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Review

Review

From Pests to Keystone Species: Ecosystem Influences and Human Perceptions of Harvester Ants (*Pogonomyrmex, Veromessor*, and *Messor* spp.)

Derek A. Uhey[1,2] **and Richard W. Hofstetter**[1]

[1]School of Forestry, Northern Arizona University, 200 E. Pine Knoll Drive, Flagstaff, AZ 86011, USA, and [2]Corresponding author, e-mail: dau9@nau.edu, dauhey44@gmail.com

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Abstract

Harvester ants (Latreille) (Formicidae: Hymenoptera) have traditionally been labeled as pests within their native ranges from perceived effects on crop production and rangeland productivity. Yet, modern research casts doubt on many of these perceived detrimental effects and instead suggests that harvester ants act as keystone species that largely benefit both ecosystems and human activities. Through nest engineering and trophic interactions (such as seed harvesting and predation), harvester ants have considerable direct and indirect effects on community structure and ecosystem functioning. Here we summarize the ecological roles of harvester ants and review their services and disservices to ecosystems and human activities. In doing so, we help clarify perceived keystone and pest roles of harvester ants and their implications for rangeland management. We find the numerous keystone roles of harvester ants to be well-supported compared to perceived pest roles. We also highlight areas where further research into their roles in natural and managed systems is needed.

Key words: rangeland, grassland, seed harvest, nest clearing, ecosystem engineer

Understanding and managing conflicts between humans and biodiversity are critical to the conservation of natural systems (McShane et al. 2011). Many of these conflicts result from confusion regarding the ecological services or disservices a species performs (e.g., Miller et al. 2007). Some species, especially non-natives, are considered 'pests' by posing threats to native ecosystems and human activities on landscapes (Deguine et al. 2021). Yet many native species have traditionally also been considered pests and persecuted as such within their native ecosystems (Hale and Koprowski 2018).

Some native species have pest perceptions that are not well-supported (e.g., Delibes-Mateos et al. 2011), but do have rigorous support as keystone species and ecosystem engineers that perform key functions in their ecological systems (e.g., European rabbits (*Oryctolagus cuniculus*; Debiles-Mateos et al. 2008), plateau pikas (*Ochotona curzoniae*; Smith and Foggin 2014) prairie dogs (*Cynomys* spp.; Miller et al. 2007), and bark beetles (*Ips typographus*; Müller et al. 2008)). Keystone species have disproportionately large (relative to their biomass) effects on community and/or ecosystem functions (Power et al. 1996), while ecosystem engineers modify habitats by modulating resource availability for other species (Jones et al. 1994). Both terms can be related, as some ecosystem engineers are also considered keystone species (e.g., Whitford and Steinberger 2010). These species are often the most important to conservation (e.g., Johnson et al. 2017). Therefore, considering keystone species as pests can create conflicts between conservation and other management goals (e.g., Miller et al. 2007, Delibes-Mateos et al. 2011, Smith and Foggin 2014, Hale and Koprowski 2018).

Many species of harvester ants (Latreille) (Formicidae: Hymenoptera) have long been considered pests of range- and croplands within their native ranges (e.g., Cole 1968, Prins et al. 1990, Taber 1999). However, recent research reveals that harvester ants have numerous positive interactions that benefit ecological stability, and potentially human activities within their ecosystems, while also casting doubts on perceived pest roles. Here we review research that demonstrates the ecological importance of harvester ants affirming their roles as keystone species and clarifying their roles as pests. We focus on situational differences that led to harvester ants either acting as keystone species or pests, while also providing a summary of their effects on ecosystems and human activities.

Harvester Ants

The term 'harvester ant' can refer to any ant species which harvest and consume seeds but is most commonly applied to ants in the genera *Pogonomyrmex* Mayr, *Veromessor* Forel, and *Messor* Forel. One hundred twenty-six species of *Messor* occur in the Old World, eleven species of *Veromessor* occur in the New World, and 68 species of *Pogonomyrmex* occur in the New World (Bolton 2021). *Pogonomyrmex* evolved roughly 55 million years ago in the Neotropics, later expanding to the Nearctic (Ward et al. 2015). The genus *Messor* has recently undergone significant taxonomic revision; and New World species are now placed in *Veromessor* while Old World species are kept in *Messor*, both genera also diverging from other ants roughly 55 million years ago (Ward et al. 2015).

Harvester ant diets consist primarily of seeds from a wide range of plants, generally preferring small-seeded annuals such as grasses and forbs (MacMahon et al. 2000). Most harvester ant species also consume arthropods, carrion, and scavenge when given the chance (Cole 1968, Whitford 1978, Whitford and Jackson 2007). In general, harvester ants are most prevalent in arid grasslands and deserts, though some species inhabit tropical forests or high-elevation tundra (Bolton 2021). The ecological influence of harvester ants is most apparent from nest clearings, which for some species can reach over 10 m in diameter and 8 m deep (Fig. 1; Taber 1999). The roughly circular areas, termed 'nest-disks', on the ground surface are cleared of vegetation by the ants and maintained for the colony's lifespan, which span decades for some species (e.g., Keeler 1993; Gordon and Kulig 1996, 1998; Keller 1998; Sanders and Gordon 2004). Densities of nests in the landscape commonly exceed 100 colonies per hectare (e.g., Holbrook et al. 2016, Baraibar et al. 2019), accounting for over 20% of total land surface area in extreme cases (Willard and Crowell 1965).

From an ecological perspective, harvester ants are one of the most intensively studied groups of ants. The majority of ecological literature focuses on a minority of highly abundant harvester ant species which form large, influential colonies in arid climates, mainly *Pogonomyrmex* in the western United States (reviewed by MacMahon et al. 2000). Recent studies also highlight similar ecological importance to Central and South American *Pogonomyrmex*, as well as Mediterranean/Arabian/African *Messor*. We focus on literature from the last two decades, building off of MacMahon et al.'s (2000) review of *Pogonomyrmex* and including ecologically similar Old World harvester ants (*Messor*) and New World *Veromessor* where possible.

Harvester Ants as Keystone Species

Keystone species perform essential ecological functions (hereafter 'keystone roles') and are most broadly defined as species that maintain the organization, stability, and function of their communities, with disproportionately large inimitable impacts on their ecosystems (Power et al. 1996, Kotliar 2000, Hale and Koprowski 2018). Common 'keystone roles' occur through ecological engineering (e.g., kangaroo rats (*Dipodomys* spp.), prairie dogs (*Cynomys* spp.), and trophic regulation (e.g., gray wolves (*Canis lupus*)). Keystone roles often facilitate ecosystem stability by enhancing resilience and recovery after disturbances (Mouquet et al. 2013).

There is strong evidence supporting harvester ants as keystone species through trophic interactions and ecological engineering (e.g.,

