Disturbance, predation risk, and social environment create predictable spatial patterns in animal foraging behavior and trophic interactions

By

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DEDICATION

This work is dedicated to my late grandfather, Dennis Daignault, whose legacy as a passionate outdoorsman and a lover of wildlife has always inspired my pursuits in field ecology and animal behavior.

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ABSTRACT

Animal foraging behavior not only affects individual fitness of animals but can also mediate the magnitude of granivory and herbivory of plant communities. As a result, understanding how aspects of the environment affect animal foraging behavior is critical to predicting how changes in the environment may directly affect animal populations and indirectly affect plant communities. Since animals must avoid attack by predators or costly encounters with conspecific competitors while foraging, animal behavior may be shaped by characteristics of the environment that predict the likelihood of predation or intraspecific competition.

Disturbances, such as fire and forest harvest, can have profound impacts on habitat characteristics (e.g., vegetative concealment from predators) that affect the identity and behavior of animals foraging in a habitat. Moreover, the legacies of historic disturbances, like past agricultural land use in restored habitats, can also impact habitat structure and, as a consequence, animal foraging behavior. By conducting an experiment that coupled canopy harvesting at sites containing both post-agricultural land use and nonagricultural land use, I found that land-use history and canopy harvesting determine the outcomes of seed-granivore interactions by modifying environmental characteristics relevant to mammal behavior. Seed predation rates in harvested plots were positively correlated with cotton rat (*Sigmodon hispidus*) foraging activity, which was lower in post-agricultural harvested plots than in nonagricultural harvested plots. In unharvested plots, seed predation increased with fox squirrel (*Sciurus niger*) activity, but fox squirrels were not affected by land-use history. In another experiment that measured white-tailed deer (*Odocoileus virginianus*) foraging and antipredator behavior across longleaf pine woodlands varying in past land use and contemporary fire frequency, I found that frequent fires generated riskier habitats for deer, but deer utilized different antipredator strategies while foraging in habitats with different land-use histories. Experimental manipulation of acoustic predator cues (i.e., coyote (*Canis latrans*) vocalizations) revealed that deer only modify their foraging behavior in response to a direct cue of predator activity in frequently burned, nonagricultural woodlands. Long-term herbivore exclosures revealed that deer herbivory only reduced deer-preferred plant species richness in infrequently burned woodlands, where deer perceptions of risk were lower. These results suggest that past and present disturbances can interact to generate "landscapes of fear" in which spatial variation in deer antipredator behavior may help explain large-scale patterns in plant communities.

Omnivorous predators, such as coyotes, that consume both animal prey and fleshy fruits may also affect plant communities as agents of seed dispersal. Since coyote foraging decisions determine individual diet and space use, understanding how aspects of the environment affect individual coyote foraging decisions is essential to understanding how environmental changes may affect seed dispersal by coyotes. By experimentally manipulating seed association with coyote scat and granivore access to seeds, I found that seed dispersal in coyote scat reduced predation of larger seeds by rodents but increased predation of smaller seeds by arthropods. Coyote scat composition was also important in affecting rodent seed predation such that seed predation was lower in the presence of meat-rich scat compared with fruit-rich scat. These results illustrate that individual coyote foraging decisions can have cascading effects on seed dispersal and survival. In an experiment evaluating how time of day and conspecific activity affect coyote foraging decisions, I found that coyotes were more likely to investigate experimental resource patches towards the end of the diel activity period and were less likely to consume resources at patches that were visited by other conspecifics. Collectively, these studies illustrate that

individual coyote foraging decisions may plan an important role in mediating seed dispersal and survival, and coyote foraging decisions may be shaped by an individual's social environment.

OVERVIEW

Spatial variation in animal foraging behavior can generate predictable patterns in trophic interactions because animal foraging decisions affect the magnitude of granivory and herbivory of plant communities. While foraging, animals must avoid attack by predators or costly encounters with conspecific competitors, so animal behavior may be shaped by characteristics of the environment that predict the likelihood of predation or intraspecific competition. While there is a growing appreciation for the myriad ways in which human activities may modify animal behavior and trophic interactions, there is still a paucity of large-scale experimental research that can measure spatial variation in trophic interactions across landscapes heterogeneous in human disturbance. Moreover, the effects of anthropogenic legacies (e.g, past agricultural land use) on animal behavior and species interactions in restored habitats has largely been unappreciated in research measuring animal responses to contemporary disturbances. Additionally, human activities not only modify environments through past and present disturbances, but they also affect species ranges, diets, and social structure. I investigate how agricultural legacies and contemporary disturbances alter habitat structure relevant to mammalian foraging decisions and perceived predation risk, generating spatial variation in antipredator behavior, seed predation, and herbivory (Chapters 1-4). In order to understand the consequences of anthropogenic modifications to species ranges, diets, and social structure, I also investigate how seed dispersal by an omnivorous predator affects post-dispersal seed predation and how the social environment of this omnivorous predator affects foraging decisions (Chapters 5-6).

