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Does Prescribed Fire Facilitate Fire Ant Invasions in Coastal Prairies or Aid Management by Improving Mound Search Efforts?

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Abstract - We established a high-intensity prescribed-fire experiment in shrub-dominated coastal prairie to quantify (1) the proportion of Red Imported Fire Ant mounds that are likely to be missed by applicators of individual mound-based chemical treatments in prairie, based on the number of mounds found in unburned prairie compared to recently burned areas, and (2) to track changes in the densities of Red Imported Fire Ant and native Red Harvester Ant mounds in response to growing-season prescribed fires conducted during drought. First, our data suggest insecticide applicators are likely to miss 48% of Red Imported Fire Ant mounds when applying individual mound treatments in shrub-infested prairie. Second, fire treatments did not increase Red Imported Fire Ant or decrease Red Harvester Ant populations. Prescribed fire may therefore provide an advantageous management option for prairie managers that does not increase densities of Red Imported Fire Ants, and maintains mound densities of Red Harvester Ants, while enhancing the ability of insecticide applicators to locate and treat individual Red Imported Fire Ant mounds.

Introduction

Historically, fire was critical to the maintenance of coastal prairies (Grace 1998), and it is being reintroduced as one of the preferred restoration and management strategies for landowners and conservationists seeking to reduce further degradation of these grassland ecosystems (Tidwell et al. 2013a, Van Auken 2000). However, many land managers are concerned that it will have unforeseen, potentially negative, consequences (Kreuter et al. 2008, Tidwell et al. 2012). Of foremost concern is that fire will promote invasions by, and increase the density of *Solenopsis invicta* Buren (Red Imported Fire Ant), which poses a serious threat to the biodiversity and economic profitability of coastal prairies. The Red Imported Fire Ant is one of the most economically important non-native species in the United States (Pimentel et al. 2000), and it causes an estimated $5 million (US) per year in livestock losses, $16 million (US) per year in control costs, and $75 million (US) per year in damages in Texas agricultural areas (Lard et al. 2002). Such expenses are a major concern for conservation and wildlife programs because the Red Imported Fire Ants have extensive economic and ecological impact; are associated with declines in the diversity, abundance, and fitness of species from nearly every faunal guild (Allen et al. 1994, Eubanks 2001, Porter and Savignano 1990, Stuble

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et al. 2009); and are implicated as a threat to the conservation of several endangered species in coastal prairie habitats, including *Tympanuchus cupido* L. (Attwater's Prairie Chicken; Wilson and Silvy 1988) and *Phrynosoma cornutum* (Harlan) (Texas Horned Lizard; Donaldson et al. 1994).

Understanding the factors that make Red Imported Fire Ants successful invaders is important to coastal prairie managers. Two prevailing hypotheses that seek to explain the successful invasion of Red Imported Fire Ants in coastal prairies include the superior aggressor/competitor hypothesis and the ecosystem transition/disturbance hypothesis. The superior aggressor/competitor hypothesis states that Red Imported Fire Ants are superior competitors to native ant species, and exhibit more aggressive behavior toward other organisms, leading to the ants' dominance and a corresponding decline of native species abundances (Porter and Savignano 1990, Wojcik 1994). Alternatively, the ecosystem transition/disturbance hypothesis proposes that Red Imported Fire Ants and native species are primarily passengers that increase and decrease as a result of contemporary disturbance regimes and widespread shifts in plant community composition and structure (King and Porter 2007; King and Tschinkel 2006, 2008; MacDougall and Turkington 2005). This is a plausible hypothesis in coastal prairies because increases in Red Imported Fire Ants and decreases in native species have coincided with a shift from prairie to shrubland vegetation throughout the ecoregion. However, this hypothesis does not explicitly differentiate between responses associated with ecosystem transitions versus those associated with disturbance. For example, it is currently not known how Red Imported Fire Ants respond to restoration activities that use fire as a disturbance. Will using fire in restoration activities decrease Red Imported Fire Ant populations and increase those of native species as a result of changing the trajectory of the system from shrubland back toward prairie (i.e., passengers of ecosystem transitions hypothesis)? Or, will using prescribed fire in coastal prairie increase Red Imported Fire Ant populations because fire is a disturbance (i.e., disturbance-mediated invasion hypothesis)? If the latter is correct, then it may force managers to choose between using fire to control woody encroachment while exacerbating the fire ant problem, or excluding the application of fire in an ecosystem dependent upon it.