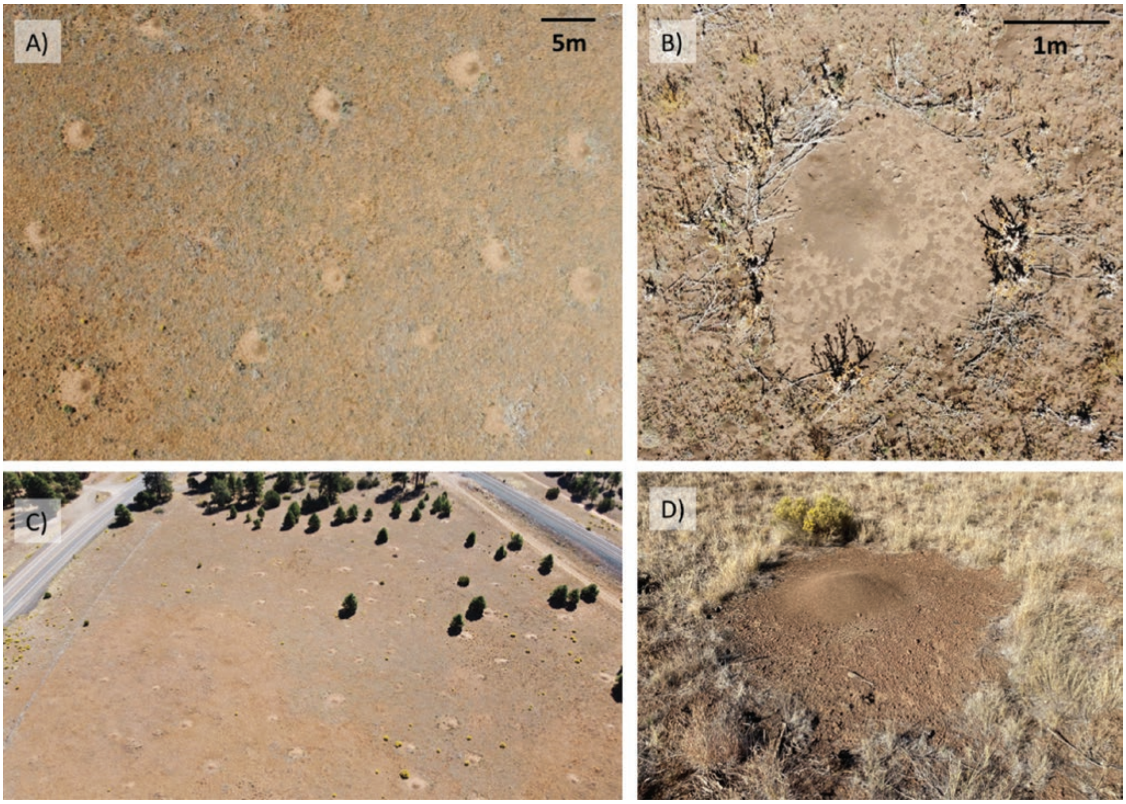

Fig. 1. Harvester ant (*P. occidentalis*) nests in high-density habitat from northern Arizona, southwestern United States. (A) Aerial (drone) view showing regular spacing of nests, (B) aerial view showing nest-clearing and nest-rim vegetation, (C) alternative aerial view of nests including tree and road for scale, and (D) angled view of nest.

Milton and Hoffman 1994, Soule and Knapp 1996). Through these roles, harvester ants directly or indirectly affect many ecosystem processes such as food-web dynamics, soil-modification, nutrient/energy flows, and disturbance regimes (MacMahon et al. 2000). By engineering nests, harvester ants structure plant and animal communities creating hotspots for nutrients and biodiversity (e.g., Wagner and Jones 2004, 2006; Whitford et al. 2007; De Almeida et al. 2020). Plant growth is often increased along nest-rims which promotes plant recovery following disturbances, thereby enhancing ecosystem stability (e.g., Nicolai et al. 2008, Mor-Mussery and Budovsky 2017, Nicolai 2019). By selectively harvesting seeds, ants can depress common plant species, thereby increasing community diversity (e.g., Nicolai and Boeken 2012). Harvester ants have a variety of direct trophic interactions with other animals including preying on other arthropods (e.g., Whitford 1978, Whitford and Jackson 2007), being preyed upon by insectivores (e.g., McIntyre 2003, Hojati et al. 2014, Sullivan et al. 2014, Mouhoub-Sayah et al. 2018) and stinging to defend nests against seed-eating vertebrates (Wiernasz et al. 2014). Below we summarize the ecological effects of harvester ants to highlight the various roles they play within their ecosystems.

Direct Effects of Harvester Ants on Ecosystems

Prey for—and Competition With—Vertebrates (pathway #1, Fig. 2)

Many insectivorous birds and lizards prey on harvester ants; some are obligate predators including several horned lizards that are species of concern for conservation (McIntyre 2003, Schmidt 2019; Fig. 2). *Pogonomyrmex occidentalis* (Cresson) is an important prey item for the endangered sage-grouse (*Centrocercus urophasianus*, Carlisle et al. 2017). *Messor* and *Veromessor* are common in the diets of many vertebrate insectivores (e.g., hedgehogs (*Atelerix algirus*) Mouhoub-Sayah et al. 2018, geckos (*Teratoscincus bedriagai*) Hojati et al. 2014). Promoting a healthy population of harvester ants is also considered conservation goals for increasing populations of some threatened insectivorous species such as horned lizards (McIntyre 2003, Sullivan et al. 2014).

Ants may compete with or facilitate granivorous rodents in complex interactions. Brown and Davidson (1977) called attention to the importance of competition of ants and rodents and found the removal of harvester ants (*Pogonomyrmex rugosus* (Emery), *P. desertorum* (Wheeler), and *Pheidole xerophila* (Wheeler)) increase kangaroo rat (*Dipodomys spectabilis*) populations and vice versa in southern Arizona. However, later papers suggest these results were not significant, and long-term data from the same experiment showed no effect of ant removal on rodents (Valone et al. 1994). Studies examining relationships with granivorous rodents are lacking in *Messor* and *Veromessor*; however, it is easy to speculate that competition for seeds with rodents is possible when seed preferences overlap. Competitive interactions with ants may be compensated for by beneficial interactions for rodents. For example, rodents can be kleptoparasites of harvester ants, raiding ant seed-caches (e.g., Clark and Clark 1989), and robbing foragers (Kline et al. 2018). Harvester ant seed-caches may be important seed-sources to rodents during times of resource-scarcity (e.g., Wiernasz et al. 2014).

Unique in the New World, *Pogonomyrmex* are armed with the most toxic insect venom known (Schmidt 2016), which likely evolved in response to rodents raiding seed-caches (Schmidt and Snelling 2009). Many species of *Pogonomyrmex* aggressively defend their nests against vertebrate intruders (Wiernasz et al. 2014). The nest area is also defended against other ant species, conspecifics, and arthropods (Wiernasz et al. 2014). While not intensively studied, it is likely that harvester ants compete for physical space with other fossorial animals.

