

Red imported fire ant, *Solenopsis invicta* (Burden) (Hymenoptera: Formicidae), abundance and arthropod community diversity affected by pasture management

Ryan B. Schmid^{1,*}, and Jonathan G. Lundgren¹

Abstract

The red imported fire ant, *Solenopsis invicta* (Buren) (Hymenoptera: Formicidae), is one of the most prolific invasive species in the southeastern US. These invaders preferentially colonize highly disturbed land and grassland habitat. Management of livestock in pasture systems can have a profound impact on the level of disturbance in grassland habitats, and we hypothesized that adaptive multi-paddock pasture management would significantly increase *S. invicta* abundance in southeastern US pastures where arthropod diversity would decrease as *S. invicta* abundance increases. We studied the effects that adaptive multi-paddock pasture management systems (based on stocking density, rotation frequency, and insecticide/anthelmintic [wormer] application rates) have on fire ant mound abundance and arthropod diversity for the soil, foliar, and dung communities. *Solenopsis invicta* mounds and mound areas were documented along transect lines in 6 pastures. Soil and foliar arthropod communities were collected along the same transect lines, and dung communities were sampled from pats within the pasture system. Pastures managed under adaptive multi-paddock practices had 3.4× more *S. invicta* mounds and 4.6× more mound area than their conventionally managed counterparts. However, arthropod diversity did not correlate with *S. invicta* abundance in any of the 3 arthropod communities sampled. This study shows adaptive multi-paddock pasture management can increase *S. invicta* mound abundance, but arthropod communities in adaptive multi-paddock pastures do not suffer decreased diversity from increased abundance of *S. invicta*.

Key Words: red imported fire ant; insect community; pasture management; grasslands

Resumen

La hormiga roja de fuego importada, *Solenopsis invicta* (Buren) (Hymenoptera: Formicidae), es una de las especies invasoras más prolíficas del sureste de Estados Unidos. Estos invasores colonizan preferentemente tierras y pastizales muy perturbados. El manejo del ganado en los sistemas de pastizales puede tener un impacto profundo en el nivel de alteración en los hábitats de los pastizales. Planteamos la hipótesis de que el manejo adaptativo de los pastos en múltiples potreros aumentaría significativamente la abundancia de *S. invicta* en los pastizales del sureste de los Estados Unidos, donde la diversidad de artrópodos disminuiría a medida que *S. invicta* aumenta su abundancia. Estudiamos los efectos que los sistemas adaptativos de manejo de pasturas en múltiples potreros (basados en la densidad de población, frecuencia de rotación y tasas de aplicación de insecticidas/antihelmínticos [gusanos/lombrices]) tienen sobre la abundancia de los montículos de la hormiga roja de fuego importada y la diversidad de artrópodos para las comunidades de suelo, foliar y estiércol. Se documentaron los montículos de *Solenopsis invicta* y las áreas de montículos a lo largo de las líneas de transectos en 6 pastizales. Se recolectaron comunidades de artrópodos foliares y del suelo a lo largo de las mismas líneas de transecto, y se tomaron muestras de las comunidades de estiércol de las zonas de pasto dentro del sistema de pastizales. Los pastos manejados bajo prácticas adaptativas de múltiples potreros tenían 3.4 veces más montículos de *S. invicta* y 4.6 veces más área de montículos que sus contrapartes manejadas convencionalmente. Sin embargo, la diversidad de artrópodos no se correlacionó con la abundancia de *S. invicta* en ninguna de las 3 comunidades de artrópodos muestreadas. Este estudio muestra que el manejo adaptativo de pastizales en varios potreros puede aumentar la abundancia de los montículos de *S. invicta*, pero las comunidades de artrópodos en los pastos adaptativos de varios potreros no sufren una disminución de la diversidad debido al aumento de la abundancia de *S. invicta*.