Based on the superior aggressor/competitor and disturbance-mediated invasion hypotheses, Red Imported Fire Ant management strategies would ideally involve direct control treatments applied over large acreages, typically with broadcast baits or individual mound-based insecticides. In non-urban areas of Texas, the current management recommendation is to apply broadcast bait first and follow with chemical treatment of individual mounds (Drees et al. 1998, 2008), while also encouraging population growth of native ant species with the hope of further suppressing Red Imported Fire Ant numbers through competition (Drees et al. 1998, 2000). However, applying broadcast baits is not feasible in areas heavily invaded by woody plants because many locations are inaccessible. This consideration places a premium on the efficacy of individual mound-based treatments in ecosystems like the shrubland-dominated coastal prairie. Yet, applying such treatments can be difficult due to the arduous task of locating Red Imported Fire Ants mounds across large, densely vegetated areas (Vogt and Wallet 2008). The presence of thick, taller vegetation is an important difference between mowed, well-groomed urban areas and wildland areas, such as prairies, savannas and shrublands. Wildland vegetation may impede insecticide applicators' ability to locate Red Imported Fire Ant mounds when conducting individual mound-based treatments.

We used an experimental fire-manipulation protocol aimed at restoring shrubland to coastal prairie in order to test management questions related to Red Imported Fire Ant invasion. First, if chemical control using individual mound-based treatments is to be successful in coastal prairie, we assume that applicators would have to find and treat nearly all Red Imported Fire Ant mounds in a given area. A prescribed-fire experiment is an ideal design to test this assumption because it enables us to estimate the rate at which Red Imported Fire Ant mounds are not found by applicators, and therefore, not treated, by comparing the number of mounds observed in an unburned, densely vegetated unit relative to the number of mounds found in a burned area where the herbaceous material that potentially hides Red Imported Fire Ant mounds has been completely removed. Second, in contrast to the other prevailing hypotheses, the passengers of ecosystem transitions hypothesis would cause managers to place greater emphasis on the restoration of the plant communities and disturbance dynamics that occurred prior to Red Imported Fire Ant invasion than chemical control techniques. If the passengers of ecosystem transitions hypothesis explains Red Imported Fire Ant invasion and drives management decisions, then Red Imported Fire Ant mound densities should decrease in this experiment and native ant mounds, such as those of *Pogonomyrmex barbatus* Smith (Red Harvester Ants), should increase as a result of restoration. In contrast, if the disturbance-mediated invasion hypothesis drives management, Red Imported Fire Ant mound densities should increase, and mound densities of native harvester ants, which have a long history of thriving in an environment with frequent fire (Zimmer and Parmenter 1998), should either remain constant or increase in abundance.

Study Site

We conducted this study on the Coastal Bend ecoregion at the Rob and Bessie Welder Wildlife Refuge. Welder Wildlife Refuge (28°06'47.75"N, 97°25'01.0"W) is a 3160-ha wildlife reserve located 71 km north of Corpus Christi, TX (Hirth 1977). Vegetation at the Welder Wildlife Refuge was consistent with the composition, structure, and long-term patterns of change of the non-agricultural plant communities in the region. Historically, the vegetation at Welder and in the southern portion of the Coastal Bend ecoregion consisted of an interspersion of tallgrass prairie and *Quercus* (oak) woodland (Drawe et al. 1978). Over time, prairie sites have transitioned to a thorn-scrub shrubland with high densities of *Prosopis glandulosa* Torr. (Honey Mesquite), *Acacia farnesiana* (L.) Willd. (Huisache), and other invasive woody plants (Drawe et al. 1978). Mean annual precipitation at the site is 915 mm

(Welder Wildlife Refuge 1956–2010 records, unpub. data), with a sporadic rainfall pattern and hurricane season in August and September leading to variable precipitation in any month (Hirth 1977). There are approximately 300 frost-free days (Fafarman and DeYoung 1986) with minimum and maximum monthly temperatures normally ranging from 23.9–34.2 °C in the summer months (mean = 29.1 °C in August) to 8.2–19.2 °C (mean = 13.7 °C in January) (data summarized from NOAA Corpus Christi Weather Station, 27.79°N, 97.40˚W, 1971–2000). Elevation is 12 m with flat and gently sloping topography (Tidwell et al. 2012). Soils are Haplustert of the Victoria clay series (USDA 2010), with dense clay to clay-loam soils in the bottomland and well-drained sandy soils in the upland.