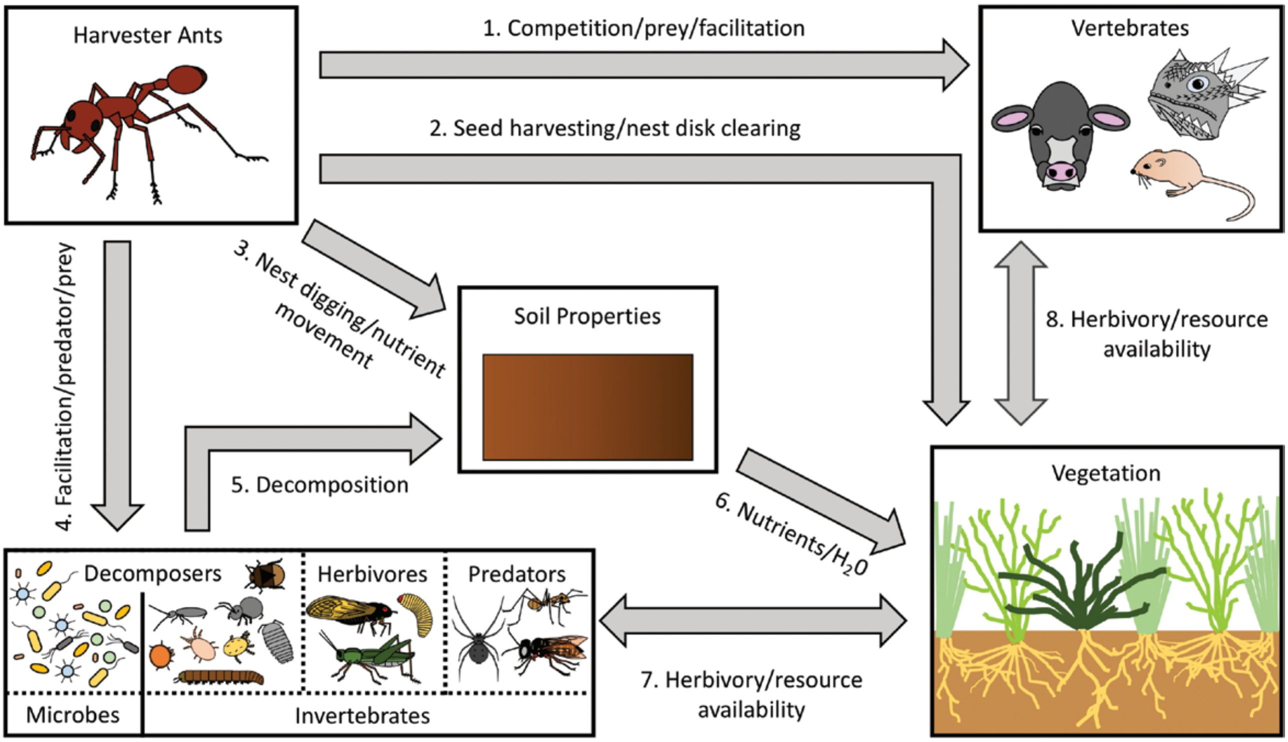

Fig. 2. Conceptual diagram of the main ecological effects (#1–10) of harvester ants on soils and communities. Effects of harvester ants on ecological communities can be direct (#1, 2, and 4); or indirect through soil properties (#3, 5, and 6); or indirect through community interactions (#7 and 8). Pathways are described in detail in text.

Seed-Harvesting and Nest-Clearing Effects on Vegetation (pathway #2, Fig. 2)

Harvester ants directly affect vegetation by selectively taking seeds from a variety of plant species and also through nest building. Some harvester ants clear 'nest-disks' (areas denuded of vegetation by worker ants) that can reach over 10 m in diameter (e.g., *Pogonomyrmex occidentalis* and *P. salinus* (Olsen), Soule and Knapp 1996). These nest clearings can occupy significant portions of vegetation across landscapes, usually 1–5% of land area in suitable habitats (MacMahon et al. 2000) but sometimes exceeding 15% (e.g., Willard and Crowell 1965, Holbrook et al. 2016). Nest building has large indirect effects on vegetation and animal communities (discussed below as an indirect effect).

Harvester ants are large-scale collectors and consumers of plant seeds having direct effects on plant communities. Plants may benefit from these relationships by having seeds dispersed (i.e., synzoochory, Gómez et al. 2019). Ants disperse seeds over short distances (<100 m) by accidentally dropping them (i.e., dyszoochory, Mull 2003, Sanchez et al. 2006) or disposing of them in refuse piles (Bulot et al. 2016). Relationships can be mutualistic, as some plants have evolved nutritious seed appendages (eliasomes) that ants remove, discarding the seed embryos (i.e., myrmecochory; e.g., Anjos et al. 2020). Lengyel et al. (2010) estimate myrmecochory is associated with 4.5% (~11,000 species) of angiosperms, highlighting the evolutionary advantage of dispersal from harvester ants.

Seed harvesting by ants for most plant species, however, is an antagonistic relationship, as seeds are eaten by ants (Whitford 1978). Most harvester ants have mass-recruitment strategies, where foraging ants return to search for food in the same general area where it was found before with foragers traveling over 20 m from nests (e.g., Beverly et al. 2009, Flanagan et al. 2012). Seed preferences and foraging intensity of ants shift in response to many factors such as seed availability (e.g., Pirk et al. 2009, Pol et al. 2011), seed traits such as energy content and morphology, resource distance, biotic factors such as neighboring colonies or predation, and weather (e.g., Crist and MacMahon 1991, 1992; Gordon and Kulig 1996; Gordon et al. 2013). Harvesting effects change over the year as ants have unimodal foraging in cooler months, bimodal foraging in warmer months (MacKay and MacKay 1989), and can be dormant in winter months (Kwapich and Tschinkel 2013). Harvester ants tend to select seeds that balance high nutrient content with an energetic trade-off for handling time (i.e., high-nutrient seeds with simple, easy-to-handle morphologies are preferred, particularly small-seed annuals (MacMahon et al. 2000)).

Foraging behaviors of harvester ants can cause compositional changes in seed banks (e.g., Crist and MacMahon 1992, DeFalco et al. 2009, Luna et al. 2018) and vegetation composition (e.g., Peters et al. 2005, Baraibar et al. 2011, Brown and Robertson 2020). However, harvester ant effects on vegetation composition through seed harvesting may be weaker than the effect of granivorous rodents (e.g., Valone et al. 1994, Anderson and MacMahon 2001). Gordon (1993) found no relation between vegetation currently growing in foraging areas and seed species collected by ants. Instead, ants mostly collected seeds distributed by wind and flooding. Harvester ants recruit to seed resources quickly, having larger effects on vulnerable seeds (i.e., seeds on the ground surface or 'seed-rain', Nicolai and Boeken 2012). The preferences of harvester ants for certain seeds can create filters that work against the establishment and seed survivorship of some plant species (e.g., Sánchez et al. 2006, Brown and Robertson 2020, Robertson and Robertson 2020).

Nest Digging Effects on Soil Properties (pathway #3, Fig. 2)

Harvester ant nests can extend many meters underground (e.g., Tschinkel 2014, 2015). Nest construction involves large-scale soil excavations, for example, 280 kg of soil material per hectare per year for *P. occidentalis* (Carlson and Whitford 1991); and 640 kg of material per hectare per year for *P. badius* (Tschinkel 2015). Ants transport food (e.g., seeds and insects) into nests and deposit trash middens of detritus on top of nests, while also clearing vegetation off nest-disks. These activities cause soils in nests to have a coarser texture, lower bulk density, higher water content, higher soil temperatures, increased nutrients (e.g., available nitrogen, phosphorus, potassium, magnesium), and higher organic matter (Wagner et al. 1997; Lei 2000; Wagner and Jones 2004, 2006; Jones and Wagner 2006; Whitford et al. 2007). Ant tunneling also aerates soil and changes soil hydrology (Lei 2000), increasing microbial respiration and decomposition (Jones and Wagner 2006). Through these changes to soil, ant nests become 'islands of fertility' or 'hotspots' supporting increased growth of vegetation along nest-rims (Wagner and Jones 2004, Gosselin et al. 2016). These effects may be magnified in the arid, nutrient-poor regions which harvester ants typically occur in.

Predation, Facilitation, and Prey for Arthropods and Microbes (pathway #4, Fig. 2)

Harvester ants provide trophic regulation of arthropods by facilitation of soil biota (both invertebrates and microbes) through habitat engineering and predation/prey relationships. Harvester ants are important prey for numerous arthropod species such as spiders (Cushing 2012) and may provide trophic control on other arthropods through their own predation (discussed below as indirect effect). Many myrmecophilous species (e.g., springtails, silverfish, crickets, cockroaches, beetles, mites, spiders, etc., aka 'houseguests') are highly adapted to life in harvester ant nests (e.g., MacKay 1983, Cushing 2012, Parmentier et al. 2020). These myrmecophiles can mimic ant nest-mate recognition cues such as pheromones or behaviors, with some specializing on consuming resources in ant waste-dumps or on ants themselves (Kronauer and Pierce 2011). Nest construction also facilitates soil microbes and other biota (e.g., bacteria, mycorrhizae, microarthropods such as springtails and mites, protozoa, and nematodes, Wagner et al. 1997, Snyder et al. 2002), which increase in biomass and activity (measured by respiration) in ant nest soil (Wagner and Jones 2004, 2006; Whitford and Jackson 2007). Harvester ant nests, therefore, host unique soil communities creating biodiversity hotspots.