Chapter 1: Past and present disturbances generate spatial variation in seed predation (Ecosphere 2020 11:e03116)

Historic agricultural land use and contemporary canopy harvesting are widespread disturbances that could generate large-scale patterns in seed fate by modifying environmental characteristics that determine granivore identity and behavior. I tested this hypothesis by tracking seed fate across seven sites containing both post-agricultural and nonagricultural land use. Past agricultural land use and contemporary canopy harvesting interacted to affect the rate of seed predation. Seed predation rates in harvested sites was positively correlated with Sigmodon hispidus foraging activity, which was lower in post-agricultural plots. In unharvested plots, seed predation increased with Sciurus niger activity, but S. niger was not affected by land-use history. This suggests that land-use history and canopy harvesting determine the outcomes of seed-granivore interactions by modifying environmental characteristics relevant to mammal behavior.

Chapter 2: Past agricultural land use affects multiple facets of ungulate antipredator behavior (Behavioral Ecology 2021 32:961-969)

Prey may dynamically adjust two antipredator strategies, vigilance and activity timing, in response to changes in perceived risk driven by vegetation cover. Agricultural legacies can modify present-day habitat structure such that the effects of contemporary disturbances, like fire regime, on vegetation cover are contingent upon land-use history. I tested this hypothesis by measuring white-tailed deer vigilance and diel activity patterns across 24 longleaf-pine woodlands varying in past land use and contemporary fire regime. In post-agricultural woodlands, deer were significantly more vigilant in woodlands with high fire frequencies than in those with low fire frequencies. Conversely, diel activity patterns of deer in nonagricultural woodlands were significantly affected by fire regime such that deer activity was nocturnal in nonagricultural woodlands with low fire frequencies but crepuscular in nonagricultural woodlands with high fire frequencies. These results suggest that landscapes containing agricultural legacies may be dynamic "landscapes of fear" in which prey use multiple antipredator strategies to respond to spatial variation in risk across disturbance regimes.

Chapter 3: Land-use history, fire regime, and large-mammal herbivory affect deer-preferred plant diversity in longleaf pine woodlands (In review at Ecography)

Disturbances have the potential to modify trophic dynamics, including the strength of top-down control of plant communities by herbivores. I tested if past agricultural land use and contemporary fire regime generated spatial variance in the impacts of ungulate herbivory on plant communities by measuring deer-preferred plant species richness at 26 longleaf-pine woodlands containing paired open and vertebrate-excluded plots. Land-use history significantly affected forage species composition, and post-agricultural sites had greater species richness than nonagricultural sites. Herbivory only affected deer-preferred species richness in woodlands with low fire frequencies. These results indicate that past and present disturbances may mediate contemporary plant-animal interactions and may explain spatial patterns in the intensity of large-mammal herbivory. Since Chapter 2 shows that deer perceive the lowest risk of predation in woodlands with low fire frequencies, these findings also suggest that the effects of fire regime on deer predation risk may have cascading effects on plant communities.

Chapter 4: White-tailed deer responses to acoustic predator cues are contingent upon past land use and contemporary fire regime (in preparation for Behavioral Ecology and Sociobiology)

Prey may use cues of predator presence to assess immediate risk of predation, and it is expected that prey should invest in costly antipredator behaviors when these cues of predation risk are detected. Features of the habitat in which the cue is detected serve as indirect cues of risk and can mediate how prey respond to direct cues of predator presence. I examined whether variation in past agricultural land use and contemporary fire regime generates predictable variation in white-tailed deer responses to acoustic cues of coyote presence. Deer did not respond to the predator cue in habitats containing infrequent fire regimes or agricultural legacies and only responded to the cue in frequently burned woodlands without agricultural legacies through increased vigilance and bout duration. These findings show that land-use legacies and contemporary fire regimes can mediate how prey respond to direct cues of risk. They also illustrate that prey may balance both the urgency and the uncertainty of a potential predator encounter through vigilance and remaining in place to acquire adequate information to launch an appropriate defense.

