REVIEW PAPER

Tallgrass prairie ants: their species composition, ecological roles, and response to management

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Abstract Ants are highly influential organisms in terrestrial ecosystems, including the tallgrass prairie, one of the most endangered ecosystems in North America. Through their tunneling, ants affect soil properties and resource availability for animals and plants. Ants also have important ecological roles as consumers of plant tissue and seeds. In the last several decades, various organizations, agencies, and agricultural producers have attempted to create wildlife habitat or reduce soil erosion by seeding thousands of hectares of bare cropland in the central United States with tallgrass prairie seed mixes. Although initially, monitoring of these restorations and of unplowed prairie remnants focused on plants and birds, in recent years the response of invertebrates such as ants has increasingly been the subject of research. An understanding of tallgrass prairie ant communities can help land managers and scientists better monitor the ecological condition of tallgrass prairie and guide management and restoration efforts. Here I review our current knowledge of ant species found within tallgrass prairie, their ecological roles, and their response to management.

Keywords Tallgrass prairie · Grassland · Ants · Formicidae · Restoration

Introduction

The tallgrass prairie is one of the most endangered ecosystems in North America and is considered a globally endangered resource (Samson and Knopf 1994; Ricketts et al. 1999). Once covering nearly 17 million hectares of the Great Plains from southern Manitoba to Texas, over 97 % of the original northern tallgrass prairie has been lost since European settlement, primarily from conversion to farmland (Samson and Knopf 1994; Samson et al. 2004). The ecosystem services associated with prairie such as reduced soil erosion, improved water quality, wildlife habitat, and recreational opportunities have been substantially reduced within landscapes now dominated by monoculture crops and urban development (Kemp and Dodds 2001). In recent decades various organizations, agencies, and agricultural producers have attempted to restore these services to the Great Plains by planting seed mixes containing native tallgrass prairie plant species into thousands of acres of bare soil on former cropland. A native prairie remnant, or remnant of tallgrass prairie that has never been plowed, may contain up to 300 plant species (Smith et al. 2010). However, the number of species used in prairie restoration seed mixes is constrained by seed availability, cost, and the goals of the restoration project and can vary from 10 to 100+ plant species. Because plants are critical in creating habitat for other organisms, the success of tallgrass restorations in simulating prairie remnants has often been measured by comparing the species composition and distribution of plants within native and restored tallgrass prairie (e.g., Kindscher and Tieszen 1998; Brye et al. 2002; Martin et al. 2005; McLachlan and Knispel 2005). However, researchers have become increasingly interested in studying the response of other taxa such as invertebrates to grassland restoration in order to gain a more complete understanding of the ecosystem and to modify management practices to manage for other organisms of interest (Davis and Utrup 2010; Orlofske et al. 2010; Déri et al. 2011).

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Because of their large influence on ecosystem structure and functioning, and because they are sensitive to environmental disturbance, ants can be an important invertebrate group to sample when monitoring an ecosystem (Hoffmann and Andersen 2003; Philpott et al. 2010; Ribas et al. 2011). Ants are one of the most influential organisms in terrestrial ecosystems for several reasons. For example, most ground-dwelling ant species are ecosystem engineers, or organisms that directly or indirectly affect the availability of resources to other species, by physically changing biotic or abiotic materials (Jones et al. 1994; Folgarait 1998). Through their tunneling, ants also mix and aerate soil, affecting soil structure and processes (e.g., soil erosion and soil formation; Baxter and Hole 1967; Jones et al. 2006) and therefore the flow of energy in ecosystems and the habitats of other species (Folgarait 1998). Finally, ants play important ecological roles as seed dispersal agents for plant species (Gomez and Espadaler 1998; Lengyel et al. 2009), predators of a variety of insects and other invertebrates (Way and Khoo 1992; Folgarait 1998), protectors of some plants against herbivory (Heil and McKey 2003) and herbivorous insects against predators and parasitoids (Buckley 1987), consumers of plants (Tobin 1994), and prey for invertebrates (Gotelli 1996; Gastreich 1999) and vertebrates (MacMahon et al. 2000; Reiss 2001).

Ants have been used as an indicator taxon in evaluations of terrestrial ecosystem restorations, particularly for rehabilitated minesites in southwestern Australia's jarrah (*Eucalyptus marginata*) forests (Majer 1983; Majer and Nichols 1998; Andersen et al. 2003; Nichols and Nichols 2003; Majer et al. 2007). These studies have shown that ant species richness and ant species composition of rehabilitated minesites generally converges towards that of unmined sites over time, although some distinct differences in species composition usually remain. Outside of Australia, comparisons have been made between the ant communities of rehabilitated ash dams and adjacent natural grasslands in South Africa (van Hamburg et al. 2004), between restored calcareous grasslands and paired reference ancient grasslands in England (Fagan et al. 2010), between a variety of restored forest and savanna habitats and their less disturbed remnant equivalents in Brazil (Ribas et al. 2012), and between restored and abandoned gullies in Columbia (Calle et al. 2013). The composition of the ant communities provided useful information about the successional stage of the restorations and the relative success of restorations in approximating natural conditions.

In recent years, understanding of prairie invertebrates has improved as researchers have studied the ant communities of tallgrass prairie remnants and restorations (e.g.,

Foster and Kettle 1999; Petersen et al. 1998, 2002, 2004; Lane and BassiriRad 2005; Phipps 2006). Although the purpose of these studies was not to specifically evaluate the usefulness of ants as ecological indicators, they provide valuable background information on tallgrass prairie ants and on the role ants play within the tallgrass prairie ecosystem. This information may be used in future studies, monitoring programs, and management techniques. In this paper, I review what is known about the species composition, ecological roles, and response to management of ants in tallgrass prairie and provide suggestions for future research. An understanding of prairie ant ecology will help land managers and conservationists better manage for these important invertebrates within tallgrass prairie.