Indirect Effects of Harvester Ants on Ecosystems

Effects of Harvester Ants on Soil Biota Functions (pathway #5, Fig. 2)

Harvester ants can positively impact soil chemistry and enhance decomposition processes through the facilitation of important soil biota such as nitrogen fixing bacteria (e.g., Wagner and Jones 2004, Jones and Wagner 2006, Boulton and Amberman 2006; Fig. 2). Enhanced microbial biomass in nest soils is documented for *Pogonomyrmex rugosus* (Wagner and Jones 2004, 2006), *P. barbatus* (Emery) (Wagner et al. 1997), *Messor* spp. (Ginzburg et al. 2008), and *Veromessor andrei* (Mayr) (Boulton et al. 2003, Boulton and Amberman 2006). Other major groups of soil biota are more diverse and abundant in harvester ant nest soils than background soils. These soil biota include protozoa, nematodes, and a variety of microarthropods (Wagner et al. 1997, Boulton et al. 2003, Wagner and Jones 2004). Experimental evidence suggests that the addition of food in the form of detritus discarded by ants is responsible for increases in the diversity and abundance of soil biota (Boulton and Amberman 2006). This evidence allows for the hypothesis that plant nutrient availability (and by extension plant growth and abundance) is increased in ant nest soils through soil biota facilitation (Wagner and Jones 2004).

Effects of Harvester Ants on Vegetation Through Soil (pathway #6, Fig. 2)

Harvester ant nest soil is a nutrient rich microhabitat that promotes plant growth on nest-rims, altering plant biomass and composition across entire landscapes (MacMahon et al. 2000). The nest-rim disk creates a niche preferred by certain plant species. Texas filaree (*Erodium texanum*), for example, grows abundantly around the edge of *Pogonomyrmex rugosus* nests (Whitford and DiMarco 1995). Plant species richness and productivity also increases along the nest-rims of many harvester ant species (e.g., Peters et al. 2005, Nicolai et al. 2008, Brown et al. 2012, Gosselin et al. 2016, Mor-Mussery and Budovsky 2017, Nicolai 2019, De Almeida et al. 2020, Pirk et al. 2020). Plants grow better in ant nest soil (Pirk et al. 2020), and plants on nest-rims benefit from having potential competitors cleared by ants. These nest-rim habitats can serve as refugia during disturbances, enhancing vegetation recovery following overgrazing (Mor-Mussery and Budovsky 2017), drought (Nicolai et al. 2008), and fire (Nicolai 2019). The greatest contribution of harvester ants to grassland ecosystems may be enhancing ecosystem stability through the creation of these specialized nest-rim habitats.

Effects of Harvester Ant Predation on Herbivores (pathway #7, Fig. 2)

Harvester ants are opportunistic predators of many arthropods, including some herbivorous pest species (Whitford 1978). While some consider harvester ants poor predators, they can be significant 'pulse' predators reducing arthropod populations close to nests (Whitford 1978, Nay and Perring 2005, Whitford and Jackson 2007). For example, *Pogonomyrmex californicus* (Buckley) can reduce carob moth (*Ectomyelois ceratoniae*) larvae on date palms (*Phoenix dactylifera*), providing some natural pest control (Nay and Perring 2005). Large portions of harvester ant arthropod prey consist of herbivorous species such as grasshoppers and Lepidoptera larvae (Whitford et al. 1976); but few studies have examined the significance of harvester ant predation in reducing herbivores or other pests.

Effects of Harvester Ants on Forage (pathway #8, Fig. 2)

Through their influences on vegetation, harvester ants impact forage quality and resource availability for vertebrates, especially grazers. Nest clearing of vegetation is usually compensated for by the enhanced growth found along nest-rims (Wight and Nichols 1966), increasing plant richness and productivity in many habitats (e.g., Peters et al. 2005, Nicolai et al. 2008, Brown et al. 2012, Gosselin et al. 2016, Mor-Mussery and Budovsky 2017, Nicolai 2019, De Almeida et al. 2020, Pirk et al. 2020). Harvester ant nest-rims, therefore, provide valuable forage for ungulates. For example, pronghorn antelope (*Antilocapra americana*, Whitford et al. 1995) and Persian gazelles (*Gazella subgutturosa*, Esmaeili and Hemami 2013) are known to preferably graze around nest-disks. As previously discussed, nest-rim habitat may help vegetation recover from disturbances (Nicolai et al. 2008, Nicolai 2019) including overgrazing (Mor-Mussery and Budovsky 2017), increasing forage availability and stability. The overall effects of harvester ants on forage seem positive, but few studies explicitly link harvester ant effects on vegetation to forage quality.

Harvester Ants as Cultural Keystone Species

Similar to the ecological concept of keystone species, ethnobotanists refer to culturally important species as 'cultural keystone species' (Gaoue et al. 2017). These species contribute in a major way to the cultural identity of a people, often with fundamental roles in medicine, materials, diets, and/or spiritual practices (Cristancho and Vining 2004). Harvester ants hold cultural importance to many indigenous peoples, most documented in the southwestern United States. For example, ritual and therapeutic use of harvester ants were common among some indigenous groups (e.g., Kitanemuk, Tübatulabal, and Chumash) of southern California before the mid-19th century. Groark (2001) summarizes accounts of young men ingesting hundreds of live *Pogonomyrmex californicus* to induce visionary quests during initiation ceremonies. Stings were used in medicine for conditions such as arthritis, paralysis, and during childbirth (Groark 1996, 2001). Harvester ants are important in the mythology of the Diné (Navajo), which avoid disturbing ant nests (Wyman and Bailey 1964, Capinera 1993). Aztecs believed harvester ants (likely *Pogonomyrmex barbatus*) brought the gift of corn, their most important crop, to the world (Taber 1999).

Which species are important to a culture can change over time (Garibaldi and Turner 2004), and it is difficult to correctly identify those species after cultural traditions are lost or changed. Coe and Gaoue (2020) highlight that identifying cultural keystone species requires robust cultural information which is currently lacking for many harvester ant species and indigenous peoples. This is potentially because traditions involving harvester ants were lost before being physically documented (e.g., Groark 1996). Harvester ants may be, or may have been, cultural keystone species and we encourage future studies to explore cultural relationships humans may share with harvester ants.

Harvester Ants as Pests

Through the early to mid-twentieth century scientists, land-managers, and farmers considered harvester ants to be pests through perceived negative impacts on rangelands and seed-crops. *Messor* have been associated as pests of seed-crops from which they harvest (e.g., Turaki et al. 2006, 2012), while *Pogonomyrmex* nest clearings are associated with decreases in forage for cattle on rangelands (Sharp and Barr 1960). Yet most of these perceived pest roles are only found in older literature and in some cases rigorous modern evidence supersedes previous pest conceptions.

Seed-Harvesting Effects on Agriculture

Harvester ants seem to pose an obvious threat to seed-crops, but the literature is surprisingly scarce on the subject. Perhaps because harvester ants prefer small-seeded annuals, mostly grasses (MacMahon et al. 2000) that are less agriculturally important, or because harvester ants often concentrate on foraging seeds on the ground surface rather than directly off the vegetation (e.g., Gordon 1993). Harvester ants also have low tolerance for soil disturbance and flooding, which reduces their numbers on tilled or flood-irrigated fields (Díaz 1992; Baraibar et al. 2009, 2019). References to seed-crop damage by *Pogonomyrmex* are rare, outdated, and mostly anecdotal (e.g., alfalfa (Barnes and Nerney 1957); clovers, small grains, grasses, and sunflowers (Randolph and Fuller 1953), red spring wheat (Borth et al. 1982)); it seems likely that harvester ants pose little threat to crops in the New World. However, some suggest *Messor galla* (Mayr) may be a seed-crop pest in Nigeria, taking seeds from crops such as cereal grains, sorghum, wheat, and rice (Turaki et al. 2006, 2012; Degri et al. 2013). Yet Baraibar et al. (2011) estimated *M. barbarus* take less than 1% of annual cereal crop yields in Spain and many studies suggest that *M. barbarus* prefer weedy species as seed sources, thereby improving, rather than harming, crop yields by reducing weeds (Baraibar et al. 2009, 2019; Westerman et al. 2012; Comas et al. 2016; Torra et al. 2016). Overall, there is little support that harvester ants are major pests to agricultural activities, but more explicit studies are needed.