Chapter 5: An omnivorous mesopredator modifies predation of omnivore-dispersed seeds (Ecosphere 2021 12:e03369)

Although many plant species are dispersed following consumption by omnivorous mesopredators, the potential for these dispersal agents to indirectly affect seed fate by modifying seed-predator behavior is poorly understood. I used an experimental manipulation of mesopredator scat and granivore guild to test whether the presence of mesopredator scat leads to different patterns of seed predation by arthropod and rodent granivores. Mesopredator scat reduced seed predation by rodents but increased seed predation by arthropods, and the effects of scat on rodent foraging were modified by scat composition related to variation in mesopredator diet. These results demonstrate that the ultimate effect of omnivorous mesopredators on plant communities may strongly depend upon dominant seed predator guilds and variation in mesopredator diets.

Chapter 6: Social environment and time of day affect individual foraging decisions of a solitary forager, *Canis latrans* (In preparation for submission to Ethology)

Animal foraging behavior is important to understand because foraging decisions determine species persistence and modify the strength of species interactions, like predation and seed dispersal. Omnivorous predators, like coyotes, may forage solitarily but have overlapping home ranges or territories with conspecifics. As a result, foraging individuals must navigate complex social environments to maximize energy intake while minimizing the costs of encounters with conspecific competitors, and the probability of encountering conspecific while foraging may predictably vary across both space and time. I examined how individual coyote foraging decisions at experimental resource patches were affected by time of day and conspecific visitation to patches. I found that solitary coyotes were more likely to investigate a resource patch towards the end of the diel activity period and were less likely to consume resources at patches that were visited by other individuals. These results suggest that coyote foraging decisions change across both space and time, likely due to spatiotemporal changes in the probability of encountering a conspecific competitor while foraging. Hence, environmental changes that modify the density or social environment of coyote populations may affect coyote foraging behavior, which may mediate coyote diet, space use, and trophic interactions.

INTRODUCTION

The nature and magnitude of important trophic interactions that may determine species persistence or extinction, such as granivory, predation, and herbivory, can be highly variable and context dependent (Harrison 1987, Louda and Collinge 1992, Schmitz et al. 2000, Shurin et al. 2002, Borer et al. 2005, 2006, Hillebrand et al. 2007, Pringle et al. 2007, Maron et al. 2014); however, habitat characteristics that modify animal foraging and antipredator behavior may predict the strength of plant-animal and predator-prey interactions (Lima and Dill 1990, Brown et al. 1999, Orrock et al. 2010, Royo et al. 2010, Lichti et al. 2017, Kohl et al. 2018, Brehm et al. 2019, Loughnan and Williams 2019, Smith et al. 2019). Human land use has considerable impacts on habitat characteristics and is the single greatest driver of global biodiversity loss due to habitat conversion, fragmentation, and other forms of degradation (Wilcove et al. 1998, Sanderson et al. 2002, Foley et al. 2005, Haddad et al. 2015). In order to effectively mitigate the effects of human land use on biodiversity, it is critical to understand how human activities that directly affect habitat structure and animal behavior may consequently affect important trophic interactions (e.g., herbivory and seed dispersal; Hobbs et al. 2009; Estes et al. 2011; Sih et al. 2011; Guiden et al. 2019; Bartel and Orrock 2022).

Predicting species interactions in human-modified landscapes is particularly difficult because habitats can experience multiple forms of human disturbance that affect habitat characteristics relevant to animal behavior. For example, human conversion of natural habitats to agriculture, leading to degraded land after agricultural abandonment, is one of the biggest factors contributing to the current biodiversity crisis (Sisk et al. 1994, Pimm et al. 1995, Dobson et al. 1997). Legacies of agricultural disturbance can persist in these lands for decades and sometimes centuries (Foster 1993, Flinn and Vellend 2005, Kopecký and Vojta 2009, Mattingly et al. 2015, Culbert et al. 2017). Many terrestrial habitats containing agricultural legacies may also experience contemporary disturbances, and the overlap of these past and present disturbances can modify both plant and animal communities (Brudvig et al. 2014, Veldman et al. 2014, Hahn and Orrock 2015). However, despite the importance of understanding trophic interactions in the context of widespread modification of habitats via past and present disturbance, large-scale studies examining the interface of these processes are rare.