Methods

We initiated an experiment aimed at restoring grassland dominance using combinations of fire and herbicide. We established eighteen 30-m x 20-m plots at the Welder Wildlife Refuge within a 60-ha area dominated by Honey Mesquite and Huisache. We randomly assigned the following fire treatments to the plots: burned once, burned repeatedly, or unburned, with six replicates of each treatment. We conducted initial prescribed-fire treatments in June 2008, and we conducted a second treatment in the plots assigned the burned-repeatedly treatment in August 2009. We randomly assigned one of the following herbicide treatments to each of three 20-m x 10-m subplots within each plot regardless of whether that plot was burned or not: herbicide all woody plants before date on which the first prescibed burning were conducted, herbicide all woody plants after the date of the first fire, or no herbicide applications. We installed fencing to exclude livestock grazing from all plots for the duration of this experiment.

We designed a systematic sampling approach to estimate the number of Red Imported Fire Ant mounds in each plot and to limit inconsistencies associated with observer bias and sampling effort. We established 9 parallel belt-transects (3 per subplot) at equidistant intervals of 3 m to provide systematic detection and tallying of Red Imported Fire Ant mounds in each plot (Fig. 1). To sample, we visually searched for Red Imported Fire Ant mounds within each belt transect, and upon detection, we differentiated active and inactive mounds by slightly agitating each one to stimulate ant activity. We included only active Red Imported Fire Ant mounds in this analysis. To estimate the number of Red Imported Fire Ant mounds that were not detected in unburned plots at the beginning of the study, we sampled burned (n = 12) and unburned (n = 6) plots within 24 hours of conducting the initial burn treatments in 2008. We analyzed data using an independent samples t-test with unequal sample sizes and met assumptions of equal variance and normal distribution. To test for differences in the number of Red Imported Fire Ant and Red Harvester Ant mounds among treatments over time, we sampled transects within 24 hours of burning in 2008 and 2009, and we sampled all plots on the same day in 2010. In plots that were not burned, we adjusted the data to represent the number of Red Imported Fire Ant mounds that we predicted to occur in the field after correcting for sampling errors associated with visually obstructed mounds that we failed to locate in searches of the unburned plots relative to burned plots at the beginning of the study. We analyzed the data using a two-factor ANOVA and log(x) transformed them to meet assumptions of equal variance and normal distribution. We made post-hoc comparisons with Tukey's HSD test.

Results

Tests for differences in the number of Red Imported Fire Ant and Red Harvester Ant mounds as a result of herbicide application on woody plants showed no significant differences among treatment groups, so we pooled the data to test for differences occurring solely as a function of the burned treatments.

Locating fire ant mounds

The likelihood of overlooking Red Imported Fire Ant mounds is significant in prairie environments ($t = 4.06$, df = 16, $P = 0.001$). Despite our systematic sampling efforts, comparisons of burned and unburned areas within 24 hours of treatment showed that 48% of the Red Imported Fire Ant mounds were unaccounted for in unburned areas at the Welder Wildlife Refuge (Fig. 2), Our inability to locate many Red Imported Fire Ant mounds was most likely due to the presence of numerous small mounds that were well hidden in unburned coastal prairie habitat (Fig. 3a). In general, such small mounds became visible only after burning removed all herbaceous vegetation (Fig. 3b), whereas large Red Imported Fire Ant mounds were easier to detect even within dense vegetation in unburned areas (Fig. 3c).

Failure to correct for the proportion of mounds not located in unburned environments would considerably alter the observed responses of Red Imported Fire Ants