Palabras Clave: hormiga roja de fuego importada; comunidad de insectos; manejo de pastos; pastizales

Invasive species are regarded as one of the main threats to native biodiversity (Simberloff 2000; Early et al. 2016). In general, invasive ants negatively affect native ant and arthropod community diversity through competitive displacement and direct predation (Porter & Savignano 1990; Human & Gordon 1997; Jourdan 1997; Hoffmann et al. 1999; Sanders et al. 2001; Holway et al. 2002). The red imported fire ant, *Solenopsis invicta* (Buren) (Hymenoptera: Formicidae), is one of the most well-known invasive ants because of environmental and economic impacts associated with this species (Apperson & Adams 1983; Lofgren 1986; Pimentel et al. 2005). Increases of *S. invicta* population

densities in invaded areas are associated negatively with overall ant species richness and abundance (Stein & Thorvilson 1989; Camilo & Phillips 1990; Chan & Guénard 2020). However, habitat disturbance is a common confounding factor in these studies because it can increase *S. invicta* abundance while simultaneously hindering native ant communities (Wojcik 1983; Buczkowski & Richmond 2012). Although this is a difficult subject to unravel, a few studies have investigated the role that disturbance type and intensity has on *S. invicta* colonization (King & Tschinkel 2008; Steele et al. 2020). For example, Steele et al. (2020) found that grazing intensity significantly increased *S. invicta* density,

¹Ecdysis Foundation, 46958 188th Street, Estelline, South Dakota 57234, USA; E-mail: ryan.schmid@ecdysis.bio (R. B. S.), jonathan.lundgren@ecdysis.bio (J. G. L.)

*Corresponding author; E-mail: ryan.schmid@ecdysis.bio

but other forms of pasture management that did not disturb the soil, e.g., dragging and mowing, were not correlated with *S. invicta* density. Moreover, actively grazed pastures have been shown to have higher *S. invicta* mound density compared with pastures without active grazing (Tucker et al. 2010).

Adaptive multi-paddock grazing is a pasture management system that was developed and refined during the latter half of the 20th century, due in part to mounting evidence for environmental benefits (Teague et al. 2011). Adaptive multi-paddock grazing uses herd management techniques like multiple paddocks per herd, high animal densities, short periods of grazing, adequate recovery periods for vegetation, and high stocking rates (Savory & Parsons 1980; Savory & Butterfield 1999; Teague 2014). Adaptive multi-paddock grazing practices can improve the health of pasture soil and plant communities by enhancing soil organic matter, water holding capacity, nutrient availability, and can increase fungal to bacterial ratios in the soil (Teague et al. 2011). These management practices also produce short, punctuated disturbances of paddocks within pastures, which creates an opportunity for *S. invicta* to colonize the disturbed area following a grazing event.

Understanding the impacts of adaptive multi-paddock grazing on *S. invicta* populations, and subsequently the arthropod community, is key to discerning if the environmental benefits of this pasture management method extends to arthropod diversity. Therefore, we documented *S. invicta* abundance and arthropod community diversity in adaptive multi-paddock and conventionally managed pasture systems. We developed 2 hypotheses for this study. First, pastures managed under adaptive multi-paddock grazing regimes would contain higher abundance of red imported fire ant mounds relative to their conventionally managed counterparts. Secondly, arthropod community diversity would decrease as *S. invicta* mound abundance increased.

Materials and Methods

SITE SELECTION

Sampling occurred within the known range of *S. invicta* in the US. Specifically, pastures were located in DeKalb County, Alabama ($n = 2$ pastures), Calhoun County, Alabama ($n = 2$ pastures), and Wilkinson County, Mississippi ($n = 2$ pastures), and fire ant mounds were observed in all those pastures. Adaptive multi-paddock and conventional grazing management systems had been employed for at least 10 yr prior to initiation of our study. Selection of treatment pairs accounted for variance in pasture management as outlined in detail by Mosier et al. (2021). Specific management criteria considered for selection of sample site pairs included land use history prior to current grazing management, soil types, cattle stocking rates, herbicide usage, legacy

of fertilization, and length of management history. Within this framework of congruent site pairs, ranch managers executed a variety of livestock grazing management practices that fit within their ranching system and goals as explained in Schmid et al. (2021). These grazing practices were used to categorize pastures into 1 of 2 treatment groups based on meeting a majority (≥ 4) of the qualifications defined in Table 1. Grazing management practices that varied between operations and used to categorize adaptive multi-paddock and conventional treatments included stocking density, rotation frequency, and insecticide/anthelmintic (wormer) use (Table 1). Grazing treatments were paired (< 8 km apart) across regional site localities.