Past agricultural land use, contemporary canopy harvesting, and contemporary fire regime are all pervasive human disturbances that modify habitat characteristics known to affect animal behavior. Canopy harvesting can alter rodent foraging behavior by eliminating canopy cover and increasing understory growth (Sullivan and Sullivan 2001, Lambert et al. 2005, Wilkinson et al. 2005, Zwolak 2009, Chen et al. 2017, Jacques et al. 2017). Since agricultural legacies also modify habitat structure (e.g., increased light availability (Hahn and Orrock 2015) and decreased shrub cover (Stuhler and Orrock 2016)), the magnitude of rodent granivory may be contingent upon the interplay of past land use and contemporary canopy harvesting. Fire is another contemporary disturbance that can cause dramatic differences in habitat structure which may affect ungulate predation risk and foraging behavior (Cherry et al. 2017); however, it is unknown if the effects of fire on ungulate predation risk and herbivory intensity are modified by agricultural legacies. In this dissertation, I evaluate how these past and present human disturbances can generate large-scale spatial variation in animal foraging behavior and may explain spatial patterns in trophic interactions, seed fate, and plant community composition.

Human activities may also modify trophic interactions by altering animal diet and social environment. Mesopredators are an ideal system for investigating the consequences of human activities on trophic interactions for multiple reasons. First, mesopredator ranges and abundances have increased rapidly across the globe due to a combination of human activities, so they are common in human-modified landscapes (Parker 1995, Crooks and Soulé 1999, Prugh et al. 2009). Second, mesopredator diets are highly variable, particularly in relation to human disturbance (Lavin et al. 2003, Dell ’arte et al. 2007, Morey et al. 2007, Grigione et al. 2011, Wallace and Gipson 2014, Prugh and Sivy 2020). Third, mesopredators may interact directly with plant species through seed dispersal (Willson 1993, Bartel and Orrock 2022, Draper et al. 2022) or indirectly by modifying granivore behavior (Orrock and Fletcher 2014, Chandler et al. 2020). Finally, the social environments of mesopredators can constrain individual resource acquisition, creating predictable individual-level variation in foraging decisions, which may affect diet (Tilson and Hamilton 1984, Gese et al. 1996, Ward et al. 2018, Bartel and Orrock 2022). In order to anticipate how human-induced changes in mesopredator ranges, diets, and social structure affect trophic interactions, it is critical to first understand how mesopredator diets affect seed fate and how the social environment of mesopredators affects individual foraging decisions (Bartel and Orrock 2022). In this dissertation, I evaluate how coyotes, which are common mesopredators throughout North America, affect seed fate as consumers of both fruit and rodent granivores and how variation in coyote diets may affect the magnitude of post-dispersal seed predation. I also evaluate how individual foraging decisions of solitary coyotes are shaped by an individual’s social environment and the likelihood of encountering conspecific competitors.

I conducted this work in the longleaf pine ecosystem at the Savannah River Site, (SRS; Aiken, SC), an 80,125-ha National Environmental Research Park (NERP). Characterized by open longleaf pine canopies that are maintained by frequent understory fires, longleaf pine woodlands are biodiversity hotspots due to the diversity of rare and endemic understory plant species (Frost 2006). SRS is within the historical range of the longleaf-pine woodland; and much of this ecosystem was converted to tillage agriculture between 1856 and 1950 (Frost 2006). These agricultural lands were small and dispersed, generating heterogeneous landscapes with plots of farmland and forests (Kilgo and Blake 2005). Agricultural lands at SRS were abandoned in 1951 and have henceforth been under management as longleaf and loblolly pine plantations (Kilgo and Blake 2005). Coyotes are widespread, omnivorous mesopredators that first arrived at SRS in 1989 (Cothran et al. 1991, Gulsby et al. 2017). Coyotes in southeastern US are omnivorous with significant diet variation (Thornton et al. 2004, Schrecengost et al. 2008, Mastro 2011, Cherry et al. 2016). Coyotes are the primary predators of deer in longleaf pine woodlands, and predation by coyotes can limit deer populations in this system (Kilgo et al. 2010, Gulsby et al. 2017). At SRS, soft mast, chiefly *Prunus* spp. and *Rubus* spp., is the most common food item from spring to late fall (Schrecengost et al. 2008), suggesting that endozoochorous seed dispersal by coyotes may be quite common. Hence, coyotes in the southeastern US stand at the intersection of multiple trophic dynamics that may indirectly affect plant communities in the longleaf pine ecosystem. Throughout this dissertation, I evaluate how the social environment shapes coyote foraging decisions, how risk of predation by coyotes affects the behavior of prey, and if prey antipredator behavior affects the magnitude of herbivory and granivory on plant communities in the longleaf pine ecosystem.