Seed-Harvesting Effects on Invasion and Restoration Dynamics

The role of seed harvesting by ants in natural settings can be variable based on harvester ant preferences for desirable or undesirable plant species. Harvester ants can be detrimental to rare native plants in which loss of seeds can have a disproportionate effect on populations (e.g., *P. salinus* harvesting *Lepidium papilliferum*, Schmasow and Robertson 2016, Brown and Robertson 2020). In situations where harvester ants prefer native over exotic plant species, they may facilitate invading plants by reducing competition from native plants. For example, *Pogonomyrmex occidentalis* and *P. salinus* avoid harvesting invasive cheatgrass seed, preferring native seed sources (Ostoja et al. 2009, Schmasow and Robertson 2016, Robertson and Robertson 2020). The preference for native over exotic seeds is also seen by *P. carbonarius* in Argentina (Aput et al. 2019).

Restoration may be negatively impacted when ants select against native plant seeds. Broadcast seeding efforts in particular may be affected, as ants are efficient predators of seeds on the ground surface (Gordon 1993, Nicolai and Boeken 2012) and may prefer many of the seed species commonly used in restoration. For example, Paolini et al. (2020) show *P. salinus* can greatly reduce native seeds (e.g., Indian ricegrass (*Achnatherum hymenoides*) and saltbrush (*Atriplex canescens*)) commonly used by the Bureau of Land Management to restore habitats degraded by cheatgrass (Paolini et al. 2020). This is especially concerning given that *P. salinus* and *P. occidentalis* nest densities have been positively correlated with cheatgrass cover (Holbrook et al. 2016, Robertson and Robertson 2020), and *P. occidentalis* workers found to be more prevalent in cheatgrass versus native habitats (Ostoja et al. 2009).

Harvester ants can also work against invasion dynamics when they exhibit a dietary preference for exotic seeds. For example, *Pogonomyrmex rugosus* in the coastal sage scrub of California prefer exotic seeds of *Erodium cicutarium* and *Brassica tournefortii* over native species, which may help prevent the establishment of these non-native plants (Briggs and Redak 2016). *Pheidole bergi* (Pearson et al. 2014) and *P. carbonarius* (Pirk et al. 2017) in Argentina may also create filters on non-native seeds. Explicit tests of preferences between native and exotic seed sources are lacking for most harvester ant species and plant combinations in most habitats. These specifics may help inform localized invasion dynamics and be important to consider for broadcast seeding efforts where harvester ants exist.

Nest-Clearing Effects on Forage in Rangelands

The perception that *Pogonomyrmex* denuded rangeland by clearing vegetation was prevalent in the first half of the twentieth century in the United States driving their original pest perceptions (Hull and Killough 1951, Sharp and Barr 1960). Considering ant nest clearings can account for up to 20% of land surface area in extreme cases (Willard and Crowell 1965), it is understandable why ranchers were concerned. Furthermore, increases in harvester ant densities in overgrazed pastures was reported as early as 1862 (Lincecum 1862), implicating these ants in degrading range condition. However, data eventually showed that harvester ants are symptoms of overgrazing, and not primary causes of poor-ranges (Sharp and Barr 1960). Still, perceived reductions in vegetation drove the elimination of *Pogonomyrmex* populations within their native ranges to increase cattle-forage (Sharp and Barr 1960, Crowell 1963). Later evidence showed reductions by nest clearing are in-fact compensated for by enhanced vegetation growth around nest-disks (Wight and Nichols 1966, Soule and Knapp 1996). Moreover, recent studies have revealed keystone roles of harvester ants aid in supporting vegetation community stability (e.g., Nicolai et al. 2008, Nicolai 2019), casting doubt on perceived pest roles of harvester ants on rangelands. The paradigm of harvester ants being rangeland pests is mostly found in literature from the 1930s–1960s (e.g., Hull and Killough 1951, Crowell 1963) and is noticeably absent from recent literature.

Nest Effects on Human Infrastructure

Ants are commonly considered pests for their ability to infiltrate buildings and/or cause damage to structures through nesting activities (e.g., Field et al. 2007). Unlike other ant species, harvester ant incursions into buildings are rare as they prefer to nest and forage in the open (Klotz et al. 2005b). Harvester ants often prefer to nest alongside roads, presumably because bare-patches of soil are where alate queens prefer to initiate nests (DeMers 1993, Itzhak 2008). There are accounts of nesting activities of *Pogonomyrmex* damaging soil stability under structures like roads (Fritz and Vickers 1942) and airport runways (Gordon 1943). Yet the lack of modern, data-based evidence suggests that cases of damage to human infrastructure from harvester ants are rare or unfounded and do not constitute a strong pest role.

Stinging Effects on Humans

Among the most recent references concerning pest roles of harvester ants in the literature, as well as pest-company websites, are the potential health risks from their stings (Pinnas 1977; Klotz et al. 2005a, b; Field et al. 2007). While *Messor* pose little threat to humans, some *Pogonomyrmex* viciously defend nests (Cole 1968) with stings that are both painful and potentially lethal to those allergic to their venom (Schmidt 2016). This powerful sting is thought to have evolved as a particularly effective measure against rodents raiding seed-caches (Schmidt and Snelling 2009), and therefore is potent against most vertebrates, including humans. While not all *Pogonomyrmex* possess powerful stings, many of the large-nested and geographically widespread species most likely to interact with humans do. *Pogonomyrmex maricopa* (Wheeler) has the most potent of the known insect venoms (LD_{50} = 0.12 mg/kg, equating to roughly 12 stings to kill a 2 kg rodent) and some *Pogonomyrmex* species are ranked among the most painful insect stings in North America (Schmidt 2016). The vast majority of sting cases for humans are not life-threatening; extrapolating the estimated lethal dose of *P. maricopa* venom in mice to an average 62 kg human equates to hundreds of stings. However, in rare cases anaphylactic shock brought on by stings requires hospitalization and may cause death (Pinnas 1977; Klotz et al. 2005a, b). Even a single sting can be a painful experience with discomfort lasting 18–72 hr (Schmidt 2016). The largest danger comes from mass-stinging when colonies are disturbed, especially when victims are unable to remove themselves from nest areas (e.g., Klotz et al. 2005a, b). Yet, the ability to remove oneself from the nest area without fear of pursuit makes harvester ants much less dangerous than other stinging hymenopterans which can fly (e.g., honey bees (*Apis* spp.) or yellowjackets (*Vespula* spp.)).

Factors Affecting Harvester Ant Distributions and Colony Densities

Habitat associations and local population densities of species can influence perceived keystone and pest roles (Delibes-Mateos et al. 2011). For example, plateau pikas are often considered pests at high densities by landowners in Asia where they compete with livestock, but are generally tolerated at moderate or low densities (e.g., Jiang and Xia 1985, 1987). Ironically, pikas are found at their highest densities on overgrazed land (Zhang et al. 2003), potentially symptoms of degraded rangelands (Holzner and Kriechbaum 2001). Harvester ants show similar density-dependent relationships, and their habitat preferences and local population densities have driven many of the perceived beneficial/detrimental roles. Below we review factors affecting harvester ant site occupation and nest density to help inform situations that create high densities of harvester ant nests that may influence perceived keystone or pest roles.

Site Occupation

The most prevalent mechanisms driving site occupation by harvester ants are abiotic factors such as soil type (Johnson 2001), precipitation (e.g., Dibner et al. 2015), temperature; and biotic factors such as competition (both inter- and intraspecific) and available seed resources (Johnson 2001). Other influencing factors include—the available species pool, demographic factors (such as birth/death rates of colonies, which tend to be low for most harvester ant species), local predators/parasites/diseases, and stochastic factors such as order of species at locale and distance to source populations (Wiernasz and Cole 1995, Johnson 2001). In general, most harvester ants 1) prefer small-seeded annual grasses and forbs, 2) rely on precipitation events for timing nuptial flights and founding new nests, 3) are limited to warmer climates, and 4) specialize in soil type (typically either sand or clay) (Johnson 2001).