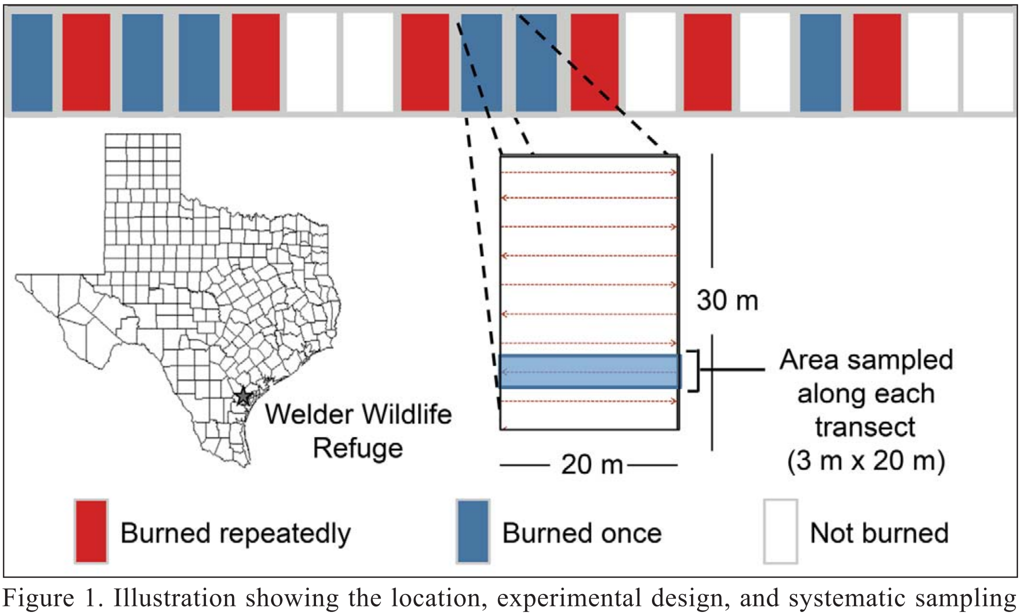

Figure 1. Illustration showing the location, experimental design, and systematic sampling design used to sample Red Imported Fire Ant and Red harvester Ants at the Welder Wildlife Refuge. Within each plot, 9 parallel belt transects were established (represented as dashed arrows) at equidistant intervals to search the entire plot for fire ant mounds.

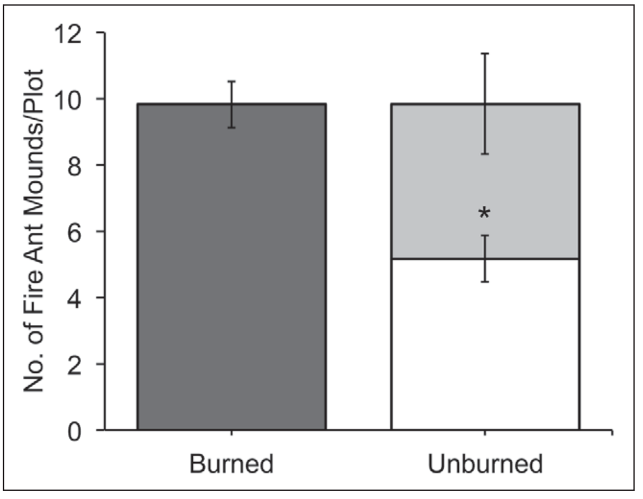

Figure 2. The number of Red Imported Fire Ant mounds (mean ± SE) found in burned (black) and unburned plots (white and gray) within 24 hours of conducting the initial burn treatments. Data were collected to estimate the number of mounds researchers failed to locate in unburned areas. The stacked columns in the unburned treatment represent the number of Red Imported Fire Ant mounds found in the field (white) and the number of mounds that were predicted to have occurred in the field after correcting for sampling error in unburned plots relative to burned plots (light grey). * indicates significant difference at $P < 0.05$ compared to the burned treatments.

Figure 3. Pictures illustrating that herbaceous vegetation can make it difficult to locate Red Imported Fire Ant mounds in unburned coastal tallgrass prairie. Many small Red Imported Fire Ant mounds were completely concealed by herbaceous vegetation in unburned plots (a), causing a large proportion of mounds to go undetected in unburned areas compared to burned plots (b). However, herbaceous vegetation does not conceal most large mounds, making them readily detectable in both unburned (c) and burned (d) areas in this study.

to burn treatments. Under the assumption that sampling error was equal among burned and unburned treatments, we would have incorrectly concluded that Red Imported Fire Ant occurrence significantly differed among treatments over time ($F_{4,53}$ = 19.0, P = 0.006), and that Red Imported Fire Ant mounds nearly doubled within 24 hours of burning in 2008 in burned-repeatedly and burned-once plots (P = 0.01 and 0.01, respectively, compared to unburned treatment; Fig. 4). In contrast, correcting for sampling error showed that the number of Red Imported Fire Ant mounds significantly differed over time ($F_{2,53}$ = 41.8, P < 0.001), but not as a function of the treatments ($F_{2,53}$ = 1.2, P = 0.30) or as a function of time–treatment interaction ($F_{4,53}$ = 1.5, P = 0.22).