References

Bartel, S. L., and J. L. Orrock. 2020. Past and present disturbances generate spatial variation in seed predation. Ecosphere 11:e03116.

Bartel, S. L., and J. L. Orrock. 2022. The important role of animal social status in vertebrate seed dispersal. Ecology Letters 00:1–16.

Borer, E. T., B. S. Halpern, and E. W. Seabloom. 2006. Asymmetry in community regulation: effects of predators and productivity. Ecology 87:2813–2820.

Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? Ecology 86:528–537.

Brehm, A. M., A. Mortelliti, G. A. Maynard, and J. Zydlewski. 2019. Land-use change and the ecological consequences of personality in small mammals. Ecology Letters 22:1387–1395.

Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385–399.

Brudvig, L. A., J. L. Orrock, E. I. Damschen, C. D. Collins, P. G. Hahn, W. B. Mattingly, J. W. Veldman, and J. L. Walker. 2014. Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities. PLoS ONE 9:e86604.

Chandler, J. L., T. R. Van Deelen, N. P. Nibbelink, and J. L. Orrock. 2020. Large-scale patterns of seed removal by small mammals differ between areas of low- versus high-wolf occupancy. Ecology and Evolution 10:7145–7156.

Chen, W., J. Zhong, S. Sun, Z. Xie, and Y. Zhou. 2017. Fuelwood collection depresses the seed-dispersal service provided by rodents. Forest Ecology and Management 406:53–60.

Cherry, M. J., K. L. Turner, M. Brent Howze, B. S. Cohen, L. Mike Conner, and R. J. Warren. 2016. Coyote diets in a longleaf pine ecosystem. Wildlife Biology 22:64–70.

Cherry, M. J., R. J. Warren, and L. M. Conner. 2017. Fire-mediated foraging tradeoffs in white-tailed deer. Ecosphere 8:e01784.

Cothran, E. G., M. H. Smith, J. O. Wolff, and J. B. Gentry. 1991. Mammals of the Savannah

River Site. SRO-NERP-21, Aiken, SC: Savannah River Site.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Culbert, P. D., I. Dorresteijn, J. Loos, M. K. Clayton, J. Fischer, and T. Kuemmerle. 2017. Legacy effects of past land use on current biodiversity in a low-intensity farming landscape in Transylvania (Romania). Landscape Ecology 32:429–444.

Dell 'arte, G. L., T. Laaksonen, K. Norrdahl, and E. Korpimä. 2007. Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. Acta Oecologica 31:276–281.

Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the future: Restoration ecology and conservation biology. Science 277:515–522.

Draper, J. P., J. K. Young, E. W. Schupp, N. G. Beckman, and T. B. Atwood. 2022. Frugivory and seed Dispersal by *Carnivorans*. Frontiers in Ecology and Evolution 0:264.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet earth. Science 333:301–306.

Flinn, K. M., and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3:243–250.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005.

Global consequences of land use. Science 309:570–574.

Foster, D. R. 1993. Land-use History and Forest Transformations in Central New England. Pages 91–110 Humans as Components of Ecosystems. Springer New York, New York, NY.

Frost, C. 2006. History and Future of the Longleaf Pine Ecosystem. Pages 9–48 *in* S. Jose, E. J. Jokela, and D. L. Miller, editors. The Longleaf Pine Ecosystem. Springer-Verlag New York, New York, NY.

Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. Canadian Journal of Zoology 74:769–783.

Grigione, M. M., P. Burman, S. Clavio, S. J. Harper, D. Manning, R. J. Sarno, M. M. Grigione, P. Burman, S. Clavio, : D Manning, S. J. Harper, and R. J. Sarno. 2011. Diet of Florida coyotes in a protected wildland and suburban habitat. Urban Ecosystems 14:655–663.

Guiden, P. W., S. L. Bartel, N. W. Byer, A. A. Shipley, and J. L. Orrock. 2019. Predator-prey interactions in the Anthropocene: Reconciling multiple aspects of novelty. Trends in Ecology and Evolution 34:616–627.

