural or unnatural perturbation that causes a physical change in the structure of a population, community, or ecosystem. The resulting environmental effects depend upon size, frequency, time of occurrence, and intensity of the disturbance (Gibson 1989). Disturbances can range from large wildfires and floods to small development of ant colonies. The intermediate disturbance hypothesis predicts that species richness is maximized when there is an intermediate level of disturbance (Huston 1979). When disturbances are rare, competitive species (k-selected) will dominate because they can typically outcompete other species for limiting resources. If disturbances are frequent, then opportunistic species (r-selected) will generally prevail and competitive species are at risk of going extinct. Species richness is maximized when disturbances are intermediate in frequency because intermittent disturbances suppress both opportunistic and competitive species and allow coexistence. Frequent, extreme disturbances can lead to destruction of ecosystems, permanently altering the landscape, flora, and fauna of an area.

One form of environmental disturbance is burrowing by subterranean animals. There are a wide variety of burrowing animals including mammals, reptiles, amphibians, birds, insects, and aquatic animals; but larger, more extensive burrowing systems are frequently characteristic of mammals. Some burrowing animals will build very comprehensive systems of connecting underground burrows and leave behind mounds of excavated soil at the entrances and exits of their burrows (Anderson 1987, Reichman and Smith 1990, Benedix 1993). The destruction of biomass caused by burrowing will increase availability of resources that can be utilized by new individuals. There are many advantages to burrowing including shelter, maintaining a homeostatic environment, food storage and avoidance of desiccation (amphipods and amphibians) and predators (Reichman and Smith 1990, Holsinger and Dickson 1977).

The actions of burrowing animals may provide an explanation for the creation of North American prairie soils (Mielke 1977). Soil provides effective physical protection and also supports many plants and animals that a variety of fossorial animals use (Reichman and Smith 1990). Animals burrowing beneath the surface of the ground can affect physical and chemical properties of soil (Miedema and Van Vuure 1977, Carlson and White 1988, Platt 1975). Burrows of small mammals can impact a variety of soil processes including organic matter turnover and inorganic material distribution, aeration, and mineralization rates (Laundre and Reynolds 1993). Environmental disturbances can also affect properties of the soil, causing deterioration of soil structure, decreasing infiltration capacity (Abbot 1989), increasing runoff (Laycock 1989) and promoting soil erosion (Bromham et al. 1999). Modifying soil composition can result in changes in the flora and fauna of an environment and have significant ecological consequences.

Burrowing animals can affect the density, species composition, and productivity of vegetation (Koide et al. 1987, Gibson 1989). Gap dynamics theory (Smith and Huston 1989) and the regeneration niche concept (Grubb 1977) predict that development of subterranean mounds and burrows should influence plant community structure by providing space for colonizer species to grow (Rogers et al. 2001). It is likely that burrowing mammals are important for maintaining and restoring the disturbance dependent aspects of native plant communities. The formation of mounds will initially inhibit live plants by suppressing their shoots which have already been established (Huntly and Inouye 1988, Stromberg et al. 1996). Mounds will, however, eventually serve as open patches in dense vegetation, sometimes enhancing germination in plant communities that are overcrowded and overgrown (Reichman and Seabloom 2002). The mortality of seedlings also tends to be very high on mounds due to exposure to herbivores and dry soil conditions. Plants that survive these conditions tend to be larger and produce more seeds than surrounding plants that show limited growth in crowded plant communities (Davis et al. 1995). Plant biomass decreases dramatically directly over mounds and burrows, yet plants adjacent to the disturbances are found to benefit because of reduced competition for resources such as water, light, and nutrients (Reichman and Seabloom 2002). In several studies, lack of burrowing by pocket gophers led to increased plant biomass which ultimately reduced light availability at the surface. Pocket gophers have been found to reduce biomass of plants through herbivory and production of mounds (Reichman and Seabloom 2002). These actions ultimately increase the heterogeneity of resources and result in a greater diversity of plant species (Huntly and Inouye 1988, Inouye et al. 1987). Rogers et al. (2001) found the effects of mounds and burrows on aboveground vegetation to be only temporary, finding no statistical differences in variability in biomass after three growing seasons.

Environmental disturbances can also cause changes in structure and composition of invertebrate communities (Majer 1983). Soil invertebrates are an extremely important and commonly overlooked component of ecosystems. Not only are they typically the most abundant (both numerically and in terms of biomass) in an ecosystem but they also form the base of food chains, function in nutrient cycling, act as aerators, decomposers, pollinators, provide tunnels for water movement, fertilize soil and function as indicator species (Lavelle et al 2006). Invertebrates are an ideal focus for studying disturbance effects because they are an important component of native ecosystems, are sensitive to environmental change, and are easily sampled in large numbers (Bromham et al. 1999). Soil invertebrate species are dependent upon each other for carbon as well as energy (Bongers and Ferris 1999). Any changes in soil structure can result in changes in corresponding invertebrate communities. A study of environmental disturbance showed that mowing resulted in a decrease of soil invertebrate abundance collected when compared to unmowed areas (Callaham et al. 2003). Alternatively, another study by Bromham et al. (1999) demonstrated that ground invertebrate fauna increased from ungrazed woodland, to grazed woodland, to grazed pasture. This trend was attributed to an increase in the most abundant orders whereas the less abundant orders showed an opposite pattern (less disturbed areas resulted in greater abundance). Ungrazed woodlands also had a higher diversity of invertebrates, most likely attributed to a larger diversity of food and habitat as a result of less disturbed vegetation.