Ant communities of native tallgrass prairie remnants

Early descriptions of tallgrass prairie ant communities were given by Shackleford (1929), Talbot (1934), and Gregg (1944). Talbot and Gregg studied the prairies of the Chicago region and noted that *Formica montana* was the dominant ant species, with Gregg (1944) estimating that this species was responsible for 95 % of the nests constructed in prairies west of Chicago. A more recent description of the tallgrass prairie ant fauna is provided by Trager (1998), who noted that a "good-sized" prairie remnant can support 25–35 ant species. Approximately 100 species of ants may be found in prairie remnants throughout the tallgrass prairie region of which about 60 are commonly found in prairies (Trager 1998). There are no endemic tallgrass prairie specialists since all prairie ants are found in other ecosystems, especially open, oak, or pine-dominated woodlands (Trager 1998).

Several different feeding guilds of ants are found in the tallgrass prairie, with the largest guild consisting of generalized predators such as members of the *Formica* genus, which prey upon other invertebrates, particularly smooth- and soft-bodied immature insects (Trager 1998). Ants in the *Formica* genus can increase the heterogeneity of the plant community (Beattie and Culver 1977), change soil profiles (Baxter and Hole 1967), slow succession (Andrews 1928), and alter soil moisture and chemistry in nests compared to adjacent soils (McCahon and Lockwood 1990). Other guilds raise sap-feeding insects such as aphids and related insects on plant roots, raid the nests of other ants for slaves and/or food, and specialize in scavenging opportunistically (Trager 1998). Many ant species obtain extrafloral nectar from glands on leaves, stems, or buds of prairie plants including common sunflower (*Helianthus annuus*), sawtooth sunflower (*H. grosseserratus*), Maximilian sunflower (*H. maximilianii*), plains sunflower (*H. petiolaris*), wild sweet potato (*Ipomoea pandurata*),

partridge pea (*Chamaecrista fasciculata*), and Illinois bundleflower (*Desmanthus illinoensis*) (Keeler 1979; Trager 1998).

Ant communities of tallgrass prairie restorations

Cropland is usually prepared for seeding of prairie plant species by disking and applying herbicides to a bare crop field (Helzer 2009; Smith et al. 2010). Because ants have underground colonies, existing populations in a cropfield may not be extirpated following disking and herbicide application (Philpott et al. 2010). However, the seeding of a new plant community dramatically changes local vegetation and soil conditions. When patches of new habitat are created in an area, they are often colonized by ants from colonies within the surrounding landscape (Elmes et al. 1998; Holec and Frouz 2005). Studies in European grasslands have found that while restoration rarely results in drastic changes in species richness, the abundance of different ant species changes with successional changes in the plant community (Dauber and Wolters 2005) and the species richness and number of open-habitat ant species gradually increases with time (Dahms et al. 2010).

One study has recorded changes in ant communities in tallgrass prairie restorations of different ages (Phipps 2006). In this study, the ants of 12 Conservation Reserve Program (CRP) tallgrass prairie sites in east-central Missouri, three in each of four age classes (0, 3, 7–8, and 14–16), were collected. The total ant abundance increased the longer the land had been in the CRP program, but species richness was generally consistent across all years. A range of 7–14 ant species were found on 0-year-old fields (0-year being the year the restoration was seeded), 9–16 species on 3-year-old fields, 16–17 species on 7–8-year-old fields, and 10–15 species on 14–16-year-old fields. Some species were observed to be early colonizers (*Pheidole pilifera*, *Hypoponera opacior*) or late colonizers (*Aphaenogaster carolinensis*).

Ants belonging to the genus *Formica* are among the dominant ants in native tallgrass prairie (Trager 1998). However, other genera may be abundant as well. In Phipps' (2006) study, the five species that dominated all ages of the CRP land in terms of total abundance, total genera, total species, and capture events were *Lasius neoniger*, *Myrmica americana*, *Solenopsis molesta*, *Tapinoma sessile*, and *Temnothorax ambiguous*. In a 20-year-old, 4-ha reconstructed prairie plot in northeastern Illinois, eleven ant species were collected and the most dominant species was *Lasius alienus* (Petersen et al. 2002). In 7- to 13-year-old tallgrass prairie restoration plots in southern Minnesota, the dominant ant species were *Aphaenogaster rudis*, *S. molesta*, and *L. neoniger* (Kittelson et al. 2008).

One species that has been noticeably rare in some tallgrass prairie restorations is the predatory ant *Formica montana*, once common in the mesic prairie of northeastern Illinois (Gregg 1944). Over 40 years after restoration of Curtis Prairie near Madison, Wisconsin, *F. montana* was still limited to a never-plowed prairie section and absent from the adjacent 50-year-old restored area (Kline and Howell 1987). *F. montana* was absent from a 20-year-old, 4-ha reconstructed prairie plot in northeastern Illinois (Petersen et al. 1998) and 7- to 13-year-old tallgrass prairie restorations in southern Minnesota (Kittelson et al. 2008). However, Moranz et al. (2013) found *F. montana* to be more prevalent in restored sites than remnant sites in their study of three 2- to 26-year old tallgrass prairie restorations and nine prairie remnants in Iowa and Missouri that were considered representative of mesic prairie in the region by the authors. The presence of *F. montana* within a restoration or remnant may be determined by site-specific factors such as soil conditions, plant productivity, and the degree of competition with other species within the landscape.