Gulsby, W. D., J. C. Kilgo, M. Vukovich, and J. A. Martin. 2017. Landscape heterogeneity reduces coyote predation on white-tailed deer fawns. Journal of Wildlife Management 81:601–609.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D. X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. Science Advances 1:e1500052.

Hahn, P. G., and J. L. Orrock. 2015. Land-use history alters contemporary insect herbivore community composition and decouples plant-herbivore relationships. Journal of Animal Ecology 84:745–754.

Harrison, S. 1987. Treefall gaps versus forest understory as environments for a defoliating moth on a tropical forest shrub. Oecologia 72:65–68.

Hillebrand, H., D. S. Gruner, E. T. Borer, M. E. S. Bracken, E. E. Cleland, J. J. Elser, W. S. Harpole, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. Proceedings of the National Academy of Science 104:10904–10909.

Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution 24:599–605.

Jacques, M.-E., S. W. Hallgren, and D. S. Wilson. 2017. Low-basal area treatment and prescribed fire to restore oak-pine savannas alter small mammal communities. Forest Ecology and Management 400:353–362.

Kilgo, J., and J. I. Blake, editors. 2005. Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site. Island Press, Washington, DC, USA.

Kilgo, J. C., H. S. Ray, C. Ruth, and K. V. Miller. 2010. Can coyotes affect deer populations in southeastern North America? Journal of Wildlife Management 74:929–933.

Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. Ecological Monographs 88:638–652.

Kopecký, M., and J. Vojta. 2009. Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. Applied Vegetation Science 12:251–260.

Lambert, T. D., J. R. Malcolm, and B. L. Zimmerman. 2005. Effects of mahogany (*Swietenia macrophylla*) logging on small mammal communities, habitat structure, and seed predation in the southeastern Amazon Basin. Forest Ecology and Management 206:381–398.

Lavin, S. R., T. R. Van Deelen, P. W. Brown, R. E. Warner, S. H. Ambrose, S. Lavin, T. Van Deelen, P. Brown, and R. Warner. 2003. Prey use by red foxes (*Vulpes vulpes*) in urban and rural areas of Illinois. Can. J. Zool 81:1070–1082.

Lichti, N. I., M. A. Steele, and R. K. Swihart. 2017. Seed fate and decision-making processes in scatter-hoarding rodents. Biological Reviews 92:474–504.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68:619–640.

Louda, S. M., and S. K. Collinge. 1992. Plant resistance to insect herbivores: A field test of the environmental stress hypothesis. Ecology 73:153–169.

Loughnan, D., and J. L. Williams. 2019. Climate and leaf traits, not latitude, explain variation in plant-herbivore interactions across a species' range. Journal of Ecology 107:913–922.

Maron, J. L., K. C. Baer, and A. L. Angert. 2014. Disentangling the drivers of context-dependent plant-animal interactions. Journal of Ecology 102:1485–1496.

Mastro, L. L. 2011. Life history and ecology of coyotes in the Mid-Atlantic states: a summary of the scientific literature. Southeastern Naturalist 10:721–730.

Mattingly, W. B., J. L. Orrock, C. D. Collins, L. A. Brudvig, E. I. Damschen, J. W. Veldman, and J. L. Walker. 2015. Historical agriculture alters the effects of fire on understory plant beta diversity. Oecologia 177:507–518.

Morey, P. S., E. M. Gese, and S. Gehrt. 2007. Spatial and temporal variation in the diet of coyotes in the Chicago Metropolitan area. American Midland Naturalist 158:147–161.

Orrock, J. L., and R. J. Fletcher. 2014. An island-wide predator manipulation reveals immediate and long-lasting matching of risk by prey. Proceedings of the Royal Society of London B: Biological Sciences 281.

Orrock, J. L., R. D. Holt, and M. L. Baskett. 2010. Refuge-mediated apparent competition in plant–consumer interactions. Ecology Letters 13:11–20.

Parker, G. 1995. Eastern Coyote: The Story of Its Success. 1st edition. Nimbus Publishing, Halifax, Nova Scotia.

Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. Science 269:347–350.

Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. Mccauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. Proceedings of the National Academy of Sciences 104:193–197.

Prugh, L. R., and K. J. Sivy. 2020. Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. Ecology Letters 23:902–918.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology 91:93–105.