The most abundant harvester ant species prefer arid grasslands with individual niches refined to specific soils, vegetation, and climates for different species (Cole 1968, Taber 1999). For example, *Pogonomyrmex occidentalis* on the Colorado Plateau in the southwestern United States can be found up to ~2,200 m in elevation in open-spaces of woodlands or shrub-dominated habitats with clay to sandy soils; and *P. rugosus* is generally found below ~1,900 m in elevation in open-grassland habitats with clay to limestone soils, with some mid-elevational habitats where both species occur (e.g., Uhey et al. 2020a,b, 2021a). Elevational limits indicate a strong role of climate in determining harvester ant ranges. These large-scale factors cause broad-scale clumping patterns in harvester ant distributions around preferred habitats (Crist and Wiens 1996, Schooley and Wiens 2003). On a fine-scale, harvester ant nest densities can vary markedly with changes in soil texture, vegetation, disturbance regimes, and interactions with other community members (Table 1). Under favorable conditions, colony densities of some species reach well over 100 colonies/hectare with regular spacing among colonies caused by intraspecific competition for territories around nests (Fig. 1; Table 1). Johnson (2001) reviews the biogeographic and community structure of harvester ant species assemblages; here we focus on factors that affect the colony densities of species that can dominate landscapes.

Table 1. Studies that estimate harvester ant nest densities and percent of total barren area caused by ant-clearings

Citation	Location	Ant species	Nest density range (ha^{-1})	Av. area % barren
Sharp and Barr (1960)	Idaho, United States	*Pogonomyrmex salinus*[a]	9–40	0.21
Willard and Crowell (1965)	Oregon, United States	*Pogonomyrmex salinus*[a]	49–74	13.84
Kirkham and Fisser (1972)	Wyoming, United States	*Pogonomyrmex salinus*[a]	0–10	2.43
Rogers and Lavigne (1974)	Colorado, United States	*Pogonomyrmex occidentalis*	3–31	0.28
Clark and Comanor (1975)	Nevada, United States	*Pogonomyrmex occidentalis*	30–43	3.34
Sneva (1979)	Oregon, United States	*Pogonomyrmex salinus*[a]	32.4–80.1	2.2
Crist and Wiens (1996)	Colorado, United States	*Pogonomyrmex occidentalis*	0–50	nr
Soule and Knapp (1996)	Oregon, United States	*Pogonomyrmex salinus*[a]	40	0.08
Kretzer and Cully (2001)	Kansas, United States	*Pogonomyrmex rugosus*	36–64	nr
		Pogonomyrmex barbatus	9–53	nr
		Pogonomyrmex occidentalis	1–20	nr
Usnick and Hart (2002)	Colorado, United States	*Pogonomyrmex occidentalis*	3.2–97	nr
Azcárate and Peco (2003	Spain	*Messor barbarus* (Linneaus)	200–300	nr
		Messor bouvieri (Bondroit)	0–130	nr
Schooley and Wiens (2003)	New Mexico, United States	*Pogonomyrmex rugosus*	10–41	0.14
Wagner and Jones (2004)	Nevada, United States	*Pogonomyrmex rugosus*	28.3–70.9	0.5
Beever and Herrick (2006)	Nevada, United States	*Pogonomyrmex* spp.	1.3–14.6	nr
Baraibar et al. (2009)	Spain	*Messor barbarus*	181–643	nr
Nicolai et al. (2010)	Texas, United States	*Pogonomyrmex barbatus*	nr	0.06
Baraibar et al. (2011)	Spain	*Messor barbarus*	140–1168	8.89
Edelman (2012)	New Mexico, United States	*Pogonomyrmex rugosus*	13–24	nr
Esmaeili and Hemami (2013)	Iran	*Messor* spp.	nr	0.29
Blanco-Moreno et al. 2014)	Spain	*Messor barbarus*	60–724	nr
Dibner et al. (2015)	Wyoming, United States	*Pogonomyrmex occidentalis*	6–60	nr
Gosselin et al. (2016)	Idaho, United States	*Pogonomyrmex salinus*[a]	30–39	0.12
Holbrook et al. (2016)	Idaho and Wyoming, United States	*Pogonomyrmex salinus*[a] and *P. occidentalis*	0–140	nr
Comas et al. (2016)	Spain	*Messor barbarus*	948	nr
Baraibar et al. (2019)	Spain	*Messor barbarus*	188–948	nr
Robertson and Robertson (2020)	Idaho, United States	*Pogonomyrmex salinus*[a]	11.97–13.57	nr

When not explicitly provided in the citation, percent barren area was calculated (when possible) using average nest-disk size. Some values were not reported (nr) in citations.

[a]Previously *P. owyheei*.

Habitat Quality

Cole (1932a, b) first noticed harvester ants are dependent on seeds from plants near nests, necessitating an abundance of preferred vegetation for colonies to thrive. Colony densities are often higher in areas with preferred seed resources (e.g., Kirkham and Fisser 1972, Pirk et al. 2009, Pol et al. 2011). Cole (1932a, b) also observed that most harvester ant species preferred certain soil conditions. Measurements of soil texture such as percent sand, silt, and clay, are strong predictors for colony densities for many harvester ant species (see Kirkham and Fisser 1972, Johnson 2000, Baraibar et al. 2019). Soil moisture is particularly important for colony founding, larval/pupal development, and storing seeds (Johnson 2000, Gordon et al. 2013), and soils differ in water retention driving ant preference for certain soils. Accordingly, precipitation is also a strong driver of harvester ant nest densities. For example, in surveys across 155 km^2 in Wyoming, United States, the strongest predictor for *P. occidentalis* nest densities was precipitation (Dibner et al. 2015), and nest densities of *P. barbatus* were reduced following drought years in New Mexico (Sanders and Gordon 2004). Cole (1932a, b) also noted that most harvester ants were seldom found in canopied habitats or shaded topography. Altitude, slope, and orientation towards the sun influence soil temperature with low temperatures decreasing nest survival probability (Crist and Williams 1999). Thus, both topography and temperature also determine nest densities (Crist and Wiens 1996). Foraging efficiency, and the risk foraging poses to ant workers, is directly impacted by temperature and humidity (MacKay and MacKay 1989, Crist and MacMahon 1991, Azcárate et al. 2007) and ultimately affects colony fitness (Gordon 2013). The highest densities of harvester ants are found in congruence with optimal temperature profiles of warm, dry climates (Dibner et al. 2015, Holbrook et al. 2016, Uhey et al. 2020a).

Disturbances

Both natural and anthropogenic disturbances affect harvester ant colony densities, although the latter is more represented in the literature. Roads, hiking trails, airport runways, and other similar human modifications that reduce vegetation cover (DeMers 1993, Terranella et al. 1999, Itzhak 2008, Uhey et al. 2021b), along with fires (Holbrook et al. 2016, Day et al. 2018) and grazing (Table 2) can increase harvester ant nest densities. Oppositely, nest densities may be decreased in areas surrounded by high-urbanization (De Jong 2015) and from tillage on farms (Díaz 1992; Baraibar et al. 2009, 2019). Disturbances that increase colony densities of harvester ants share similarities in opening habitats by reducing vegetation. These changes may also facilitate nest-founding of harvester ants which prefer bare ground to initiate nests and growth of their preferred seed-sources. Disturbances that decrease harvester ant nest densities are similar in that they reduce soil stability and increase shading, thereby destabilizing nesting conditions.