Some researchers have compared the effect of planting low or high diversity seed mixes on ant communities. In an observational study, Davis and Utrup (2010) compared the invertebrates of low-diversity (4–5 grass species) and high-diversity (at least 25 forb and grass species) tallgrass prairie restorations in south-central Nebraska and found no difference in total abundance, family richness, and diversity of invertebrates between the low and high diversity sites, including ants. However, the plantings differed in age, with the high-diversity plantings being 4–8 years old while the low-diversity plantings were 10–20 years old. The authors observed that because the high-diversity plantings were still in the early stages of successional development, differences in the plant community and associated differences in the invertebrate community may have not yet emerged. Similarly, Nemec et al. (2014) found no response of ant abundance, richness, or Shannon–Weaver diversity to seed mix richness or seeding density in 55 m × 55 m experimental plots seeded with low-diversity (15 grass and forb species) and high-diversity (97 grass and forb species) tallgrass prairie restoration plots. These plots were sampled in the second-fourth growing seasons when weedy, unseeded plants were abundant in all treatments and conservative plant species that begin growing several years after a restoration is seeded had not yet appeared in the high diversity plantings. The authors of both studies recommended longer term research or research on older restorations is needed to compare invertebrate communities once more species in the high diversity seed mixes have become

established and differences in the low and high diversity plant communities are more distinct. The diversity of grass species in seed mixes may also be of particular importance, with one study (Unstad 2012) finding that the strongest predictor of Shannon diversity for ants was the number of grass species per square meter.

Comparisons of ant communities between remnants and restorations

According to my review of the literature, most tallgrass prairie ant species have been recorded in both native and restored tallgrass prairie across a variety of studies ("Appendix"). To my knowledge some species have been recorded in native tallgrass prairie but not restorations (*Aphaenogaster treatae*, *Formica lasioides*, *F. obscuripes*, *Leptothorax pergandei*) while others have been recorded in restorations but not in native remnants (*F. subintegra*, *Hypoponera opacior*, *Lasius claviger*) in the published literature ("Appendix").

Several studies have been designed to compare ant communities between native and restored tallgrass prairie in an area. Kittelson et al. (2008) compared a prairie restoration and a prairie remnant in southern Minnesota. The authors found significantly higher ant species richness per plot in the prairie remnant, which also had higher plant diversity, especially forbs, than the restoration. Panzer et al. (1995) used aerial nets and sweep nets to collect a variety of insect taxa from remnant and restored prairies in the Chicago, Illinois region over a 12-year period and created lists of remnant-dependent insects, defined to be the "obligatory association of species with remnants of fragmented ecosystems" by creating a list of species that were scarce or absent from degraded areas. They observed that because prairie ant species seem to occur in a variety of habitats and are often generalist predators, they are not a good group to use as indicators of quality prairie remnants. The authors also noted that their list of remnant-dependent species is of limited use in areas outside of Chicago.

Although Panzer et al. (1995) did not detail the methods they used to survey prairies, Orlofske et al. (2010) used a more standardized approach to capture ants using sweep nets along three 25 × 2 belt transects randomly located within remnant and restored tallgrass prairie in central Iowa. They then used indicator species analysis, which identifies a taxon's site specificity, or the abundance of a taxon at a subset of sites, and the taxon's site fidelity, or the number of sites of a given type where the taxon occurs (Dufrene and Legendre 1997) to identify insect families that are significantly associated with native remnant or restored prairies. In contrast to Panzer et al. (1995), the authors found that ants were a significant indicator taxon associated with remnant prairies.

Impacts of invasive ants on tallgrass prairie ant communities

Invasive ants are ants introduced by humans that penetrate natural areas, disrupting ecosystems by killing young birds and mammals, displacing native ants, reducing the abundance of other invertebrates, and altering food web structures (Holway et al. 2002). The most destructive invasive ant in the United States, the red imported fire ant (*Solenopsis invicta*), was introduced into the United States in the 1930s or 1940s near Mobile, Alabama (Callcott and Collins 1996) and has since spread throughout the southeastern United States, including Oklahoma, Texas, and Arkansas, the southern portion of the tallgrass prairie region (NAPIS 2011). Although the red imported fire ant will likely continue to expand its range in the United States, it is unlikely to substantially invade the tallgrass prairie states north of Oklahoma and Arkansas in the next century because of climatic limitations, even when projected temperature changes from global warming are accounted for (Korzukhin et al. 2001; Morrison et al. 2005).

The red imported fire ant favors open and disturbed areas (e.g., parking lots, roadsides, open fields; Callcott et al. 2000; Wojcik et al. 2001) but also occurs in a range of natural habitats, including woodland and prairie (Morris and Steigman 1993; Allen et al. 2001; Forys et al. 2001; Wojcik et al. 2001). Red imported fire ants maintain large supercolonies and display strong interspecific aggression, often outcompeting other ant species for resources and decreasing the overall diversity and abundance of native ants (Wojcik et al. 2001; Holway et al. 2002; Epperson and Allen 2010). However, while some native ant species have been displaced in infested areas, others have survived and even increased in abundance and distribution following red imported fire ant invasion (Wojcik et al. 2001; Morrison and Porter 2003). Two studies have looked at the impact of red imported fire ants on native ants in blackland prairie, a region of tallgrass prairie in central Texas. Morris and Steigman (1993) found that native ant species richness declined 66 % and native ant abundance declined 99 % in a blackland prairie infested by red imported fire ants. Porter and Savignano (1990) studied the impacts of fire ants on ant communities of the Brackenridge Field Laboratory, which included a mixture of woody and grassy vegetation characteristic of the Edwards Plateau and the Blackland Prairie region. Native ant species richness was 70 % lower in infested areas and native ant abundance was 90 % lower

in infested areas. However, these effects were temporary because when the area was resampled 12 years later, fire ants were still the most abundant species but native ant diversity had returned to pre-invasion levels (Morrison 2002).