Previous studies have shown the effects of small mammal burrowing on overlying vegetation characteristics and soil chemical composition (Whicker and Detling 1988, Kalisz and Davis 1992, Rogers et al. 2001, Coppock et al. 1983) and other studies have looked at the effects of mowing (Todd et al. 1992, Seastedt 1985), fire (Callaham et al. 2003) and grazing (Bromham et al. 2009) on soil invertebrate communities. This is however the first study to attempt to connect the effects of burrowing to soil invertebrate communities. This study focuses on the subterranean burrowing effects of simulated *Spermophilus franklinii* (Franklin's ground squirrel) burrows on soil invertebrate communities. Franklin's ground squirrel is a species of subterranean mammal once commonly found throughout midwestern North America (Lewis and Rongstad 1992) and is now rare over much of its range. They develop extensive burrow systems with mounds of soil at burrow entrances. Their declining numbers have been attributed mainly to the destruction of their preferred tallgrass prairie habitats (Heske et al. 2001). Franklin's ground squirrel is a relatively large (475-568 mm, 400-950 g), grayish-brown, inconspicuous species which builds underground tunneling systems and spends most of its time below ground. Their burrows range from simple to complex in structure but seldom vary in depth (45 cm) and diameter (8.25 cm) (Haberman and Fleharty 1971). Burrows typically have several branches. One branch consists of a nesting area approximately 30 x 25 x 20 cmthat is padded with dried plant material (Haberman and Fleharty 1972), whereas other tunnel branches have dead ends and usually include storage areas for food (Jones et al. 1983) or feces (Schwartz and Schwartz 1981). Burrows are usually built on steep slopes for drainage and typically have two to three entrances to facilitate escape from predators (Haberman and Fleharty 1972).

Trampling, feeding, fecal material, and wallowing are sources of intermediate disturbance in prairies. During historic times most of these disturbances have been removed. In prairie ecosystems, burrowing is an intermediate level disturbance. Following the intermediate disturbance hypothesis, I predict that soil samples taken in quadrats with the greatest disturbance (vole and burrow presence) will result in higher soil invertebrate diversity. I predict that sampling locations possessing the greatest disturbance (entrance of the burrow and mound or “tailing”) will result in lower total invertebrate abundance as compared to adjacent undisturbed locations. I also hypothesize that soil samples collected away from the burrows compared to less disturbed sampling locations associated with burrows (halfway between the entrance and deepest part of the burrow and deepest part of the burrow) will not show any significant difference in either abundance or diversity.

MATERIALS AND METHODS

Study Site

The study site was located at Jim Edgar Panther Creek (JEPC) State Fish and Wildlife Area (40°00′15” N 90°10’00” W), Cass County, Illinois. The area is owned by the Illinois Department of Natural Resources and is 6,698 ha of prairie and woods. JEPC has been restoring many parts of the non-native areas back to native grasses. JEPC provides a habitat for rich diversity of plants and animals which includes several endangered species. A large preponderance of native forbs and grasses characteristic of *S. franklinii* habitat was chosen for experimental manipulations. A relatively high proportion of native plants further representing *S. franklinii* habitat made for an ideal landscape for this study. Common native plant species found at this site include *Andropogon gerardii* (Big Bluestem), *Schizachyrium scoparium* (Little Bluestem), *Bouteloua curtipendula* (Side Oats Grama), *Lithospermum incisum* (Fringed Puccoon), *Ruellia humilis* (Wild Petunia) and *Silphium terebinthenacium* (Prairie Dock). Common carnivores at JEPC include *Canis latrans* (Wild Coyote), *Vulpes vulpes* (Red Fox) and *Urocyon cinereoargenteus* (Gray Fox). Soil composition and depth were important factors in choosing plot locations. Because Franklin’s ground squirrel is a relatively weak digger neither compact soil nor dolomite prairie could be chosen for replication of the burrowing systems. According to the United States Department of

Agriculture (NRCS 2003) the study site is located on Beardstown loam which is a mix of loamy and sandy alluvium with the organic matter content in the surface layer to be between 2.0 and 4.0 percent.

