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An arthropod survival strategy in a frequently burned forest

The sound of burning stems and leaves filled our ears and smoke swirled as we marched into the longleaf pine forest to assess the experimental burn. As we walked over the ash of burned vegetation, seedbanks and plant parts lay beneath our feet waiting to grow. But what we couldn't see were the arthropods fleeing the fire. How are these invertebrates adapted to fire? They probably smell it coming, but do they feel the heat or see the smoke? Do they hear the noise that we hear as we near the flames?

Fire has been structuring terrestrial ecosystems since the Silurian Period (Glasspool et al. 2004, Pausas and Keeley 2009) and remains a key process in these systems. Prairies, savannas, and coniferous forests, like longleaf pine (*Pinus palustris* Mill.), cannot persist without periodic burning (Bradstock et al. 2005). Fire-adapted plant species have physiological adaptations such as thick, insulating bark and the ability to rapidly resprout post-burn. These adaptations confer greater resiliency to frequent disturbance. While we know fire maintains plant diversity in these ecosystems, less is known about the impacts of fire on other taxa in fire-adapted systems. Recently, we discovered a potential mechanism by which arthropods, the smallest animals in the longleaf pine ecosystem, survive frequent disturbance by fire. We suggest that tiny, yet highly sensitive, sensory adaptations may aid in an interesting arthropod behavior that takes place before the fire arrives: *insect ears.*

Arthropods found in fire-adapted habitats have specific traits and dispersal strategies to deal with frequent fires (New 2014). For example, they seek refugia during fires where temperatures may be lower (Robinson et al. 2013). Refugia are areas adjacent to or within a burn area that enhance arthropod survival during a fire, facilitate persistence of individuals, or allow for post-fire recovery. These may include insulated underground burrows, fire-resistant termite mounds, or patches of unburned vegetation (Robinson et al. 2013). Dispersal is another obvious response to fire for arthropods, and as a result, winged orders have higher survivorship than less-mobile taxa (New 2014).

When we arrived in the middle of our prescribed fire at Eglin Air Force base in Florida in May 2014, we noticed the maneuvering of a group of Mississippi kites as they gorged themselves on arthropods fleeing in front of the oncoming flames. We also spotted a group of several wingless juvenile grasshoppers walking up the side of a tree toward the canopy. Longleaf pine forests are characteristically open, with a monospecific overstory of pine, a sparse midstory, and a high-diversity understory. Fires burning in longleaf pine forests are typically high-frequency, low-intensity, and predominately run through surface fuels with little effect on the canopy. Later that afternoon, we started wondering out loud if these marching arthropods were also escaping the flames and what warning signals they used to make a timely getaway. If refugia and dispersal are the most important factors in predicting success of arthropod fire avoidance, how were these less-mobile and immature arthropods avoiding the dangers of natural fires?

To address this question, we formulated methods for an experiment using sticky traps to capture insects moving up tree boles during the fire. We chose such traps as they can be engineered from any sticky substance, including duct tape purchased that night from the local hardware store. For each of the subsequent burns, sticky traps were set approximately 2 m high, putting them out of reach of the surface flames. Ten traps were set on the boles of longleaf pine trees pre-ignition and also in paired unburned sites, with contents collected after fires had moved through. Sticky traps are ideal as they effectively capture small arthropods and preserve orientation upon contact with the sticky surface allowing for documentation of upward movement (Fig. 1).

After a subsequent fire, we saw that our sticky traps were covered with mostly juvenile, wingless, and non-flying arthropods. Traps within the fires caught 615% more arthropods compared to traps outside the fire perimeter ($n = 1666$ inside, $n = 271$ outside). Most specimens collected were grasshoppers and crickets ($n = 1361$), including a few winged adults ($n = 56$), but primarily wingless nymphs ($n = 1305$; Orthoptera: Acrididae, Gryllidae, Tettigoniidae). Traps also yielded several other non-flying arthropods such as spiders ($n = 67$; Aranea: Buthidae, Salticidae) and arachnids ($n = 134$; Opiliones), walking sticks ($n = 17$; Phasmatodea), cockroaches ($n = 3$; Blattodea), praying mantids ($n = 57$; Mantodea), ants ($n = 89$; Hymenoptera: Formicidae), and immature stages of antlions ($n = 24$; Neuroptera: Myrmeleontidae) and true bugs ($n = 128$; Hemiptera: Cercopidae, Cicadellidae, Pentatomidae). Although there was not much difference between burned and unburned areas in flying arthropods, there were proportionately more non-flying arthropods collected from the burn treatment.