A more recent ant invader in tallgrass prairie is the Japanese pavement ant, *Tetramorium tsushimae*. The pavement ant may have been introduced to the United States as early as the first half of the twentieth century but was first observed in 1988 within the city of St. Louis, Missouri and a few adjacent townships (Steiner et al. 2006). The Japanese pavement ant has since invaded disturbed tallgrass prairie and other open habitats such as parks in the area surrounding St. Louis (Steiner et al. 2006; Reuther 2009). It has several characteristics of a successful invasive ant species, including unicoloniality (creating one large super-colony), omnivory, generalist nesting preferences, and a preference for disturbed areas (Reuther 2009). It is able to outcompete common, opportunistic native ants such as *L. neoniger* and *T. sessile* for food resources, and has displaced common native ant genera such as *Crematogaster*, *Formica*, *Camponotus*, *Myrmica*, *Lasius*, *Tapinoma*, *Prenolepis*, and *Paratrechina* (Steiner et al. 2006; Reuther 2009). The Japanese pavement ant has the potential to expand throughout the Midwest and significantly affect the native ant community (Steiner et al. 2006; Reuther 2009).

If the negative ecological impacts of an invasive ant are large and land managers have the resources to monitor and address the encroachment of invasive ants into an area, Hoffmann et al. (2011) propose a five-phase management framework for managing invasive ants: (1) a pre-emptive phase that analyzes the risks of a potential incursion; (2) a scoping phase that involves gathering information on potential incursions; (3) a treatment phase; (4) a post-treatment monitoring phase; and (5) a program completion phase in which managers summarize the lessons learned from the project. Although there is little published on techniques for reducing or eradicating Japanese pavement ant populations, an integrated management approach consisting of cultural and biological control methods and targeted insecticide use has been applied for managing fire ant infestations (Drees et al. 2013).

Ants as ecosystem engineers in tallgrass prairie

Through nest construction, ants alter the physical and chemical properties of soil by increasing drainage and aeration through the creation of underground galleries (Folgarait 1998). Ants also transform organic matter and add nutrients to the soil through food storage, aphid tending, and the accumulation of feces and corpses (Folgarait 1998). Ant nests may be entirely subterranean or may form an aboveground mound (Folgarait 1998). Mounds may be small and temporary, or may be larger and more permanent, with mounds from *Formica* sp. in tallgrass prairie lasting as much as 30 years (Henderson et al. 1989) and attaining densities up to 1,148 active mounds per hectare (Baxter and Hole 1967). Mound-building ant species in tallgrass prairie include *Formica* species and *Lasius claviger* (Henderson et al. 1989; Petersen et al. 2002; Foster 2004). Densities of mound-building ants may be lower in young tallgrass prairie restorations than in native prairie and it may take mound-building ants several years to colonize a restoration (Foster 2004).

Ant mounds can influence the density, biomass, and distribution of plants in a prairie. In a 17-year-old high diversity (∼150 plant species), 7.5-ha mesic tallgrass prairie restoration in northeastern Illinois, surface coverage of three warm-season grasses was significantly higher in quadrats containing ant nests than in quadrats lacking ant nests (Petersen et al. 2002). The density of big bluestem shoots was also significantly higher in clumps growing on nests of the mound-building species *L. claviger* than in clumps lacking nests (Petersen et al. 2002). Plant growth may be enhanced by the loosened soil and increased aeration and drainage on ant mounds (Petersen et al. 2002). Seed predation by ant colonies may also reduce competition with plants growing on the mound (Petersen et al. 2002). In addition, the herbivorous aphids that are tended by ants often carry plant diseases, which may influence the diversity and distribution of some prairie plants (Trager 1990).

The local disturbances caused by ant mounds also increase the heterogeneity of the local environment (Cammeraat and Risch 2008). Some plant species may be particularly associated with ant mounds. For example, little bluestem (*Andropogon scoparius*) had significantly higher cover on ant hills compared with adjacent undisturbed native tallgrass prairie (Gibson 1989). Big bluestem (*Andropogon gerardii*) and heath aster (*Aster ericoides*) had significantly higher cover on the adjacent undisturbed tallgrass prairie than on the anthills (Gibson 1989). In contrast, Foster (2004) found that big bluestem cover was significantly lower off of mounds in a restored prairie than on prairie. Partridge pea occurred significantly less often off mounds compared to on mounds in restored prairie and goldenrod occurred significantly less often off mounds compared to on mounds in native prairie (Foster 2004).

Differences in the affinity of plant species for ant mounds may in part reflect differences in the nutrient needs of the plants and the effects of the ants on the soil. For example, *L. claviger* did not significantly affect organic content or aboveground biomass of grasses, but floral richness was significantly higher when nests of *L. claviger*

were present in a tallgrass prairie restoration (Petersen et al. 2004). Unusually high contents of available potassium and phosphorous that have been recorded in ant mounds may have several causes. For example, these nutrients may be derived from plant sap from aphids, a product from the ants' rapid mineralization of organic matter, or from the ants' addition of B horizon material to the soil (Baxter and Hole 1967).