Red Imported Fire Ant and Red Harvester Ant response

When we analyzed data corrected for our inability to locate Red Imported Fire Ant mounds in unburned prairie, we found that the number did not significantly differ among burned-repeatedly, burned-once, and unburned treatments in any year (P > 0.05 for all pairwise comparisons; Fig. 4). However, Red Imported Fire Ant mound densities were highly variable among years. The number of fire ant mounds decreased significantly from 2008 to 2009 (P < 0.001), but numbers rebounded and did not differ from pre-treatment levels in 2010 (P = 0.15). Similarly, the number of Red Harvester Ant mounds did not differ among burned and unburned treatments ($F_{2,53}$ = 3.1, P = 0.06; Fig. 5). Unlike our results for Red Imported Fire Ants, the number of Red Harvester Ant mounds was relatively constant over the timeline of this study ($F_{2,53}$ = 0.2, P = 0.79; Fig. 5), with only an increase in the number of Red Harvester Ant mounds two years after the fire treatment in plots that were burned once (Fig. 5). However, this change in the burned-once treatments was not significantly different from the burned repeatedly (P = 0.73) or unburned treatments (P = 0.31).

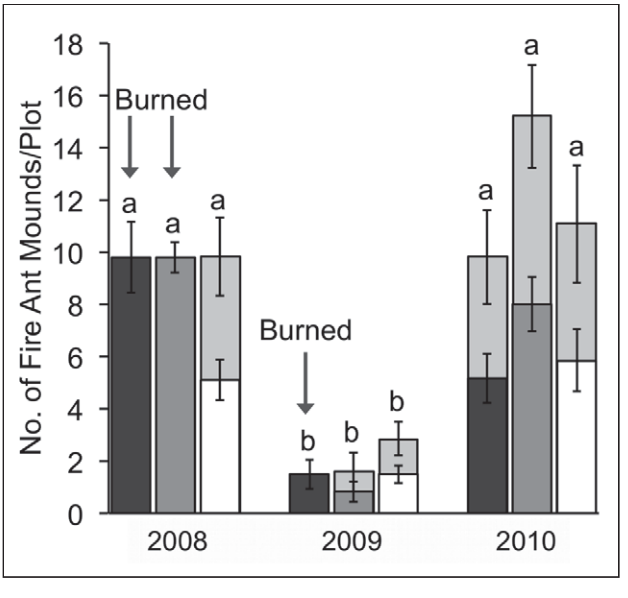

Figure 4. The number of Red Imported Fire Ant mounds (mean ± SE) found in burned repeatedly (black), burned once (dark grey), and unburned (white) treatments. The stacked columns represent the number of Red Imported Fire Ant mounds that were predicted to have occurred in the field (light grey) after correcting for sampling error in unburned plots relative to burned plots at the beginning of the study (Fig. 2); uncorrected data are shown but were not incorporated into the statistical model. Different letters indicate significant differences between treatments (P < 0.05).

Discussion

Our failure to locate nearly one-half of Red Imported Fire Ant mounds in unburned areas has important implications for the control and management of this species in coastal prairies. Insecticides are the most common means of treating Red Imported Fire Ant infestations (Drees et al. 1998, Myers et al. 1998, Williams 1994), but their efficacy on populations in non-urban areas where broadcast bait applications are restricted is largely dependent on the ability of a pesticide applicator to locate and treat individual mounds. Clearly, the ability to successfully locate and treat individual mounds is reduced in prairie environments with high levels of woody and herbaceous plant canopy cover (Figs. 2, 3). Given these search limitations, one would not expect mound-based chemical applications to completely eradicate Red Imported Fire Ant populations in unburned coastal grasslands. These circumstances may help explain the increased density and distribution of Red Imported Fire Ant in non-urban areas, even when insecticides are widely used as part of a control plan (Kemp et al. 2000). Red Imported Fire Ant control efforts in areas like the coastal plain prairie may be more effective if pesticide applicators apply mound-based treatments immediately after prescribed fire, when dense herbaceous vegetation that obscures mounds has been completely removed.

Our findings do not support the disturbance-mediated invasion hypothesis; rather, they indicate that the use of prescribed fire does not result in an increase in Red Imported Fire Ant abundances in coastal prairie ecosystems. This suggests that Red Imported Fire Ants respond differently to fire than they do to many other ecological perturbations. Red Imported Fire Ant populations have been shown to increase in areas disturbed by mowing (King and Tshinkel 2008), plowing (King and Tshinkel 2008), grazing (Hill et al. 2008, Tucker et al. 2010), and other human-driven activities (Forys et al. 2002, King et al. 2009, Stiles and Jones 1998, Todd et al. 2008). Like fire, these human-caused disturbances remove or reduce herbaceous vegetation. Red Imported Fire Ant abundances are typically higher in areas with less vegetation because the ants prefer sites with sufficient sunlight