Sanderson, E. W., M. Jaiteh, M. Levy, K. H. Redford, A. V Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. Bioscience 52:891–904.

Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. The American Naturalist

155:141–153.

Schrecengost, J. D., J. C. Kilgo, D. Mallard, H. S. Ray, and K. V Miller. 2008. Seasonal food habits of the coyote in the South Carolina Coastal Plain. Southeastern Naturalist 7:135–144.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4:367–387.

Sisk, T. D., A. Launer, K. R. Switky, and P. R. Ehrlich. 1994. Identifying extinction threats. BioScience 44:592–604.

Smith, J. A., E. Donadio, J. N. Pauli, M. J. Sheriff, O. R. Bidder, and A. D. Middleton. 2019. Habitat complexity mediates the predator–prey space race. Ecology 100.

Stuhler, J. D., and J. L. Orrock. 2016. Past agricultural land use and present-day fire regimes can interact to determine the nature of seed predation. Oecologia 181:463–473.

Sullivan, T. P., and D. S. Sullivan. 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and Population Dynamics of Small Mammals. Journal of Applied Ecology 38:1234–1252.

Thornton, D. H., M. E. Sunquist, and M. B. Main. 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in south-central Florida. Journal of Mammalogy 85:973–982.

Tilson, R. L., and W. J. Hamilton. 1984. Social dominance and feeding patterns of spotted hyaenas. Animal Behaviour 32:715–724.

Veldman, J. W., L. A. Brudvig, E. I. Damschen, J. L. Orrock, W. B. Mattingly, and J. L. Walker.

2014. Fire frequency, agricultural history and the multivariate control of pine savanna understorey plant diversity. Journal of Vegetation Science 25:1438–1449.

Wallace, M. C., and P. S. Gipson. 2014. Comparison of coyote (*Canis latrans*) diets in continuous and fragmented short-grass prairie in the Texas Panhandle. Texas Journal of Science 66:25–41.

Ward, J. N., J. W. Hinton, K. L. Johannsen, M. L. Karlin, K. V. Miller, and M. J. Chamberlain. 2018. Home range size, vegetation density, and season influences prey use by coyotes (*Canis latrans*). PLoS ONE 13:1–22.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48:607–615.

Wilkinson, L., J. T. Fisher, and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Page Mammal Review.

Willson, M. F. 1993. Mammals as seed-dispersal mutualists in North America. Oikos 67:159–176.

Zwolak, R. 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. Forest Ecology and Management 258:539–545.

CHAPTER 1

Past and present disturbances generate spatial variation in seed predation

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Abstract

Seed survival is a key process for plant populations; variation in the activity and abundance of animals that consume seeds can lead to dramatic shifts in seed fate. Because granivores may respond to contemporary disturbance as well as to enduring changes in habitats caused by past disturbances, understanding seed fate requires studies capable of evaluating how past and present disturbances modify granivore communities, foraging activity, and ultimately, seed predation. Historic agricultural land use and contemporary canopy harvesting are widespread disturbances that could generate large-scale patterns of seed fate by modifying environmental characteristics that determine granivore identity and behavior. To evaluate whether land-use history and canopy harvesting affect seed–animal interactions, we conducted an experiment distributed across 80,000 ha of longleaf pine woodlands that coupled large-scale canopy harvesting at seven 4-ha sites containing both post-agricultural land use and nonagricultural land use in South Carolina, United States. We deployed a total of 28,000 nail-tagged seeds and recovered the tags to quantify seed fate. Past agricultural land use and contemporary canopy harvesting interacted to affect the rate of seed predation. Seed predation rates in harvested sites depended on land-use history: Seed predation was 30% lower in post-agricultural plots than in nonagricultural plots. This interaction was driven by the differential effect of land-use history and canopy harvesting on rodent activity. Camera traps revealed that Sigmodon hispidus only foraged in harvested plots and was most active in nonagricultural plots. In harvested plots, seed removal increased with S. hispidus activity. In unharvested plots, seed removal increased with Sciurus niger activity, but S. niger was not affected by land-use history. In finding that land-use history and canopy harvesting determine the outcomes of seed–animal interactions, we show that understanding patterns of seed predation is contingent upon the interplay of disturbances in both the distant past and recent past. These results suggest that patterns of past land use and present land use may help reconcile the considerable variation in seed fate observed in ecological communities.