Experimental Design

Experimental plots were constructed in June 2013. Eight, 10 m x 10 m plots were randomly positioned throughout the field site. The 10 m x 10 m plots were subdivided to create 4, 5 m x 5 m quadrats. A 45.7 cm deep x 10 cm wide trench was dug between adjacent quadrats and around the perimeter of the 10 m x 10 m plot. Hardware cloth (1.2 cm mesh size) was placed vertically 45.7 cm below ground and 45.7 cm above ground around two of the four quadrats in each plot, and soil was replaced after inserting the hardware cloth. The hardware cloth was inserted to help prevent usage of burrows and underground tunneling by other small burrowing mammals. This treatment was especially important for the exclusion of *Microtus* spp., which is abundant in this area and generally only burrows 20 cm below the surface (Davis and Kalisz 1992). Hardware cloth with 1.2 cm mesh size was chosen because *Microtus* spp. can pass through 2.5 cm cloth and any smaller may have excluded soil invertebrates.

A randomized block design was used in this experiment with each of the four quadrats representing a different treatment combination (subgroup) of two treatment factors: burrow (present or not) and mammal (present or not). The two openings (entrances) for each linear burrow were located 1.5

m from the edge of the quadrat as well as at least 1 m from each trenched edge to minimize edge effects (Fig. 2). Burrows were constructed with a gas powered auger using a 125 cm x 8.25 cm bit at an angle of approximately 30^{o}. Excavations at each end of the burrow resulted in a soil mound remaining atop the ground and near the entrance of the burrow. The burrows were joined in the middle at the deepest part, roughly 40 cm below the surface. The augur dimensions represent a similar diameter to the burrowing done by Franklin's ground squirrel and auguring was repeated several times throughout the study to imitate use of the burrow by the squirrel.

Data Collection

Data collection was conducted at four locations along the burrow: on the soil mound outside the burrow entrance, at the entrance of the burrow, halfway between the entrance and deepest part of the burrow, and at the deepest part of the burrow. Collection was performed using a soil corer with a 10 cm depth and a 7.6 cm diameter. At each of the four collection locations, three samples (soil cores) were taken. One sample was taken directly over the burrow or mound, one sample taken 1 m to the right of the burrow, and one sample taken 1 m to the left of the burrow in undisturbed areas (Fig 2). Soil cores were then placed in separate, individual zip lock bags for transportation to laboratory. Soil samples were then sifted through by hand in a plastic tray to collect all soil invertebrates found in soil core. After sifting by hand, the remaining soil was placed in a Burlese funnel system to ensure no invertebrates were missed by hand sorting. After removal from the soil, invertebrates were placed in ethanol for subsequent identification. Organisms were then identified to order and separated according to each soil sample. Experimental data were collected on two separate occasions: once in October 2013, 3 months post-burrow construction and once again in June 2014, during the summer season. Samples taken in October 2013 were during a drought.