Ant mounds can have strong influences on soil properties in tallgrass prairie restorations, with large differences recorded between mound and non-mound soil. For example, percent soil moisture and soil bulk density were consistently lower on mounds compared to off mounds in both restored and native tallgrass prairie (Foster 2004). However, differences in soil properties may diminish over the age of a restoration, with one study finding the difference between six of seven measured soil properties in mound and non-mound prairie soil to be highest at an 8-year-old site, with the differences lower at the 16- or 26-year-old site and in a nearby native prairie (Lane and BassiriRad 2005).

The density of ant mounds can also change over time. During the first 16 years following restoration, the area per mound increased with increasing time since restoration, but there was no significant increase in the density of ant mounds. However, between 16 and 26 years of restoration, the density of the mounds increased sharply while the average size of the mounds declined (Lane and BassiriRad 2005).

Ants can also affect the distribution of a plant species in an ecosystem by seed predation. While ants are a dominant seed predator in some desert and woodland ecosystems (Andersen 1987; Brown et al. 1979), vertebrates are the dominant seed predators in tallgrass prairie (Reed et al. 2004). There is a relatively low abundance of granivorous ants in tallgrass prairie compared to less productive types of prairie such as shortgrass and mixed grass prairie (DuBois 1985). The deeper litter layer in tallgrass prairie compared to other types of grassland may make seed detection more difficult (Reed et al. 2006). In addition, many of the warm-season grasses and forbs that dominate tallgrass prairie become inactive and drop their seeds in the fall, when ant colonies become dormant (Reed et al. 2006).

Effects of management activities and fragmentation on tallgrass prairie ants

Because grassland plant and animal communities evolved with fire and grazing, these disturbances are commonly used management tools in native and restored tallgrass prairie. Fire is commonly used to control invasive plants, remove woody shrubs, or encourage native plant growth

(Underwood and Fisher 2006). Grassland invertebrate responses to fire and grazing are often species specific and are influenced by habitat size, frequency, intensity, and duration of the disturbance (Joern and Laws 2013). Previous research has shown that invertebrate populations are seldom eradicated by single fires and species present beneath the soil surface in the spring and fall when prairies are burned are generally not threatened by the direct effects of fires (Panzer 2002). The direct effects of fire on ants are small because only a portion of an ant colony is likely to be caught aboveground, soil nests are generally very deep, and soil cracks provide refuges during the fire (Underwood and Fisher 2006). Indirect effects of a fire have a larger impact on an ant community because the removal of aboveground biomass changes food supply and nesting sites, while burned areas receive more sunlight, which might influence nest-site temperature and foraging activity (Underwood and Fisher 2006).

Some studies have reported the abundance of ants to increase following fire in tallgrass prairie (Panzer 2002), while others report few effects of fire on ant abundance, diversity, or richness (Nagel 1973; Van Amburg et al. 1981; Debinski et al. 2011). Although the abundance and richness of the ant community may not necessarily change following fire, burning may affect the composition of the ant community. For example, litter-inhabiting, cryptic species and twig-, stem- and acorn-nesting species, which make up a large portion of woodland ant fauna, are virtually absent in regularly burned prairies, while mound-building and subterranean root-aphid tending species more abundant (Trager 1990).

Grazing affects soil structure, increases runoff, decreases infiltration capacity, simplifies aboveground vegetation and litter, and removes seed resources from the environment (Underwood and Fisher 2006). Little research has been conducted on the effects of grazing on tallgrass prairie ants, but studies in other grasslands indicate that the effect of grazing on ants is influenced by the interaction of the species of grazer and vegetation type (Joern and Laws 2013). A study in European grasslands showed little impact of grazing on ant species richness or the frequency of ant species, although the composition of ant species changes (Pihlgren et al. 2010). Similar ant species composition, richness, and abundance in desert grasslands in Arizona under varying degrees of livestock grazing were observed (Whitford et al. 1999). Grazing had no effect on the diversity of ants within another desert grassland study in Arizona (Kerley and Whitford 2000), and caused no significant change in the abundance of harvester ant colonies (*Pogonomyrmex salinus*) in north-central Wyoming rangelands (Kirkham and Fisser 1972).

Recent studies have indicated that functional groups respond more consistently to disturbance than other more

traditional metrics such as species richness and abundance in forested and grassland ecosystems (Stephens and Wagner 2006; Hoffmann and James 2011). The same observation has recently been found for tallgrass prairie. For example, when Debinski et al. (2011) studied the effect of fire and grazing treatments on ants using ant species richness or total ant abundance, they found no effect, and when studying the effect of these disturbances at the species level, they only showed a treatment effect for one species, *F. montana*. When the authors analyzed data from the same study using functional groups based on food acquisition strategy they observed multiple treatment effects at the functional group level (Moranz et al. 2013). The authors used four ant functional groups: (1) dominants actively and mutually exclude each other and most generalists from their foraging territories, and tend to monopolize large prey and honeydew sources, (2) subdominants locally monopolize large prey and honeydew sources (except against dominants), (3) generalists recruit en masse to rich food sources by means of odor trails, but may be chased off by more dominant species, and (4) opportunists do not mass-recruit nest mates to rich food, but use a ''grab and run'' strategy, and are more specialized on small food sources such as very small insect prey and stray droplets of honeydew on the ground, litter, or low foliage. The authors found that functional groups differed in their response to disturbance. For example, although no ant functional groups were eliminated by fire, opportunist ants were more abundant in burn-only sites than graze-and-burn sites while generalists were more numerous in graze-and-burn sites than in burn-only sites. In addition, frequent fires (fire return interval of 3 years or less) favored dominance by the ant species *F. montana*, reducing the abundance of generalist ants. In contrast, grazing reduced dominance by an ant species in the tallgrass prairie ant community.