Grazing

Increases in harvester ant nest densities are especially associated with cattle grazing in the western United States (Cole 1968). Cattle grazing impacts spatial patterns of ant nests (Schooley and Wiens 2003) which is likely caused by alteration of soil and vegetation characteristics by grazers. Explicit tests between harvester ant nest densities and grazing are rare and confined to *Pogonomyrmex* in the western U.S. (Table 2). In most cases, grazed plots had higher nest densities than control plots. Grazing reduces vegetation cover, which could facilitate nesting of harvester ants. Grazing may also increase preferred seed resources for ants. However, too much grazing seems to lower ant nest densities, as high-intensity grazed plots tend to have low nest densities. Usnick and Hart (2002) hypothesize too many cattle disrupt nest construction and foraging through hoof-traffic. In general, moderate (not heavy) grazing seems to be beneficial to harvester ants.

Intraspecific Competition

Intraspecific competition is generally considered the predominant factor structuring harvester ant communities (Johnson 2001). In areas with preferable conditions, harvester ant colonies can occur in high densities that are regularly spaced through intraspecific competition with other colonies (Fig. 1; Wiernasz and Cole 1995, Crist and Wiens 1996, Schooley and Wiens 2003, Dibner et al. 2015). Foraging ants may travel as far as 50 m from their nest which inevitably leads to interactions with other colonies (e.g., Hölldobler 1976, Gordon and Kulig 1996). Foraging territories are established through forager interactions (usually nonviolent) which divide available habitat among different colonies (Hölldobler 1976, Gordon 2013, Lubertazzi et al. 2013). These territorial interactions limit nest density by preventing new colonies from establishing and producing over-dispersed (regular) patterns on fine-scales (Dibner et al. 2015).

Interspecific Interactions

Harvester ants compete with other ant species for space and scavenging resources (e.g., Sanders and Gordon 2004). Interspecific competition for seeds with other harvester ant species is probably rare, as co-occurring species usually partition seed resources or habitats (e.g., Solida et al. 2011, Saar et al. 2018). However, other ant genera, especially non-native ants can have detrimental effects on harvester ants. For example, Argentine (*Linepithema humile*) and fire ants (*Solenopsis invicta*) directly reduce harvester ant populations by raiding nests (Porter and Savignano 1990, Zee and Holway 2006).

Table 2. Studies comparing harvester ant nest densities across grazing-treatments show patterns of (↑) increases with grazing, (↓) decreases with grazing, (↑↓) increases with light- and/or moderate-grazing but decreases under heavy-grazing, and null/no pattern

Citation	Location	Ant species	Treatments	Colony density relationship with grazing
Kirkham and Fisser (1972)	Wyoming, United States	*Pogonomyrmex salinus*[a]	4 grazing intensities	null
Rogers et al. (1972)	Colorado, United States	*Pogonomyrmex occidentalis*	4 grazing intensities	↑ moderate, ↓ heavy
Crist and Wiens (1996)	Colorado, United States	*Pogonomyrmex occidentalis*	light vs moderate vs heavy	↓
Usnick and Hart (2002)	Colorado, United States	*Pogonomyrmex occidentalis*	light vs moderate vs heavy	↑ moderate, ↓ heavy
Schooley and Wiens (2003)	New Mexico, United States	*Pogonomyrmex rugosus*	grazed vs ungrazed	↑
Beever and Herrick (2006)	Nevada, United States	*Pogonomyrmex* spp.	grazed vs ungrazed	↓

Note some studies only compare grazed/ungrazed treatments, while others compare multiple grazing intensities.

[a] Previously *P. owyheei*.

In some cases, harvester ant nest densities are lower in areas with high densities of burrowing rodents which potentially disrupt ant nest construction (Sanders and Gordon 2004) and also pose the threat of raiding ant seed-caches. Sometimes rodents kleptoparasitize harvester ants (e.g., Clark and Clark 1989, Wiernasz et al. 2014, Kline et al. 2018). However, long-term removal experiments examining the interaction between granivorous rodents and ants showed only equivocal results with no constant patterns (Valone et al. 1994). Interspecific competition is probably less important than intraspecific competition and abiotic factors (reviewed by Johnson 2001). On the other hand, there is evidence of facilitative relationships with rodents that burrow. For example, nesting banner-tailed kangaroo rats (*Dipodomys spectabilis*) create ideal soil conditions for founding-queens of *P. rugosus* and increase the growth of preferred plant species by enhancing seed resources (Edelman 2012). Harvester ant queens near kangaroo rat nests have higher survival rates, and the nests of both ants and kangaroo rats across landscapes are spatially associated (Edelman 2012). Increased colony densities have been reported for *P. occidentalis* on abandoned pocket gopher (*Thomomys talpoides*) mounds (Hopton 2001) and *P. rugosus* on prairie dog (*Cynomys ludovicianus*) mounds (Kretzer and Culley 2001). However, in the same study Kretzer and Culley (2001) found no increase on prairie dog mounds for *P. occidentalis* or *P. barbatus*, and Alba-Lynn and Detling (2008) found no spatial relationships between prairie dog mounds and *P. occidentalis* nests. Relationships between harvester ants and burrowing rodents may be variable, and only noticeable once rodents have abandoned burrows, creating ideal nesting locations (i.e., bare ground) for ants.

Clarifying Keystone and Pest Roles in Management

Compared to pest roles, keystone roles for harvester ants are thoroughly documented in the literature. The distribution of keystone species can impose spatial structure on landscapes, influencing ecosystem function and stability (Hastings et al. 2007). Termites, for example, impart substrate heterogeneity through nest construction, enhancing plant growth and increasing the robustness of landscapes to desertification (Bonachela et al. 2015). Harvester ant nests seem to play similar keystone roles within their ecosystems (Nicolai et al. 2008, 2019). Still, harvester ants can play both keystone and pest roles depending on the human-perceived context. Here we clarify these roles and give management recommendations.

Harvester ant activities can be viewed as having pest- or keystone roles depending on circumstance, but keystone roles are far better supported (Supp Table 1 [online only]; Fig. 3). When ants harvest seeds that are undesirable, such as weeds or invasive species, they may be beneficial to agriculture and/or restoration. However, when ants harvest desirable native or crop species, they may be considered detrimental. Overall, the pest role from seed harvesting in agriculture is likely negligible, however, there is more support for negative effects to broadcast seeding restoration. Nest building creates beneficial microhabitats for vegetation and other biodiversity, but may be detrimental depending on location and density in rare instances. Specifically, nests may cause damage when located under anthropogenic structures like roads and airport runways, although there is no recent evidence for this. Nests may also affect productivity on