Unique arthropod survival strategies exist in other fire-adapted systems. In Australia, during experimental

FIG. 1. Sticky trap contents collected during a fire from within a burn unit. Arthropods were engaged in vertical dispersal as indicated by their orientation, which is preserved upon contact with the trap.

burning of the flammable grass tree (*Xanthorrhoea* spp.), a diverse assemblage of arthropods sought refuge and survived between the tightly packed tree leaves (Brennan et al. 2011). In longleaf pine forests, arthropods fly toward adjacent unburned areas, or as we documented in Florida, walk, crawl, or jump up tree boles toward the canopy. What cues are used for dispersal toward refugia during fires? Shortly after cutting down our first set of arthropod-laden sticky traps, we came up with additional hypotheses related to arthropod sensilla that respond to touch, smell, light, and sound. We all agreed there must be some sensory cue responsible for the initiation of the dispersal response.

The highly developed sensory systems in arthropods suggest several hypotheses, such as specialized chemoreceptors that sense compounds unique to smoke associated with longleaf fires, or perhaps sensilla that respond to radiant heat. Pyrophilous insects possess both adaptations (New 2014). Yet from our vantage point, we were well-upwind of the advancing flames and smoke, and distant enough to not feel any of the heat from combustion. Thus, we present a third hypothesis: the auditory sensilla in arthropods, such as tympana in Orthopterans and Lepidopterans, respond to acoustic signals from the burning fuels and may trigger dispersal behavior. Therefore, the arthropods may be responding to the sounds of the fire. This hypothesis has been tested by Grafe et al. (2002), who showed that estivating frogs flee from the sounds of fire.

Both vertebrates (Beane 2006) and arthropods use specialized hearing organs for intraspecific communication and detection of predators. The hearing range of arthropods with tympanal structures are commonly within the 100 Hz to 3 kHz range, with some Lepidopterans able to detect frequencies up to 240 kHz (Straub and Lakes-Harlan 2014). Characterizations of fire acoustics indicate that clearest signals of burning are found in the frequency range of 200–500 Hz (Viegas et al. 2008). Because the frequency ranges associated

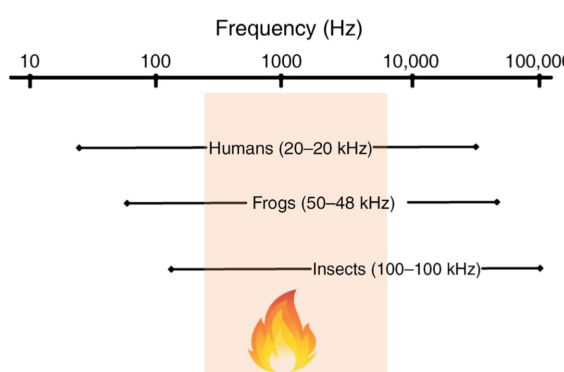

FIG. 2. The overlapping acoustic frequency ranges of fire and arthropod sound detection support the hypothesis that the sounds of fire may serve as an audible cue for dispersal.

with fire lie well within the arthropod hearing range (Fig. 2), it is feasible that fire acoustics serve as a dispersal cue for arthropods in this system.

Although many studies have investigated arthropod recolonization before and after fires, determining whether the populations sampled post-burn have survived the fire or are new colonizers has proven difficult (Robinson et al. 2013, New 2014). The survival of arthropods that have dispersed into the canopy during fires and their potential as a source of recolonization remains unknown. Fires are characteristically heterogeneous in terms of severity and impact (Bradstock et al. 2005). In forests with low-intensity surface fires and short residence times, such as those found in the longleaf pine ecosystem, the canopy has cooler temperatures and reduced combustion compared with the understory. Thus, it is likely that arthropods may move upward into the cooler canopy. This may allow them to survive the burn, and subsequently recolonize the burned area below. Future studies linked with prescribed burns could focus on these dispersal patterns to provide insight to the mechanisms of post-burn colonization. Additionally, documenting dispersal, survival, and colonization events could be an important consideration for arthropod conservation strategies in longleaf pine and other fire-adapted ecosystems.

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