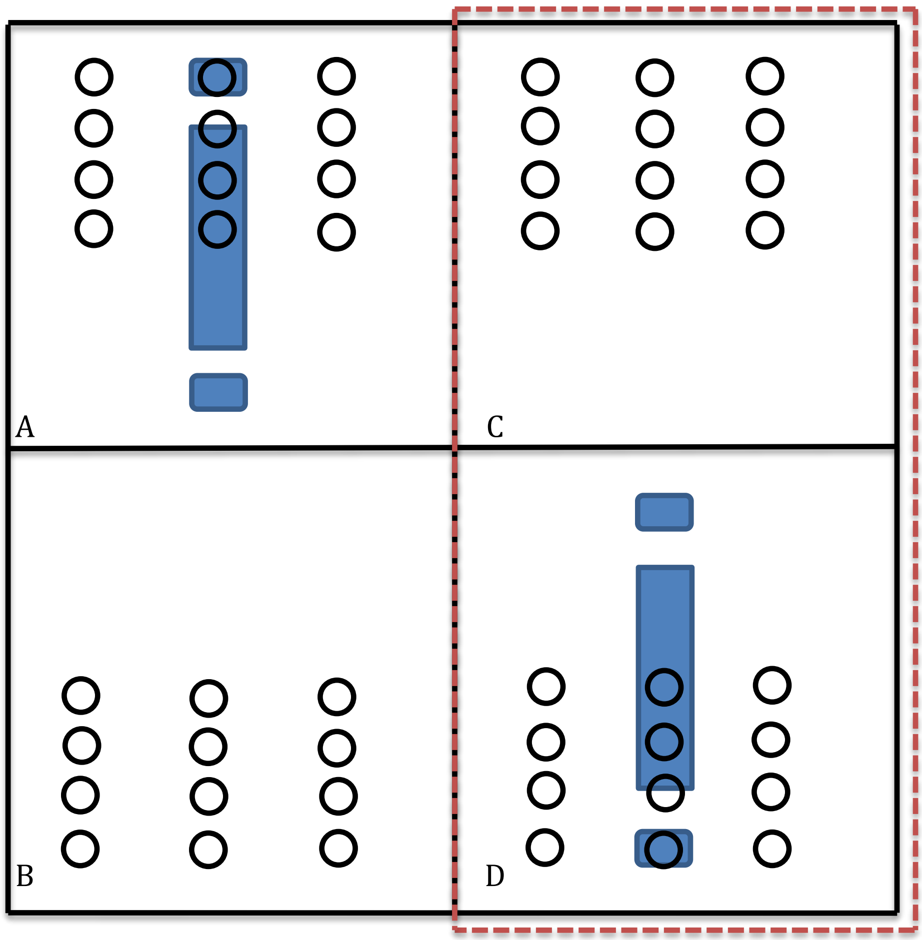

Fig 2. – 10 m x 10 m plot divided into 4- 5 m x 5 m quadrats, each quadrat representing a different experimental factor. A – yes burrow and yes animal B – no burrow and yes animal, C – no burrow and no animal, D – yes burrow and no animal. The dashed box represents the hardware cloth location and its semi-permeable nature.

Statistical Analysis

Invertebrate abundance was analyzed using MANOVA testing, with orders as response variables. This was a 2 x 2 factorial design with categorical variables being burrow and animal. Inference was based on type III sum of squares, with alpha = 0.1 using SAS/STAT® software (SAS Institute 2009). Shannon-Weiner diversity indexes were calculated for each quadrat. 1-way ANOVA testing was performed on individual abundances at each sampling location (8 locations), regardless of the order of invertebrates. In the event of a significant ANOVA, Student-Newman-Keuls test was performed as a post-hoc test to identify individual differences. Samples collected 1 m left and 1 m right for each location (mound, entrance, halfway, burrow) were averaged together for analysis.

RESULTS

During the two sampling periods, 768 soil cores were collected. These cores contained 316 invertebrates comprising 10 orders in fall 2013 and 974 invertebrates and 11 orders collected in spring 2014 (Fig. 3), for a total of 1,290 invertebrates in 13 different orders. Eight orders were collected in both years while of the remaining five orders, two were collected in 2013 and three collected in 2014. Nine different orders with the greatest abundances were included in statistical analysis: Hymenoptera, Haplotaxida, Hemiptera, Homoptera, Coleoptera, Isopoda, Aranea, Lepidoptera, and Dermaptera (Fig. 3). The other orders collected had insufficient abundances to be considered for analysis.

Invertebrate abundance during fall 2013 was not adequate for statistical analysis independently (values added to 2014 abundances and used in MANOVA). Total abundances for each order used in analysis are reported as separate fall 2013 and spring 2014 collections. 2014 values are higher in both individual orders as well as overall treatments (Fig. 3). Data for 2013 and 2014 show similar trends: Hymenoptera had the highest abundance, followed by Haplotaxida, Hemiptera, and Homoptera. The remaining orders, coleoptera, isopoda, araneae, lepidoptera, and dermaptera are all very similar in value and are interchangeable in succession between years (with the exception of 2014 Coleoptera, which was similar to Homoptera and Hemiptera).

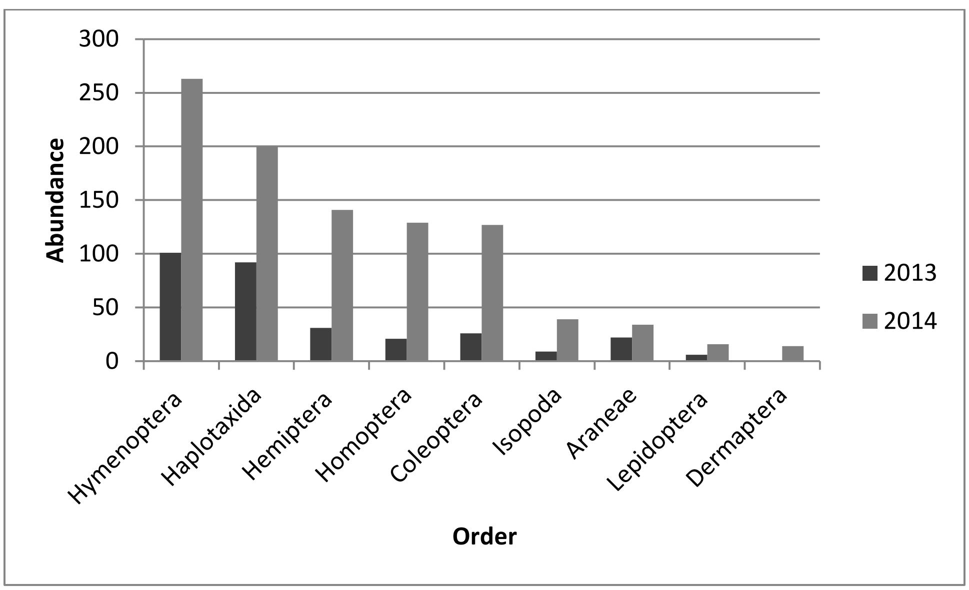

Fig. 3. Total invertebrate abundance collected by order

There was a highly significant difference in abundance among locations ($F_{7,248}$ = 9.47, P < 0 .0001). There were four distinguishable groups which were statistically significantly different from each other (Fig. 4). Sampling location halfway (A) had the greatest mean and was statistically significantly higher from meter halfway (B), meter deep (B), and entrance (C). Sampling location entrance (C) had the lowest of all the means and was significantly lower than all of the other sampling locations. Sampling location meter halfway (B) and meter deep (B) had the next lowest abundances and were statistically significantly lower than all other locations with the exception of entrance.