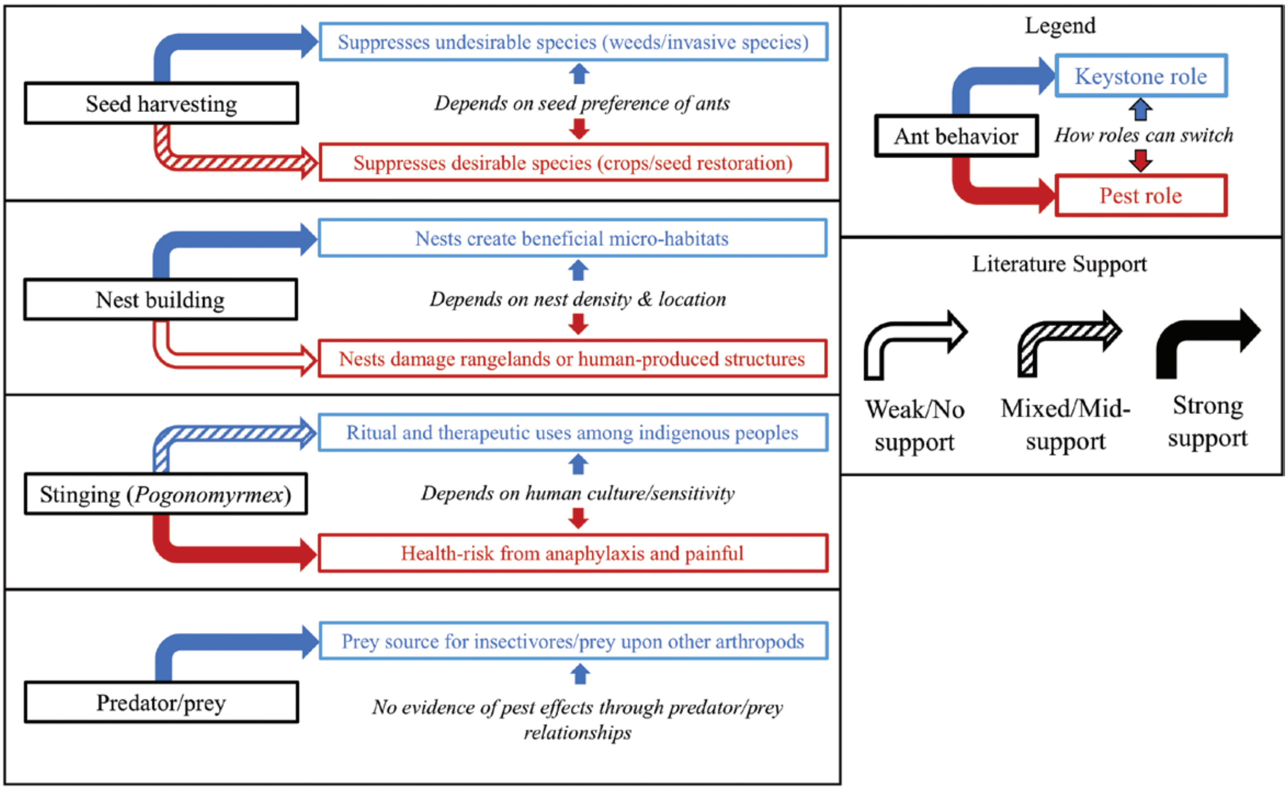

Fig. 3. Clarification of the pest- and keystone roles of harvester ants. Black boxes contain ant activities that can be viewed as pest- or keystone roles. Top arrows represent keystone roles, while lower arrows represent pest roles. Perceived roles can switch from pest to keystone for some ant activities depending on circumstance and have different levels of literature support represented by arrow fill. 'Weak support' is assigned in cases where literature is scarce or outdated, 'mixed support' when literature is either contradictory or requires more investigation, or 'strong support' when the literature is recent and conclusive (Supp Table 1 [online only]). See online version for color figure.

rangelands when at extremely high densities, although recent evidence points towards harvester ants exhibiting positive roles on primary productivity in rangelands, essentially negating the historical rangeland pest paradigm. Stinging in *Pogonomyrmex* can be viewed as culturally important, although further study is needed for this keystone role, or as a human health risk. Trophic relationships of ants with other insectivores and arthropod prey are beneficial in supporting native biodiversity, with no reported pest roles associated with it.

Control Recommendations

Large-scale control of harvester ant populations seems unlikely to benefit rangeland conditions or most seed-crops, but the practical danger from stings suggests targeted elimination may sometimes be necessary for areas of concentrated human habitation. Poisoned baits are effective at eliminating individual harvester ant nests (Crowell 1963, Race 1964, Lavigne 1966, Borth et al. 1982, Salas-Araiza et al. 2020) but can have detrimental effects on nontarget organisms. Mechanical control of harvester ants by shading (e.g., Bucy and Breed 2006, Tschinikel 2014), flooding, or tilling (Baraibar et al. 2011, 2019) nest areas may provide an alternative to pesticides but have yet to be tested systematically. We propose that in general, control is rarely needed and only necessary where harvester ants pose immediate health risks (e.g., playgrounds, small backyards).

Bioindicators for Conservation Management

Harvester ants may be important to monitor and potentially facilitate for conservation-based management of their habitats. Several studies suggest that healthy populations of harvester ants should be a part of restoration and/or conservation goals (Carlisle et al. 2017, De Almeida et al. 2020) because of their beneficial roles in aiding vegetation recovery. In some cases, facilitating harvester ant colonization by either directly adding queens from other areas or managing conditions to be favorable for harvester ant establishment may yield direct restoration tools, as suggested for Mediterranean *Messor* (De Almeida et al. 2020). Harvester ants are abundant, easily sampled, responsive to disturbances, and have long-lived colonies (MacMahon et al. 2000) making them ideal surrogates for quantifying ecological health. Entire ant communities are recognized and used as bioindicators for ecological health (e.g., Andersen et al. 2002), but harvester ants on their own may also be just as useful. *Pogonomyrmex rugosus*, for example, bioaccumulates heavy metals suggesting its use in monitoring mining restoration success (Del Toro et al. 2010). *Pogonomyrmex barbatus* foraging performance decreases with forest regeneration suggesting its use in monitoring forest restoration (Hernandez-Flores et al. 2016). *Pogonomyrmex occidentalis* nest densities correlate positively with sage-grouse populations (Carlisle et al. 2017) and other harvester ants are necessary prey items for threatened horned lizards (McIntyre 2003, Schmidt 2019), showing their importance for the conservation of endemic insectivores. The links of harvester ant nest densities with grazing intensity (Rogers et al. 1972, Crist and Wiens 1996, Usnick and Hart 2002, Schooley and Wiens 2003, Beever and Herrick 2006), invasive grass species (Holbrook et al. 2016), and climate (Dibner et al. 2015), along with the ease of aerial/satellite detection of their nests, suggest strong potential for use in remote sensing.

Considerations for Vegetation Restoration in Harvester Ant Habitats

Restoration plans in areas with high densities of harvester ants should consider ant effects on vegetation and ant preference for vegetation when planting and seeding. Harvester ants can select native (co-evolved) dominant grasses (e.g., Robertson and Robertson 2020), the same species common to broadcast seeding restoration (Paolini et al. 2020). Harvester ants can be beneficial to restoration, however, only when they prefer and suppress non-native seeds (Briggs and Redak 2016). Seeding efforts near nests may find more success by using plant species not preferred by ants, applying seeds when ant activity is low during colder times of the year, sowing seeds into the soil, or distancing seed-application from nests where possible. Restoration efforts that directly plant seedlings should also consider that ants will clear vegetation planted too close to nests, although they are less able to remove woody vegetation (Taber 1999).

Research Needs

The effects of harvester ants on vegetation are numerous, context-dependent, and many aspects of their influences on ecosystems are still unknown. Our knowledge is heavily skewed towards a small number of *Pogonomyrmex* species from just a few habitat types in the western United States; and baseline information is needed for many regions and harvester ant species. The relationship between harvester ants with plant communities should be of particular concern for future studies. Some questions to consider: How important are harvester ant nest-rim habitats to vegetation recovery following disturbances such as drought and fire? Are harvester ants facilitators or simply beneficiaries of non-native invasions such as cheatgrass (e.g., Holbrook et al. 2016)? In which scenarios do harvester ants prefer native (e.g., Paolini et al. 2020) or invasive seeds (e.g., Briggs and Redak 2016), and does their preference alter local invasion dynamics or seed restoration? And finally, can harvester ant nest densities be used as indicators for rangeland quality or invasive species monitoring? Answers to these questions are likely to change from system to system, but a baseline knowledge of these specifics will likely improve restoration of grass and rangelands where harvester ants are present.

Conclusions

Harvester ants are important regulators of plant and animal community structure, shaping landscape patterns and contributing to the ecosystem stability of most arid grasslands. In healthy grassland systems, harvester ants play keystone roles by enhancing plant diversity and creating landscape heterogeneity. Yet their roles in invasion dynamics can switch from beneficial to determinantal depending on seed preferences. Furthermore, relationships between harvester ants and cattle grazing, and their collective impacts on vegetation remain unclear. In general, the perception of harvester ants as pests is unsupported. We hope that the recognition and knowledge of the keystone roles of harvester ants in grassland communities can help reduce human conflicts with these native ants.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

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