SAMPLING PROCEDURE

Sampling occurred from 29 Sept to 1 Oct 2018. A total of six 46 m transect lines (spaced 25 m apart) were established within each pasture. The first set of 3 transects was located in one area of the pasture with the remaining 3 placed a minimum of 100 m from that first set. Two separate areas were chosen for transect establishment because of similar soil characteristics within pasture and across treatment pairs as outlined by Mosier et al. (2021). All sampling from individual transects within a pasture were compiled to form 1 dataset for each arthropod community per pasture. *Solenopsis invicta* mounds observed within 1 m of transect lines were counted along with the area of each mound following the method outlined by Porter et al. (1992) for sampling fire ant mound densities and areas along transects. Foliar-dwelling arthropods were sampled from pasture vegetation along 3 of the same transect lines that *S. invicta* mounds were sampled. Pasture foliage was swept with a 38 cm diam sweep net, with 25 sweeps occurring perpendicular to each side of a transect (total of 50 sweeps per transect). The soil arthropod community was sampled twice on 4 of the transects (total of 8 samples per pasture) using soil cores (10 cm diam, 10 cm deep). Dung arthropod community was sampled from randomly selected manure pats from each pasture (total of 5 pats per pasture). Age of dung pats ranged from 2 to 5 d old, because this age contains peak arthropod abundance and diversity (Pecenka & Lundgren 2018). Arthropods within soil cores and dung pats were extracted using a Berlese system over 7 d, which ensured that each soil/dung core had completely dried and all arthropods had left the core. Soil and dung cores were placed on ice upon extraction from the field then loaded into the Berlese system as soon as possible after extraction (within 60 h of collection). Arthropods collected from sweep samples and Berlese system were stored in 70% ethanol until they could be identified and catalogued. Each specimen was identified to the lowest taxonomic level, representing functional morphospecies. Larvae were considered as distinct morphospecies because of their discrete differences in ecological function. Voucher specimens were deposited in the Mark F. Longfellow Biological Collection at Blue Dasher Farm, Estelline, South Dakota, USA.

Table 1. Categorized ranching system and associated composite rank score of individual ranches used in study based on cattle stocking density, herd rotation frequency, and insecticide/anthelmintic (wormer) use. Ranches whose rank scores are ≥ 4 were considered adaptive multi-paddock grazing; those with rank scores ≤ 3 were considered conventional. The 3 management practices were scored 0 to 2, with higher numbers reflecting adaptive multi-paddock practices. Stocking density (animal units) was divided into < 5 animal units per ha (0), 5 to 10 animal units per ha (1), and > 10 animal units per ha (2). Rotation frequency was divided into > 30 d rotation (0), 10 to 30 d rotation (1), and < 10 d rotation (2). Insecticide/wormer application was divided into multiple applications (0), application once per yr to individuals in herd that required treatment (1), and no insecticide or wormers (2).

Location (county and state, USA)	Stock density	Rotation frequency	Insecticide/wormer	Composite rank score	System designation
Wilkinson, Mississippi	2	2	1	5	Adaptive multi-paddock
Wilkinson, Mississippi	0	2	0	2	Conventional
Calhoun, Alabama	2	2	2	6	Adaptive multi-paddock
Calhoun, Alabama	0	0	0	0	Conventional
Dekalb, Alabama	2	2	1	5	Adaptive multi-paddock
Dekalb, Alabama	0	0	1	1	Conventional

DATA ANALYSIS

Mean *S. invicta* mound abundance and area were compared between grazing treatments (adaptive multi-paddock and conventional grazing) using 1-way ANOVA, with the data conforming to the assumptions of ANOVA. Linear regression analysis was conducted to gain greater insight on correlations between *S. invicta* abundance, and arthropod community diversity and species richness for soil, foliar, and dung inhabiting arthropod communities. All statistics were performed using Systat 13 (Systat Software, Inc., Point Richmond, California, USA).

Results

ARTHROPOD COMMUNITIES

There were 15,705 arthropod specimens, representing 184 morphospecies, collected from the soil samples. The complete inventory of arthropod morphospecies collected from this study are presented in Schmid et al. (2021). In the foliar community from sweep net samples, 13,376 arthropods were collected, representing 371 morphospecies. Dung arthropod sampling resulted in 3,465 specimens, representing 110 morphospecies. Acari and Collembola represented 14,983 and 3,603 specimens, respectively, of the total 32,546 collected arthropod specimens from the 3 communities. Lack of taxonomic keys and technical expertise to identify these 2 groups beyond the order Acarina and the family level for Collembola prevented the inclusion of these groups in diversity analysis.