Conservationists seeking to improve the species diversity and abundance of tallgrass prairie ants can reduce fragmentation by increasing connectivity between patches of habitat (Fahrig 2003). The more isolated a patch is from similar habitats, the lower the dispersal and colonization rates and the greater the influence of the surrounding landscape matrix on communities. Crist (2009) reviewed the effects of landscape fragmentation on ants in a variety of habitats worldwide. He found the species composition of ants to change with the size and relative isolation of habitats from similar habitats, which can have implications for ecosystem functioning such as soil nutrient dynamics in habitat patches if certain ant species are lost. Unstad (2012) studied effects of landscape fragmentation on ant communities in tallgrass prairie remnants in southeastern Nebraska and the abundance of ants to be positively associated with the amount of nearby haymeadow. He recommended that conservation efforts should prioritize individual large patches of tallgrass prairie or small sites that are close to each other.

Conclusions

In conclusion, ants play important roles in the tallgrass prairie ecosystem, affecting soil structure and processes and plant biomass and species composition. To date, studies that have been conducted on tallgrass prairie ants have focused on the influence of ants on soil structure and plant diversity and the species composition of ant communities in remnants or restorations of various ages, management strategies, or levels of seed mix species richness in restorations. Because of rapidly changing environmental conditions such as climate change, fragmentation-related effects such as edge effects, and the widespread occurrence of invasive species, the field of ecosystem restoration is focusing less on restorations as a mean of replicating historic (often defined as pre-European settlement) conditions and more on restoring the ecosystem services associated with an ecosystem (Perring et al. 2013). For this reason, future research on tallgrass prairie ants could contribute to our understanding of the ecosystem services provided by ants and the ecological roles of ants within tallgrass prairie rather than comparing the ant communities of native and restored prairies. The interactions of ants with the tallgrass prairie plant community is better understood than the interactions of ants with the tallgrass prairie fauna. The role of ants as predators of tallgrass prairie invertebrates or as prey for invertebrates and vertebrates has been little studied, although these ecological relationships could have implications for managing other prairie taxa and in managing pests in agroecosystems. Future research needs include studies that improve knowledge of: (1) the interaction between ants and other invertebrates in tallgrass prairie; (2) the influence of tallgrass prairie management strategies and restoration techniques on ant communities of prairie remnants and restorations; and (3) the design of tallgrass prairie restorations that enhance the role of ants in pest control within adjacent farmland. Such research can guide recommendations for managing tallgrass prairie to benefit this important insect group.

Appendix

See Table 1.

Table 1 Ant species that may be found in tallgrass prairie

Species	Habitat and range	Ecology	Native tallgrass prairie records	Restored tallgrass prairie records
Aphaenogaster rudis Enzmann	Woods, woods' edges, open areas near woods[1]; Ontario south to NJ, NC, AL, west to OH, IN, MO[1]	Insects, seeds, pollen of ground nesting bees, elaiosomes of forest myrmecocohrous plant seeds[1]	MN[7] (r.a. = 0.753) NE[32], OH[29]	MN[7] (r.a. = 0.348); NE[33]
A. treatae Forel	Semi-open to open grassy prairies and fields[1]; Ontario south to FL, west to MI, OH, IL, AL[1]	Mostly insects, including other ants, some grass seeds[1]	IL[6], MO[6], OH[29]	
Crematogaster cerasi (Fitch)	Woods, woods' edges, semi-open and open areas[1]; Quebec south to GA and FL, west to MI, SD, AR, NM[1]	Found on goldenrod (*Solidago* sp.) and on dead insects[1], eats elaiosomes of seeds, occurs at extrafloral nectaries, tends hemipterans for honeydew[18]	IL[6], NE[32]	MO[8] (total r.a. over restorations 0–16 years old = 0.005)
Crematogaster lineolata (Say)	Woods, semi-open areas, open fields, meadows[1], rocky prairies and glades[19]; Quebec, Ontario south to FL, west to MI, ND, CO, TX[1]	Scavenger, predator, tends hemipterans for honeydew[1,19,30]	MO[6], OH[29], NE[32]	IL[10] (r.a. = 0.011;1 nest in 20-year-old, 4-ha prairie) MO[8] (total r.a. over restorations 0–16 years old = 0.005)
Formica dolosa Buren	Oak or oak-pine savanna, open woodland, dry-mesic prairie near woods' edge[20]; New England west to WI and IA, south to FL, gulf coast states and TX[21]	Preys on small animals, esp. soft-bodied, herbivorous insects, gets honeydew from tending hemipterans and from honeydew spilled onto leaf-litter[20]	NE[32], OH[29]	KS[3] (low densities); NE[33]
F. incerta Buren	Mesic and dry-mesic prairie, parks, fields, lawns[21]; New England and Great Lakes states west to MN, NE, CO, south to southern Appalachians[21]	Visits extrafloral nectaries of sunflowers (*Helianthus* sp.), partridge peas (*Chamaecrista fasciculata*), and other prairie plants, tends aphids and membracids for honeydew[21]; often first *Formica* species to become abundant on restored grassland[21]	IL[14] MN[7] (r.a. = 0.054); NE[9,32] OH[29]	IL[8] (total r.a. over restorations 0–16 years old = 0.019) NE[9,33]
F. lasioides Emery	Grasslands, fields, woods' edges, woodlands[1]; Nova Scotia, Quebec west to British Columbia, south to MA, MI, OH, SD, CO, NM, AZ, CA[1]	Found on milkweed (*Asclepias*) bloom[1], preys upon tussock moth larvae[22] and tent caterpillar larvae[23]; eats elaiosomes of *Corydalis aurea* seeds[24]	NE[9], OH[29]	
F. montana Wheeler	Open fields and prairies[1]; central OH, west to Manitoba, ND, SD, NE, KS[1]	Found on bloom of goldendrod, tends membracids and aphids for honeydew[1]	IL[4,15,16], NE[9], WI[15]	IL[12] (mounds present in 8–26 year old reconstructions) NE[9,33]
F. neogagates Viereck	Mesic woods[1], deciduous and conifer woodlands, grasslands[25], Nova Scotia, Quebec, west to AK, south to NC, IL, IA, NE, NM, NV, AZ, CA[1]	Tends hemipterans for honeydew[1,25]; generalist feeder[25] eats elaiosomes of *Corydalis aurea* seeds[24]	MN[7] (r.a. = 0.027)	MN[7] (r.a. = 0.008)
F. nitidiventris (=*F. pallidefulva* Emery)[a]	Open fields, mowed areas, meadows, woods' edges[1]; Ontario, Quebec south to GA, west to WI, SD, WY, CO, NM[1]	Tends membracids for honeydew, found on bloom of *Solidago* sp. And *Asclepias syriaca*[1]; seeds of myrmecochore U. perfoliata[1]	IL[14,15,16], NE[9]	IL[10] (r.a. = 0.157; 5 nests in 20-year old, 4-ha prairie) IL[13] (nests in 17-year-old, 7.5 ha prairie), NE[9,33]
F. obscuripes Forel	Open areas and dry grasslands[1]; Quebec, MI, IN, IL, Manitoba west to British Columbia, south to NM, NV, UT, CA[1]	Omnivorous on dead and moribund invertebrates, tends aphids and other homopterans for honeydew[1]	MN[7] (relative abundance = 0.001)	