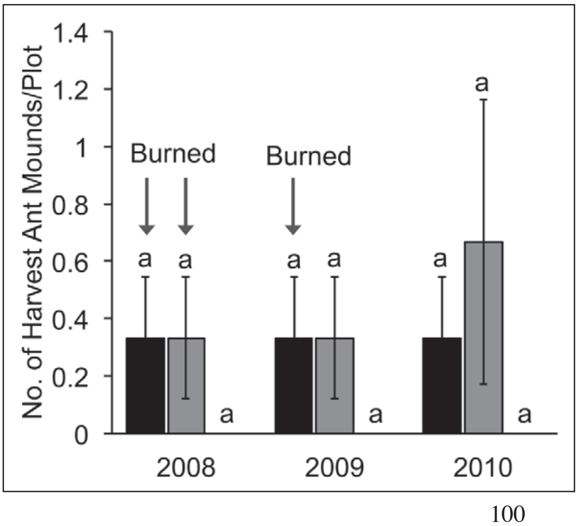

Figure 5. The number of Red Harvester Ant mounds (mean ± SE) found in burned repeatedly (black), burned once (dark grey), and unburned (white) treatments. No Red Harvester Ant mounds were located in the unburned treatment in any year. Different letters indicate significant differences between treatments ($P < 0.05$).

to allow brood thermoregulation (Plowes et al. 2007, Porter and Tschinkel 1993, Sternberg et al. 2006). The differential responses of Red Imported Fire Ants to fire relative to other disturbances suggest the disturbance-mediated invasion hypothesis should be refined to account for differences in the intensity, duration, frequency, or severity of different disturbances. Such a distinction is important because mechanical equipment used to manage woody plants in coastal prairie creates a disturbance similar to plowing or mowing and is likely to cause similar increases in Red Imported Fire Ant abundances. Fire may, therefore, be the best option available for preventing the establishment of woody plants in coastal prairies invaded by Red Imported Fire Ants.

It is unclear whether our findings would be confirmed in studies of Red Imported Fire Ant populations following more traditional, low-intensity prescribed fires that are conducted during periods of average or above-average precipitation. We carried out the controlled fires in our study during periods of severe drought, leading to considerable grass curing, low fine fuel moistures, and high fire intensities (e.g., Taylor et al. 2012; Twidwell et al. 2009, 2013b). Multiple authors have suggested Red Imported Fire Ants are negatively affected by drought (Hung and Vinson 1978, Kidd and Apperson 1984, Stuble et al. 2009), and fire-mediated responses of dominant ant species have been shown to be specific to the timing, seasonality, and intensity of fires (Andersen et al. 2007). Consequently, the reason Red Imported Fire Ant populations did not increase as a result of burning in this study may be because the timing of our fire treatments coincided with drought episodes.

The number of Red Imported Fire Ant and Red Harvester Ant mounds did not change as a result of our experimental restoration treatments and therefore, our data do not support the passengers of ecosystem transitions hypothesis. It is important to acknowledge however, that the time frame of this study is likely insufficient to document colony turnover and displacement dynamics. In addition, even though our fire and herbicide treatments have dramatically altered the composition and structure of the woody plant community (Twidwell 2012), the ecosystem has not been fully restored to coastal tallgrass prairie. As a result, it is likely too early to determine whether restoration treatments are having a long-term effect on Imported Red Fire Ant and Red Harvester Ant abundances. Moreover, using alternate sampling techniques, such as pitfall traps, would provide a more precise measure of how populations of Red Imported Fire Ant and Red Harvester Ant are responding to the initial restoration treatments (Schlick-Steiner et al. 2006).

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Literature Cited

Allen, C.R., S. Demaris, and R.S. Lutz. 1994. Red Imported Fire Ant impact on wildlife: An overview. Texas Journal of Science 46:51–59.

Andersen, A.N., C.L. Parr, L.M. Lowe, W.J. Muller. 2007. Contrasting fire-related resilience of ecologically dominant ants in tropical savannas of northern Australia. Diversity and Distributions 13:438–446.

Donaldson, W., A.H. Price, and J. Morse. 1994. The current status and future prospects of the Texas Horned Lizard (*Phrynosoma cornutum*) in Texas. Texas Journal of Science 46:97–113.

Drawe, D.L., A.D. Chamrad, and T.W. Box. 1978. Plant communities of the Welder Wildlife Refuge. Rob and Bessie Welder Wildlife Foundation Contribution No. 5, Series B, Revised, Sinton, TX.