In both 2013 and 2014, total abundance among treatment groups were not statistically significantly different from each other (Fig. 5). Treatment and absence of treatment did not appear to have an effect on invertebrate abundances for either collection date. Abundances did vary between plots, however not intensely enough to cause significance.

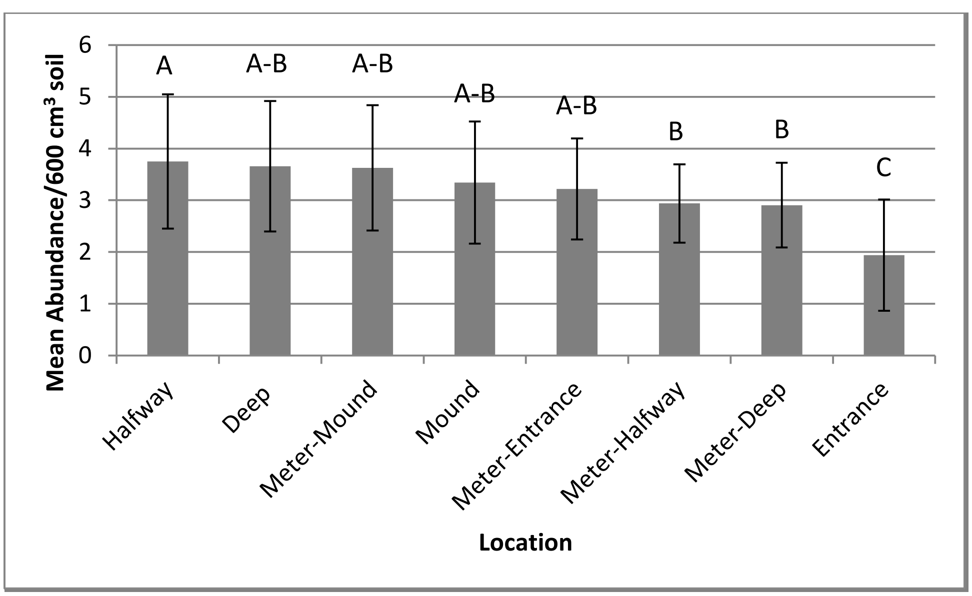

Fig. 4. – Mean abundance/600 cm^3 soil for each sampling location with standard errors.

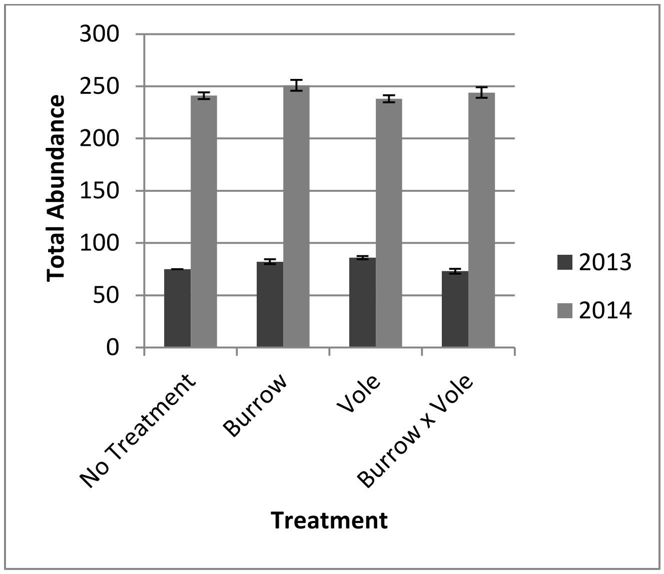

Fig. 5. 2013 and 2014 total invertebrate abundance as compared among the four treatment types.

In 2014, there were no significant treatment or treatment interaction effects on invertebrate abundance. They did however have significant effects on different orders for the three individual treatments. For simulated burrowing, some invertebrate orders were marginally significant. Wilks' Lambda test showed no overall burrowing effect for the experimental model ($F_{3,28} = 0.38$, $P = 0.9345$).

The presence of voles shows a statistically significant effect on the abundance of dermaptera in the soil ($F_{3,28} = 3.23$, $P = 0.0831$, Fig. 7A). There is an effect on dermaptera abundance when voles are present, irregardless of burrows. All other orders showed no statistically significant effects correlated to the presence of voles. Wilks' Lambda showed no significant overall effect of voles on invertebrate abundance and diversity ($F_{3,28} = 0.55$, $P = 0.8218$).