Table 1 continued

Species	Habitat and range	Ecology	Native tallgrass prairie records	Restored tallgrass prairie records
F. pallidefulva Latreille	Open fields and semi-open areas[1], NY, NJ south to FL, west to OH, IL, CO, OK, TX[1]	Generalist forager, tends aphids and membracids for honeydew, preys on caterpillars and earthworms[24]; visits extrafloral nectaries of partridge pea in FL[1]	IL[6], MN[7] (r.a. = 0.007); MO[6]; NE[32], OH[29]	MO[8] (total relative abundance over restorations 0–16 years old = 0.005); MO[6]
F. subintegra Emery	Open woods, woods' edges, open fields near woods' edge[1]; Newfoundland, Nova Scotia, Ontario south to SC, TN, west to ND, IA, KS[1]	Raid on *Aphaenogaster* ant colony as food[1]		MO[8] (total r.a. over restorations 0–16 years old = 0.001)
F. subsericea Say	KS[2] Open woods, woods' edges, open areas near woods[1]; New Brunswick, Quebec south to N FL, west to Manitoba, MT, IA, KS, MO, MS[1]	Honeydew, seeds gathered from myrmecochorous plants; On bloom of *Rubus* sp. *Solidago* sp., *Daucus carota*[1]	KS[2,3] IL[4,5] IL, MO[8], IL[15], OH[29]	KS[2] (low densities), IL[6], IL[11] (r.a. = 0.034; 1 nest in 20-year-old, 4 ha prairie); IL[14] (nests present in 17-year-old, 7–5 ha prairie); MN[7] (relative abundance = 0.007); MO[8] (total relative abundance over restorations 0–16 years old = 0.011)
Hypoponera opacior	Open prairie and grassland, open woods[1]; VA to FL, west to OH, IN, IL, IA, CO, TX, NV; OR, CA; Mexico south to Chile, Argentina, West Indies[1]	Generalist predator of small soil arthropods[26]		MO[8] (total relative abundance over restorations 0–16 years old = 0.001)
Lasius alienus	Woods or woods' edges, open fields and meadows[1]; Nova Scotia, New Brunswick south to FL, west to SE Manitoba, ND, SD, NE, KS, AR, MS[1]	Tends membracids and aphids for honeydew, eats living and dead insects, gathers seeds of *Luzula echinata* and *Uvularia perfoliata* for elaiosomes[1], nests under rocks, in leaf litter, on bare ground[1,13]	IL[5,14,15] MO[6]	IL[10] (r.a. = 0.702; 16 nests in 20-year-old, 4-ha prairie) IL[13] (nests in 17-year-old, 7–5 ha prairie), MO[8] (total r.a. over restorations 0–16 years old = 0.059); MO[5]
L. claviger (Roger)	Mesic habitats; open woods, woods' edges, semi-open areas[1,17]	Feeds on honeydew of root-feeding aphids and mealy bugs[1,17], largely subterranean, forages below the soil surface[1,17]		IL[10]: 4 nests in a 20-year-old, 4-ha restored prairie IL[11]: 61 nests in an 18-year old, 7.1-ha restored prairie IL[12]: mounds present in 8–26 year old restorations IL[13]: nests present in 17-year-old, 7.5-ha prairie
L. neoniger	Open lawns, meadows, fields, near woods' edges[1]; Quebec, Maine south to northern FL, across southern Canada west to ID, WY, CO, NM[1]	Tends honeydew excreting insects but largely carnivorous[1]	MN[7] (relative abundance = 0.062); MO[6]; IL[16] NE[32]; OH[29]	MN[7] (relative abundance over restorations 0–16 years old = 0.205); MO[6], NE[10,33]
Leptothorax ambiguus	Open woods, open fields and meadows[1]; Quebec to VA, west to MI, ND, SD, IA, NE[1]	Honeydew and other nectar sources[1]; nests in goldenrod galls[1]	MO[6], NE[32]	MO[6]
L. pergandei Emery	Semi-open or open exposed or dry barren areas[1]; District of Columbia south to GA, TN, west to IL, NE, TX[1]	Occasionally taken at bait[1]	MO[6], NE[32]	