Drees, B.M., C.L. Barr, D.R. Shanklin, D.K. Pollet, K. Flanders. 1998. Managing Red Imported Fire Ants in agriculture. B-6076. Texas Imported Fire Ant Research and Management Plan. Texas A&M University, College Station, TX. 20 pp.

Drees, B.M., K. Schofield, E. Brown, P. Nester, M. Keck, and K. Flanders. 2008. Fire ant control: The two-step method and other approaches. L-5496. Texas Agrilife Extension, College Station, TX.

Eubanks, M.D. 2001. Estimates of the direct and indirect effects of Red Imported Fire Ants on biological control in field crops. Biological Control 21:35–43.

Fafarman, K.R., and C.A. DeYoung. 1986. Evaluation of spotlight counts of deer in South Texas. Wildlife Society Bulletin 14:180–185.

Forys E.A., C.R. Allen, and D.P. Wojcik. 2002. Influence of the proximity and amount of human development and roads on the occurrence of the Red Imported Fire Ant in the lower Florida Keys. Biological Conservation 108:27–33.

Grace, J.B. 1998. Can prescribed fire save the endangered coastal prairie ecosystem from Chinese Tallow invasion? Endangered Species Update 15:70–76.

Hill, J.G., K.S. Summerville, and R.L. Brown. 2008. Habitat associations of ant species (Hymenoptera: Formicidae) in a heterogeneous Mississippi landscape. Environmental Entomology 37:453–463.

Hirth, D.H. 1977. Social behavior of White-Tailed Deer in relation to habitat. Wildlife Monographs 53:3–55.

Hung, A.C.F, and S.B. Vinson. 1978. Factors affecting the distribution of fire ants in Texas (Myrmicinae: Formicidae) Southwestern Naturalist 23:205–213.

Kemp, S.F., R.D. deShazo, J.E. Moffitt, D.F. Williams, and W.A. Buhner. 2000. Expanding habitat of the imported fire ant (*Solenopsis invicta*): A public health concern. Journal of Allergy and Clinical Immunology 105:683–691.

Kidd, K.A., and C.S. Apperson. 1984. Environmental factors affecting relative distribution of foraging Red Imported Fire Ants in a soybean field on soil and plants. Journal of Agricultural Entomology 1:212–218.

King, J.R., and S.D. Porter. 2007. Body size, colony size, abundance, and ecological impact of exotic ants in Florida's upland ecosystems. Evolutionary Ecology Research 9:757–774.

King, J.R., and W.R. Tschinkel. 2006. Experimental evidence that the introduced fire ant, *Solenopsis invicta*, does not competitively suppress co-occurring ants in a disturbed habitat. Journal of Animal Ecology 75:1370–1378.

King, J.R., and W.R. Tschinkel. 2008. Experimental evidence that human impacts drive fire ant invasions and ecological change. Proceedings of the National Academy of Sciences 105:20,339–20,343.

King, J.R., W.R. Tschinkel, and K.G. Ross. 2009. A case study of human exacerbation of the invasive species problem: Transport and establishment of polygyne fire ants in Tallahassee, Florida. Biological Invasions 11:373–377.

Kreuter, U.P., J.B. Woodard, C.A. Taylor, and W.R. Teague. 2008. Perceptions of Texas landowners regarding fire and its use. Rangeland Ecology and Management 61:456–464.

Lard, C., D.B. Willis, V. Salin, and S. Robison. 2002. Economic assessments of Red Imported Fire Ant on Texas' urban and agricultural sectors. Southwestern Entomologist 25:123–137.

MacDougall, A.S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55.

Myers, J.H., A. Savoie, E. van Randen. 1998. Eradication and pest management. Annual Review of Entomology 43:471–491.

Pimentel, D., L. Lach, R. Zuniqa, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53–65.

Plowes, R.M., J.G. Dunn, and L.E. Gilbert. 2007. The urban fire ant paradox: Native fire ants persist in an urban refuge while invasive fire ants dominate natural habitats. Biological Invasions 9:825–836.

Porter, S.D., and D.A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts the arthropod community. Ecology 71:2095–2106.

Porter, S.D., and W.R. Tschinkel. 1987. Foraging in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae): Effects of weather and season. Environmental Entomology 16:802–808.

Porter, S.D., and W.R. Tschinkel. 1993. Fire ant thermal preferences: Behavioral control of growth and metabolism. Behavioral Ecology and Sociobiology 32:321–329.