SOLENOPSIS INVICTA COMMUNITY IN LIVESTOCK MANAGEMENT SYSTEMS AND CORRELATION WITH ARTHROPOD DIVERSITY

Solenopsis invicta mound abundance differed significantly between grazing treatments ($F = 11.77$; $df = 1,4$; $P = 0.03$) (Fig. 1A). Mean ant mound abundance was 3.4× greater in adaptive multi-paddock managed pastures than conventional pastures. The higher abundance of *S. invicta* mounds resulted in a significantly larger spatial area of mounds per pasture ($F = 33.06$; $df = 1,4$; $P = 0.01$) (Fig. 1B). Mean area of these mounds within adaptive multi-paddock pastures were 4.6× larger than conventional pastures. However, *S. invicta* mound abundance did not significantly correlate with species richness or diversity for any of the arthropod communities (Table 2).

Discussion

Our study revealed significant differences in *S. invicta* mound abundance and area within pasture systems under differing management systems. Greater mound abundance with larger spatial areas were observed consistently within adaptive multi-paddock managed pastures relative to their conventionally managed counterparts. These results support the findings of Steele et al. (2020) that found increased red imported fire ant densities within intensively managed pastures. However, we found that mound abundance was not correlated with arthropod community (soil, foliar, and dung) diversity or species richness. This result disproves our hypothesis that *S. invicta* abundance would correlate negatively with arthropod community diversity.

The first result of this study indicated that pastures grazed under adaptive multi-paddock management had a greater abundance of *S. invicta* mounds relative to conventionally managed pastures. Many ranchers would not interpret this as a positive result, because red imported fire ants typically are regarded as a pest species in the US (live-

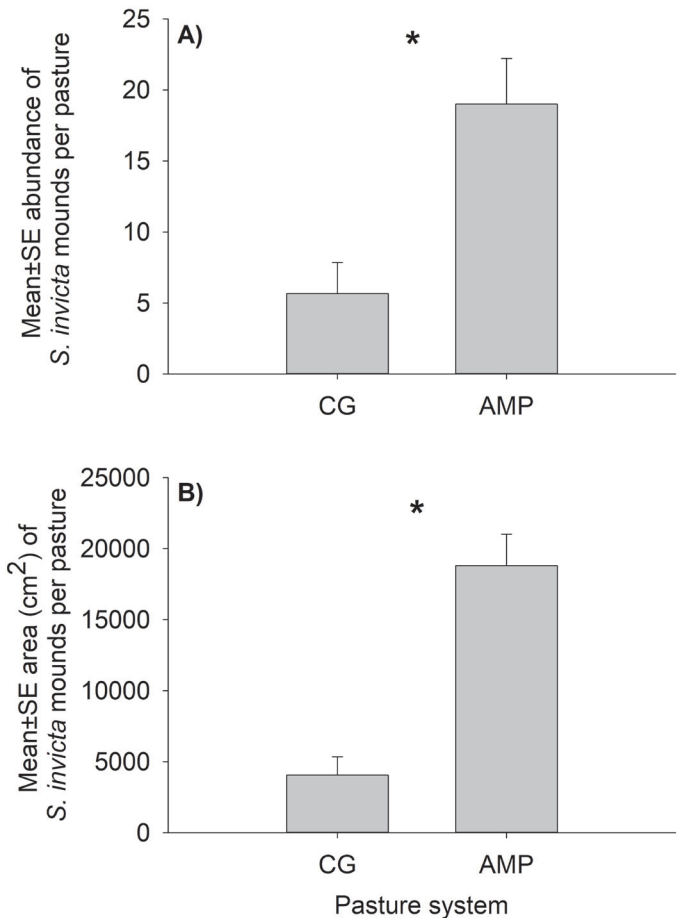


Fig. 1. Mean \pm SE *Solenopsis invicta* mound abundance (A) and mound area (B) in adaptive multi-paddock and conventionally grazed (CG) pastures ($n = 6$). Statistical analysis was conducted using 1-way analysis of variance (ANOVA), $*\alpha = 0.05$.