Table 1 continued

Species	Habitat and range	Ecology	Native tallgrass prairie records	Restored tallgrass prairie records
Monomorium minimum Buckley	Open and semi-open areas[1]; PN and District of Columbia south to GA, TX, west to MI, ND, ID, CO, NM[1]	Feeds on dead arthropods[1,27]	IL[5], MN[7] (r.a. = 0.003); MO[6]; NE[32] OH[29]	MO[8] (total r.a. over restorations 0–16 years old = 0.004); MO[5]
Myrmica americana	Open fields, prairies, meadows, grasslands, edges of woods[1]; Quebec, Maine south to NC, TN, west to Manitoba, ND, CO, UT, NV, AZ[1]	Animal matter and plant juices[1]	MO[9]; NE[10,32]	MO[8] (total r.a. over restorations 0–16 years old = 0.106) MO[5]; NE[9,33]
M. emeryana	Occasional in dry-mesic and mesic prairie restorations, also in old fields[28]	Predator and scavenger of small arthropods, tends honeydew-excreting hemipterans[28]	NE[9]	MO[8] (total r.a. over restorations 0–16 years old = 0.002)
Paratrechina parvula	Woods, open woods, open areas near woods[1]; MA south to FL, west to MI, IL, ND, NE, KS, OK, TX[1]	Seeds of mymecochorus plant *Trilium erectum* for elaiosomes, visits extrafloral nectaries of partridge pea in FL[1]	MN[7] (r.a. = 0.083); NE[32], OH[29]	MN[7] (r.a. = 0.041)
Pheidole pilifera	Open fields and meadows[1]; NY, MA south to GA, west to ND, NE, KS[1]	Granivorous, may take dead insects[1]	IL[5], NE[32]	MO[8] (total r.a. over restorations 0–16 years old = 0.007); NE[33]
Ponera pennsylvanica	Variety of moist woodlands, less commonly, open habitats[1]; MI, ND, SD, NE, IL, OH, MO, TX, IN. KS, OK, AR[1]	Carnivorous, feeding on small insects[1]	IL[5], MN[7] (r.a. = 0.001), MO[6], NE[32]	IL[10] (r.a. = 0.002), MO[8] (total r.a. over restorations 0–16 years old = 0.004); MO[5]
Solenopsis molesta	Open woods, fields, meadows[1]; Quebec, Ontario south to FL, west to WA, CA[1]	Highly predacious, nearly omnivorous[1]; smallest prairie ant[31]; nests in mounds of other ants, under rocks, or in ground[1,31]	IL[5,15], MN[7] (r.a. = 0.007); MO[6]; NE[32] OH[29]	MN[7] (r.a. = 0.365) IL[10] (r.a. = 0.005; 4 nests in 20-year-old, 4-ha prairie) IL[13] (nests present in 17-year-old, 7.5 ha prairie) MO[5,8] (total r.a. over restorations 0–16 years old = 0.138); NE[33]
Tapinoma sessile	Woods, woods' edges, open fields and meadows[1]; Nova Scotia, Quebec S to FL, west to WA, CA; Mexico[1]	Honeydew, flesh of other organisms[1] eats elaiosomes of *Corydalis aurea* seeds[25]	IL[5,14], NE[32]	IL[10] (r.a. = 0.011; 1 nest present in 20-year-old, 4-ha prairie), MO[8] (total r.a. over restorations 0–16 years old = 0.236) MO[5], NE[33]
Temnothorax ambiguus	Dry-mesic and mesic grasslands in Midwest[29]	Honeydew ejected onto foliage and litter[29]	OH[29]	MO[8] (total r.a. over restorations 0–16 years old = 0.174)
Tetramorium caespitum	Open or partially shaded situations, disturbed sites[1]; Quebec, Ontraio, MI, Atlantic coastal region of NE US, west to TN, NE, MO, WA, NV, CA[1]	Often taken at fruit baits, seeds, eat tubers, roots and stalks of plants, attend honeydew insects[1]	IL[5], NE[32] OH[29]	IL[11] (r.a. = 0.030; 3 nests in 20-year-old, 4-ha prairie) IL[14] (nests present in 17-year-old, 7–5 ha prairie)

r.a.—relative abundance, and is listed when known

[a] *F. nitidiventris* is now recognized as a color variant of *F. pallidefulva* rather than a separate species (Trager et al. 2007)

[1] Coovert (2005), [2] Foster (2004), [3] Foster and Kettle (1999), [4] Gregg (1944), [5] Newman and Wolff (1990), [6] Trager (1990), [7] Kittelson et al. (2008), [8] Phipps (2006), [9] Nemec (2003), [10] Petersen et al. (1998), [11] Petersen et al. (2004), [12] Lane and BassiriRad (2005), [13] Petersen et al. (2002), [14] Shackleford (1929), [15] Talbot (1934), [16] Gregg (1944), [17] Trager (2013a), [18] Trager (2013b), [19] Trager (2013c), [20] Trager (2013d), [21] Trager et al. (2007), [22] Harrison (1994), [23] Ayre and Hitchon (1968), [24] Hanzawa et al. (1985), [25] Trager (2013e), [26] Trager (2013f), [27] Adams and Traniello (1981), [28] Trager (2013g), [29] Friedrich (2010), [30] Fisher and Cover (2007), [31] Trager (1998), [32] Unstad (2012), [33] Nemec et al. (2014)

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