Schlick-Steiner, B.C., F.M. Steiner, K. Moder, A. Bruckner, K. Fiedler, and E. Christian. 2006. Assessing ant assemblages: Pitfall trapping versus nest counting (*Hymenoptera, Formicidae*). Insectes Sociaux 53:274–28

Sternberg, T., G. Perry, and C. Britton. 2006. Grass repellency to the Red Imported Fire Ant. Rangeland Ecology and Management 59:330–333.

Stiles, J.H., and R.H. Jones. 1998. Distribution of the Red Imported Fire Ant, *Solenopsis invicta*, in road and powerline habitats. Landscape Ecology 13:335–346.

Stuble, K.L., L.K. Kirkman, and C.R. Carroll. 2009. Patterns of abundance of fire ants and native ants in a native ecosystem. Ecological Entomology 34: 520–526.

Taylor, C.A., Jr., D. Twidwell, N.E. Garza, C. Rosser, J.K. Hoffman, and T.D. Brooks. 2012. Long-term effects of fire, livestock herbivory removal, and weather variability in Texas semiarid savanna. Rangeland Ecology and Management 65:21–30.

Todd, B.D., B.B. Rothermel, R.N. Reed, T.M. Luhring, K. Schlatter, L. Trenkamp, and J.W. Gibbons. 2008. Habitat alteration increases invasive fire ant abundance to the detriment of amphibians and reptiles. Biological Invasions 10:539–546.

Tucker, J.W., Jr., G.R. Schrott, and R. Bowman. 2010. Fire ants, cattle grazing, and the endangered Florida Grasshopper Sparrow. Southeastern Naturalist 9:237–250.

Twidwell, D. 2012. From theory to application: Extreme fire, resilience, restoration, and education in social-ecological disciplines. Ph.D. Dissertation. University of Texas A&M, College Station, TX.

Twidwell, D., S.D. Fuhlendorf, D.M. Engle, C.A. Taylor, Jr. 2009. Surface-fuel sampling strategies: Linking fuel measurements and fire effects. Rangeland Ecology and Management 62:223–229.

Twidell, D., W.E. Rogers, B. McMahon, B. Thomas, UP. Kreuter, and T.L. Blankenship. 2012. Prescribed fire effects on richness and invasion in coastal prairie. Invasive Plant Science and Managment 5:330–340.

Twidell, D., W.E. Rogers, S.D. Fuhlendorf, C.L. Wonkka, D.M. Engle, J.R. Weir, U.P. Kreuter, and C.A. Taylor, Jr. 2013a. The rising Great Plains fire campaign: Citizens' response to woody plant encroachment. Frontiers in Ecology and the Enviroment 11:e64–e71.

Twidell, D., S.D. Fuhlendorf, C.A. Taylor, Jr., and W.E. Rogers. 2013b. Refining thresholds in coupled fire–vegetation models to improve management of encroaching woody plants in grasslands. Journal of Applied Ecology 50:603–613.

USDA, NRCS. 2010. The Soil Survey database. Available online at http://www.websoilsurvey.nrcs.usda.gov. Accessed 20 April 2010.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology, Evolution, and Systematics 31:197–215.

Vogt, J.T., and B. Wallet. 2008. Feasibility of using template-based and object-based automated detection methods for quantifying Red and hybrid Imported Fire Ant (*Solenopsis invicta* and *S. invicta x richteri*) mounds in aerial digital imagery. The Rangeland Journal 30:291–295.

Williams, D.F. 1994. Control of the introduced pest the imported fire ant *Solenopsis invicta* in the United States. Pp. 282–292. *In* D.F. Williams (Ed.). Exotic Ants: Biology, Impact, and Control of Introduced Species. Westview Press, Boulder, CO.

Wilson, D.E., and N.J. Silvy. 1988. Impact of the imported fire ants on birds. Pp. 70–74. *In* The Red Imported Fire Ant: Assessment and Recommendations. Proceedings of the Governor's Conference. Sportsmen Conservationists of Texas, Austin, TX.

Wojcik, D.P. 1994. Impact of the Red Imported Fire Ant on native ant species in Florida. Pp. 269–281. *In* D.F. Williams (Ed.). Exotic Ants: Biology, Impact, and Control of Introduced Species. Westview Press, Boulder, CO.

Zimmer, K., and R.R. Parmenter. 1998. Harvester ants and fire in a desert grassland: Ecological responses of *Pogonomyrmex rugosus* (Hymenoptera: Formicidae) to experimental wild fires in central New Mexico. Environmental Entomology 27:282–287.