The presence of both burrows and voles has a statistically significant effect on homoptera ($F_{3,28}$ = 3.90, P = 0.05, Fig. 6B) and coleoptera abundance ($F_{3,28}$ = 3.68, P = 0.07, Fig. 6D). Analysis shows a significant effect caused by burrow/vole interactions. The two levels of burrow and vole presence/absence show an intersection indicating a significant effect when present together. The interaction plot for isopods is marginally significant with the presence of both voles and burrows ($F_{3,28}$ = 2.83, P = 0.10, Fig. 6C). Independently, neither variable is significant. The discrepancy in isopod abundance between the presence/absence of burrows and voles is not great enough to warrant significance. When burrows are absent; the invertebrate abundances collected comparing vole presence and absence are very similar, regardless of how great the variation is when burrows are present. This causes the difference to be non-significant.

Wilks' Lambda shows an overall burrow x vole interaction effect on invertebrate abundances ($F_{3,28}$ = 2.24, P = 0.06).

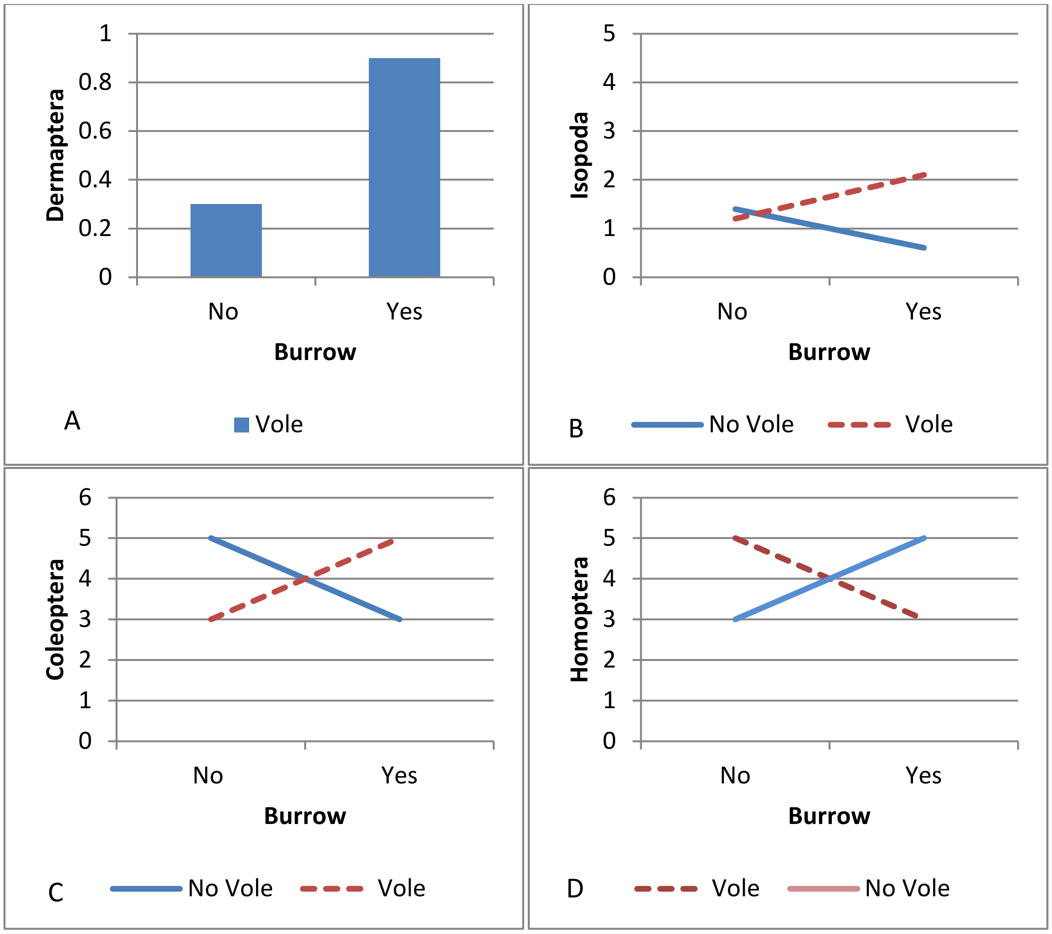

Fig. 6. Treatment effects showing significance on different invertebrate orders. A – Effects of voles on dermaptera abundance, B,C,D – Effects of burrow x vole interaction on isopoda, coleoptera, and homoptera abundance.

There were no significant effects on Shannon-Weiner diversity indices resulting from burrow ($F_{3,28}$ = 0.02, P = 0.90) or burrow x vole interaction ($F_{3,28}$ = 0.00, P = 0.98). There was a significant effect resulting from the presence of voles on Shannon-Weiner diversity indices ($F_{3,28}$ = 2.74, P = 0.10, Fig. 7). This results in refutation of the hypothesis that there would be an increase in soil invertebrate diversity in quadrats with. These results however support the hypothesis that the most disturbed areas will result in lower invertebrate abundance and undisturbed locations will not show any differences in abundance or diversity.