stock producers included). However, this ant species can be beneficial to some aspects of cattle production. For instance, *S. invicta* has been shown to reduce important pests of the cattle industry, including the lone star tick (*Amblyomma americanum* [L.]; Acari: Ixodidae), horn fly (*Haematobia irritans* [L.]; Diptera: Muscidae), and stable fly (*Stomoxys calcitrans* [L.]; Diptera: Muscidae) (Harris & Burns 1972; Burns & Melancon 1977; Summerlin & Kunz 1978; Tschinkel 2006). Despite the impact of *S. invicta* on these dung-dwelling fly pests, this ant species does not affect the reproduction and activity of beneficial dung beetles (Tschinkel 2006; Steele 2016). These studies suggest *S. invicta* can be beneficial for pest control in livestock production, and livestock grazing on adaptive multi-paddock pastures may experience fewer tick and fly pests because of this. Because our arthropod community inventories did not sample for ticks or flies on livestock in the pastures, we are unable to examine this hypothesis with this dataset.

The second result of our study showed no significant correlation between *S. invicta* mound abundance and arthropod diversity or species richness. The implication of this finding is that adaptive multi-paddock managed pastures do not experience decreased arthropod diversity despite increased fire ant abundance. The reason for this might be due to the environmental effects that adaptive multi-paddock grazing causes to pastures. It has been shown that adaptive multi-paddock managed pastures increase plant diversity, ground cover, fungal/bacterial ratio, soil organic matter, and water holding capacity (Teague et al. 2011; Hillenbrand et al. 2019). Altering the previously mentioned

Table 2. Regression analysis results comparing *Solenopsis invicta* mound abundance with arthropod community (soil, foliar, and dung communities) species richness and diversity (Shannon H').

	Soil arthropods			Foliar arthropods			Dung arthropods		
	df	F-ratio	P-value*	df	F-ratio	P-value*	df	F-ratio	P-value*
Species richness	1, 4	0.04	0.86	1, 4	1.44	0.30	1, 4	1.24	0.33
Diversity (Shannon H')	1, 4	0.77	0.43	1, 4	1.47	0.29	1, 4	4.70	0.10

* $\alpha = 0.05$.

environmental features has a cascade of effects on different facets of arthropod communities, e.g., enhanced predator evenness, increased herbivore robustness, and decreased pestiferous insects (Welti et al. 2017; Bhandari et al. 2018; Aldebrón et al. 2020). It is difficult to determine which of the aforementioned environmental characteristics known to be affected by adaptive multi-paddock management may be influencing the dynamic between arthropod diversity and red imported fire ants. Several potential hypotheses could explain this phenomenon, e.g., niche partitioning, habitat complexity, intermediate disturbance, etc. (Joern & Laws 2013). Because our study was based on correlation and not causality, we are unable to determine the mechanism(s) that maintained arthropod diversity greater than expected in the adaptive multi-paddock pastures. However, the potential for adaptive multi-paddock pasture management to support biodiversity despite higher numbers of an invasive species (such as the fire ant) warrants further investigation, a subject of utmost importance as arthropod diversity is in decline around the world (Leather 2018; Sánchez-Bayo & Wyckhuys 2019; Wagner 2020).

Prior to the start of this study, ranch managers indicated they thought that adaptive multi-paddock pastures would have fewer *S. invicta* mounds. Ranchers provided anecdotal evidence to support their opinion, citing observations of more mounds of red imported fire ant near areas of high human traffic in conventionally managed pastures (gates, water tanks, mineral/salt feeders, etc.). We hypothesize that adaptive multi-paddock pasture management assists ranchers by providing greater functionality (compared with conventional methods) because the greater abundance of *S. invicta* mounds found in our sampled adaptive multi-paddock pastures did not interfere with daily cattle operations. This facet is worth noting for further investigations in ranching systems.

In summary, the ability of adaptive multi-paddock pastures to maintain diversity despite greater abundance of *S. invicta* deserves further study, especially during this period of global arthropod diversity decline (Sánchez-Bayo & Wyckhuys 2019). Moreover, our study highlighted the need for future research to understand how adaptive multi-paddock ranching can change environmental features that can affect *S. invicta* abundance and distribution. A pasture management method, such as adaptive multi-paddock, that can protect biodiversity while maintaining functionality and productivity deserves additional investigation, because the value of such a system would be important for conservation and ranching alike.