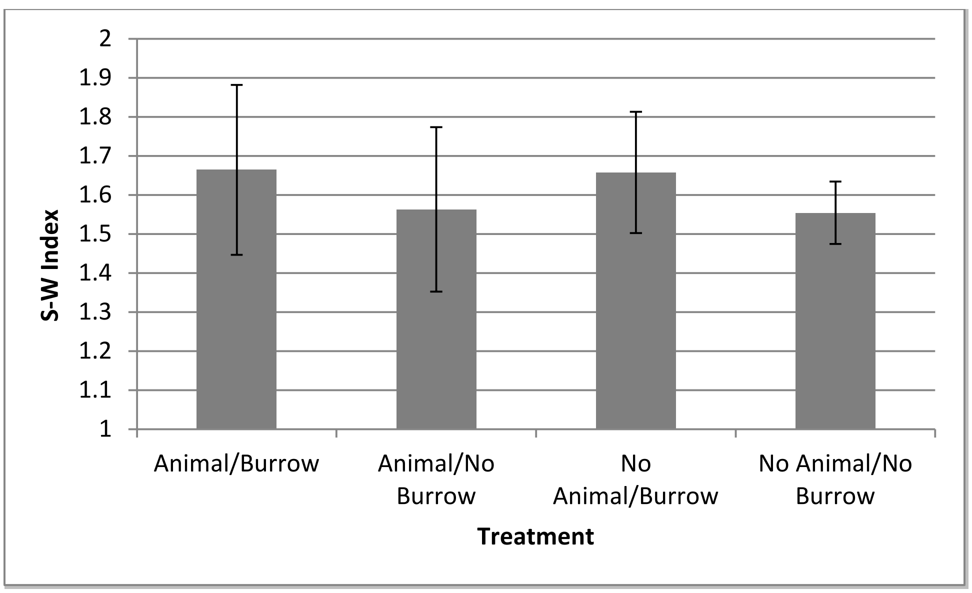

Fig. 7. Shannon-Weiner means and differences among treatments.

DISCUSSION

Overall simulated burrowing had limited effects on invertebrate abundance. There was however a significant difference in abundance among the different sampling locations. The four distinguishable groups demonstrate that simulated burrowing does have an effect on soil invertebrate abundance. Most notable effects were found at the entrance of the burrows, which had the lowest abundance of all sampling locations (33% to 50% lower than other sampling locations). The entrance of the burrow had the greatest amount of disturbance and also the least amount of vegetative coverage. This resulted from the gap caused by the auguring and the mound being less open as it was surrounded by dense vegetation. Because these plots were established in tallgrass prairies, the habitat of *Spermophilus franklinii*, there was reasonably dense vegetative cover at most sampling locations. Lack of cover at the entrance of the burrow resulted in the reduction of invertebrate abundance. All other sampling locations consisted of moderately dense cover which offered refuge for the invertebrates. In addition, since there was no cover at the entrance of the burrow sunlight caused the soil to dry out at a higher rate and made this location more open to predators. This made it less suitable for inhabitance by invertebrates. Further research could link change in soil invertebrate abundance with changes in plant and microbial communities.

Invertebrate abundance collection was much greater during the sampling of 2014 over that of 2013. This can most likely be attributed to the increased precipitation in 2014 and drought-like conditions occurring during the 2013 collection dates. The summer of 2013 preceding collection dates saw lower than normal temperatures and also reported only 0.08 cm of rain in August, the month before collection. This made soil conditions very dry and compact and not only resulted in difficult sampling circumstances but also extremely low invertebrate abundances. A similar study in 2005 showed that sites where land condition was poor resulted in a decline in the richness and abundance of soil macroinvertebrates (Dawes-Gromadzki 2005). In this study in Australia's tropical savannah, hymenoptera and haplotaxida also dominated the invertebrate assemblages sampled, which is consistent with our results. Abundance in spring 2014 was greater as increased precipitation (12.2 cm in May) caused soil conditions to be much more favorable for sampling as well as invertebrate inhabitance. This is consistent with the increase in soil invertebrate abundance collected from (316 to 974) in 2014 compared to 2013. The invertebrate orders collected in 2013 and 2014 were very similar in diversity and the rank orders were comparable as well: Hymenoptera, Haplotaxida, Hemiptera and Homoptera had highest abundances in both years. The other orders collected, which had abundances too low to be considered for analysis, included scutigeromorpha, ixodida, acari and opiliones.

Hymenoptera was the order with the highest abundance in both years of sampling. The hymenoptera collected in these samples consisted mainly of the family Formicidae but included other families as well. They had a consistent presence in all sampling locations and also possessed unusually high values, as when soil collections were taken on nests constructed in the soil and with the use of plant material. The disruption by the various types of treatments did not seem to have a major effect on hymenoptera as their abundances were not significantly altered between sampling locations. The only location this was different was at the entrance of the burrow; however, hymenoptera still had the highest abundance at this location. Formicidae quickly abandon already established nests at the first sign of a threat, which is one reason why their abundances may have been lower at the entrance of the burrow where the greatest disturbance was found.