Acknowledgments

We thank Liz Adey, Mike Bredeson, Nicole Schultz, Alec Peterson, Sierra Stendahl, and Cassidy Weathers for help collecting specimens. Kelton Welch identified the insect specimens for this study. We also would like to give a huge thanks to all the farmers that participated in this study, and to Allen Williams and the GrassFed Exchange for helping to survey adaptive multi-paddock farmers in the southeastern US. Applied Ecological Services and Arizona State University led the strati-

fication and site selection of the farms. Funding for this project came from the Arizona State University Foundation. This research is part of a larger research project analyzing whether adaptive multi-paddock grazing can contribute to soil carbon sequestration, improvement of ecosystem resilience, and improvement of socio-ecological resilience.

References Cited

- Aldebrón C, Jones MS, Snyder WE, Blubaugh CK. 2020. Soil organic matter links organic farming to enhanced predator evenness. *Biological Control* 146: 104278. doi.org/10.1016/j.biocontrol.2020.104278 (last accessed 1 Dec 2021).
- Apperson CS, Adams CT. 1983. Medical and agricultural importance of red imported fire ant. *Florida Entomologist* 66: 121–126.
- Bhandari KB, West CP, Longing SD. 2018. Communities of canopy-dwelling arthropods in response to diverse forages. *Agricultural & Environmental Letters* 3. doi:10.2134/ael2018.07.0037 (last accessed 1 Dec 2021).
- Buczowski G, Richmond DS. 2012. The effect of urbanization on ant abundance and diversity: a temporal examination of factors affecting biodiversity. *PLoS ONE* 7: e41729. doi: 10.1371/journal.pone.0041729 (last accessed 1 Dec 2021).
- Burns EC, Melancon DG. 1977. Effect of imported fire ant (Hymenoptera: Formicidae) invasion on lone star tick (Acarina: Ixodidae) populations. *Journal of Medical Entomology* 14: 247–249.
- Camilo GR, Phillips Jr SA. 1990. Evolution of ant communities in response to invasion by the fire ant *Solenopsis invicta*, pp. 190–198 *In* Vander Meer R [ed.], *Applied Myrmecology: A World Perspective*. Westview Press, Boulder, Colorado, USA.
- Chan KH, Guénard B. 2020. Ecological and socio-economic impacts of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), on urban agricultural ecosystems. *Urban Ecosystems* 23: 1–12.
- Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, Blumenthal DM, Gonzalez P, Grosholz ED, Ibanez I, Miller LP, Sorte CJB, Tatem AJ. 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications* 7. doi: 10.1038/ncomms12485 (last accessed 1 Dec 2021).
- Harris WG, Burns EC. 1972. Predation on the lone star tick by the imported fire ant. *Environmental Entomology* 1: 362–365.
- Hillenbrand M, Thompson R, Wang F, Apfelbaum S, Teague R. 2019. Impacts of holistic planned grazing with bison compared to continuous grazing with cattle in South Dakota shortgrass prairie. *Agriculture, Ecosystems & Environment* 279: 156–168.
- Hoffmann BD, Andersen AN, Hill GJE. 1999. Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. *Oecologia* 120: 595–604.
- Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ. 2002. The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics* 33: 181–233.
- Human KG, Gordon DM. 1997. Effects of Argentine ants on invertebrate biodiversity in Northern California. *Conservation Biology* 11: 1242–1248.
- Joern A, Laws AN. 2013. Ecological mechanisms underlying arthropod species diversity in grasslands. *Annual Review of Entomology* 58: 19–36.
- Jourdan H. 1997. Threats on Pacific islands: the spread of the tramp ant *Wasmannia auropunctata* (Hymenoptera: Formicidae). *Pacific Conservation Biology* 3: 61–64.
- King JR, Tschinkel WR. 2008. Experimental evidence that human impacts drive fire ant invasions and ecological change. *Proceedings of the National Academy of Sciences* 105: 20339–20343.
- Leather SR. 2018. “Ecological Armageddon” – more evidence for the drastic decline in insect numbers. *Annals of Applied Biology* 172: 1–3.
- Lofgren CS. 1986. The economic importance and control of imported fire ants in the United States, pp. 227–255 *In* Vinson SB [ed.], *Economic Impact and Control of Social Insects*. Praeger, New York, USA.