The order Haplotaxida were found in great abundances. The presence of earthworms has been shown to increase the biomass of plants (Scheu et al. 1998) and nutrient availability to plants (Scheu and Parkinson 1994), contributing to the major role they play in tallgrass prairies. Haplotaxida have been found to be absent in sites of poor land condition (Dawes-Gromadzki 2005), which may be the reason why their abundances were so low in 2013. Alternatively (in the Dawes-Gromadzki study) in sites of good land condition, earthworms dominated the invertebrates sampled. Treatments (vole/burrow) did not seem to have a major effect on their abundance including at burrow entrances and mounds, where abundance was predicted to be lower. These organisms typically stay beneath the surface of the soil which is why they were anticipated to be less abundanct at the mound and entrance of the burrow where soil was disturbed.

The synergistic interactions of burrows and voles had the greatest effect of all the treatment types. The presence of both had a significant effect on orders homoptera, coleoptera and isopoda. The presence of burrows and voles independently did not have any major effects on invertebrate abundance, which may be an indication that their presence individually does not have enough capacity to alter abundance. The presence of burrows has been shown to alter plant community composition and development for a limited time; however, after three years the effects seem to be greatly diminished. The same may be true for soil invertebrates. Without the continuous use of the burrow by an animal and other contributing factors (e.g., deposition of excrement, food storage) burrowing will not affect the soil invertebrate community composition. A combination of both burrows and voles provides a sufficient enough disturbance to affect soil invertebrate abundance. Perhaps more intricate burrowing (as found with most burrowing animals, yet almost impossible to simulate) and including other factors typical of burrowing (e.g., continuous usage, excrement deposition, constant removal of soil, leaving behind food remains) might have a greater effect on invertebrates. The simulation of burrows in this experiment was representative of the main disturbance caused by burrowing, which is the removal and displacement of soil to the ground surface above. Only sampling occupied in addition to burrows formerly created but unoccupied will truly show whether the results obtained in this experiment are indicative of what is occurring in nature.

The sole presence of an animal (vole) did have an overall effect on soil invertebrate diversity. Independent of burrow presence and the interactive effect of both burrow and vole, the significance of vole presence on invertebrate diversity can be difficult to explain. Perhaps the best explanation is that without the presence of voles to maintain consistency of disturbances (no matter how small) through movement, feeding, excretion and plant usage burrowing alone will not have a significant effect on soil invertebrate communities (ex: low frequency/low intensity). This explanation is consistent with the intermediate disturbance hypothesis that states a medium amount of disturbance will increase or maximize diversity. Independent presence of burrows has an initial disturbance; however, without the presence of an animal disturbance is not maintained throughout time. Herbivores have been found to affect the rate of terrestrial nitrogen cycling by having an influence on the amount and condition of organic matter in the soil and on the ground surface (Sirotnak and Huntly 2000). The change in the organic matter content in the soil can thus affect what kind and amount of invertebrates found in the soil. A longer study would be required to test predictions of consistent increase or decrease in soil invertebrate abundance with presence or absence of voles.

There was no statistical significance shown between overall invertebrate abundance and individual treatment type for 2013 or 2014. This result is just as interesting as there being a significant difference because it brings about the question as why there is no difference. Perhaps because sampling was performed on top of the soil and not truly within the disturbance itself (with the exception of burrow entrance and mound) lack of treatment effects indicates that the disturbance was not sufficient enough to cause an effect on soil invertebrates around the disturbed area. In addition, the treatments in this study may not have closely simulated burrowing because they lacked characteristics such as continuous usage, deposition of excrement, remnants of food products and removal of soil.

A source of sampling error in this experiment was disturbing insects while collecting samples from locations in close proximity (without creating a separate disturbance). Sampling at a location only one meter away from the next location might have influenced invertebrate abundance at the next location, whether from physically knocking organisms from surrounding vegetation or frightening them away. These effects could be more likely in areas with no vegetative cover, such as the burrow entrance or mound, where invertebrate abundances were lowest.

Another possible source of sampling error is size of soil samples collected. A relatively small soil corer was used in this study to minimize both collection time and soil disturbance. It is possible, though, that larger individual soil samples would have resulted in higher invertebrate abundances and species diversity, and might have been more representative of the soil invertebrate community. Given more time and funding, another year of sampling would be welcomed for comparison. In addition, soil conditions (e.g., temperature, moisture) could be compared with invertebrate abundances in and around burrows.

As demonstrated in this study, simulated burrowing does have an effect on soil invertebrate community composition although not as pronounced as expected. Future sampling of invertebrates in addition to soil and plant sampling would be recommended to quantify interactions among all three factors.

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