- Mosier S, Apfelbaum S, Byck P, Calderon F, Teague R, Thompson R, Cotrufo MF. 2021. Adaptive multi-paddock grazing enhances soil carbon and nitrogen stocks and stabilization through mineral association in southeastern US grazing lands. *Journal of Environmental Management* 288: 112409. doi.org/10.1016/j.jenvman.2021.112409 (last accessed 1 Dec 2021).
- Pecenka JR, Lundgren JG. 2018. The importance of dung beetles and arthropod communities on degradation of cattle dung pats in eastern South Dakota. *PeerJ* 6: e5220. DOI: 10.7717/peerj.5220 (last accessed 1 Dec 2021).
- Pimentel D, Zuniga R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288.
- Porter SD, Fowler HG, Mackay WP. 1992. Fire ant mound densities in the United States and Brazil (Hymenoptera: Formicidae). *Journal of Economic Entomology* 85: 1154–1161.
- Porter SD, Savignano DA. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* 71: 2095–2106.
- Porter SD, Williams DF, Patterson RS, Fowler HG. 1997. Intercontinental differences in the abundance of *Solenopsis* fire ants (Hymenoptera: Formicidae): escape from natural enemies? *Environmental Entomology* 26: 373–384.
- Sánchez-Bayo F, Wyckhuys KAG. 2019. Worldwide decline of the entomofauna: a review of its drivers. *Biological Conservation* 232: 8–27.
- Sanders NJ, Barton KE, Gordon DM. 2001. Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. *Oecologia* 127: 123–130.
- Savory A, Butterfield J. 1999. *Holistic Management: A New Framework for Decision Making*. Second edition. Island Press, Washington, DC, USA.
- Savory A, Parsons SD. 1980. The Savory grazing method. *Rangelands* 2: 234–237.
- Schmid RB, Welch KD, Lundgren JG. 2021. An inventory of the foliar, soil, and dung arthropod communities in pastures of the southeastern United States. *Ecology and Evolution* 11: 10761–10768.
- Simberloff D. 2000. Nonindigenous species: a global threat to biodiversity and stability, pp. 325–334 *In* Raven PH [ed.], *Nature and Human Society: The Quest for a Sustainable World*. National Academies Press, Washington, DC, USA.
- Steele C. 2016. Pasture management, the red imported fire ant (*Solenopsis invicta*) and dung beetle mediated ecosystem services. MS Thesis, College of Sciences. University of Central Florida, Orlando, Florida, USA. <http://purl.fcla.edu/fcla/etd/CFE0006400> (last accessed 1 Dec 2021).
- Steele CH, King JR, Boughton EH, Jenkins D. 2020. Distribution of the red imported fire ant *Solenopsis invicta* (Hymenoptera: Formicidae) in Central Florida pastures. *Environmental Entomology* 49: 956–962.
- Stein MB, Thorvilson HG. 1989. Ant species sympatric with the red imported fire ant in southeastern Texas. *Southwestern Entomologist* 14: 225–231.
- Summerlin JW, Kunz SE. 1978. Predation of the red imported fire ant on stable flies. *Southwestern Entomologist* 3: 260–262.
- Teague R. 2014. Deficiencies in the Briske et al. Rebuttal of the Savory method. *Rangelands* 36: 28–29.
- Teague WR, Dowhower SL, Baker SA, Haile N, DeLaune PB, Conover DM. 2011. Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie. *Agriculture, Ecosystems & Environment* 141: 310–322.
- Tschinkel WR. 2006. *The Fire Ants*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.
- Tucker JW, Schrott GR, Bowman R. 2010. Fire ants, cattle grazing, and the endangered Florida grasshopper sparrow. *Southeastern Naturalist* 9: 237–250.
- Wagner DL. 2020. Insect declines in the Anthropocene. *Annual Review of Entomology* 65: 457–480.
- Welti E, Helzer C, Joern A. 2017. Impacts of plant diversity on arthropod communities and plant–herbivore network architecture. *Ecosphere* 8: e01983. doi.org/10.1002/ecs2.1983 (last accessed 1 Dec 2021).
- Wojcik DP. 1983. Comparison of the ecology of red imported fire ants in North and South America. *Florida Entomologist* 66: 101–111.