Introduction

Seed limitation is a key process affecting large-scale patterns of plant distributions and diversity (Louda 1982, Clark et al. 1998, Zobel et al. 2000, Orrock et al. 2006, Standish et al. 2007, Öster et al. 2009). Seed limitation occurs through two processes: seeds may never arrive at a microsite favorable for establishment (dispersal limitation; Turnbull et al. 2000), or seeds may be destroyed by predators either before or after dispersal (predator limitation; Crawley 2000). Because seed predation may be tightly linked to the abundance and activity of animals that consume seeds (Ji-Qi and Zhi-Bin 2004), environmental characteristics that modify animal behavior, abundance, and community composition can place important constraints on seed survival (Orrock et al. 2010, Lichti et al. 2014, 2017, Brehm et al. 2019). Despite the importance of understanding how the environment can modify seed-animal interactions, deciphering the effect of the environment can be complex because multiple environmental components can affect the activity, abundance, and community composition of foraging animals (Brown and Kotler 2004, Orrock et al. 2010, Kelt et al. 2019).

Past agricultural land use and contemporary canopy harvesting are two pervasive human disturbances that modify environmental characteristics that determine granivore identity and behavior. Agricultural land use is widespread in terrestrial systems: 42-68% of land cover has been impacted by agriculture since 1700, and land recovered from agriculture increased over this period by 10-44x10^6 km^2 (Hurtt et al. 2006). Agricultural legacies on plant communities can persist for centuries (Foster 1993, Flinn and Vellend 2005, Kopecký and Vojta 2009, Mattingly et al. 2015, Culbert et al. 2017). Past land use can interact with contemporary disturbances like canopy harvesting to determine plant performance (Hahn and Orrock 2016), consumer pressure (Hahn and Orrock 2015, Stuhler and Orrock 2016), and community structure (Brudvig and Damschen 2011). Harvesting of mature trees is implemented worldwide for both commercial and restoration purposes (Toman et al. 1996, Simberloff 1999, Drever et al. 2006), and it can drive changes in seed predation by animals (Bellocq et al. 2005, Lambert et al. 2005, Chen et al. 2017). Despite evidence showing that seed limitation is fundamental in determining plant community structure after agricultural land use and canopy harvesting (Turley et al. 2017, Barker et al. 2019), it is unclear whether past agriculture and contemporary canopy harvesting generate patterns of seed predation by changing granivore identity and behavior.

Rodents are primary seed predators in many ecosystems (Hulme 1994, Bermejo et al. 1998, Corlett 1998, Kappler et al. 2012, Stuhler and Orrock 2016, Gómez et al. 2019); and rodent seed predation can generate large-scale patterns of plant distributions (Maron and Simms 1997, Crawley 2000, Orrock et al. 2006, Bricker et al. 2010, Culot et al. 2017). Habitat structure is a particularly well-known driver of rodent foraging behavior (Dueser and Shugart 1978, Orrock et al. 2004, 2010, Zwolak 2009, Guiden and Orrock 2017); hence, disturbances that transform habitat structure could change the magnitude and spatial patterns of rodent foraging to modify seed fate (Guiden and Orrock 2017). By eliminating canopy cover and increasing understory growth, canopy harvesting can alter rodent granivore identity and foraging behavior (Sullivan and Sullivan 2001, Lambert et al. 2005, Fisher and Wilkinson 2005, Zwolak 2009, Chen et al. 2017, Jacques et al. 2017). Since agricultural legacies also modify habitat structure (e.g., increased light availability (Hahn and Orrock 2015) and decreased shrub cover (Stuhler and Orrock 2016)), predicting how rodents will respond to harvesting may be contingent upon past land use. Despite the potentially important role of past agricultural legacies in determining the outcomes of contemporary disturbances, no research has investigated if past agricultural land use interacts with a globally ubiquitous disturbance, canopy harvesting, to generate spatial variation in rodent species activity and seed predation. Considering that rodent granivores may also be essential agents of seed dispersal (Vander Wall 2001, Vander Wall et al. 2005, Jansen et al. 2012, Lichti et al. 2017), explicit tracking of the seed fate after rodent handling is essential to understanding how rodent responses to disturbances are linked to spatial patterns of seed predation. Understanding the roles of past and present disturbances and rodent granivory in generating patterns of seed predation therefore requires landscape-level manipulations of past and present disturbances paired with small-scale monitoring of granivore identity, behavior, and seed fate.

In order to understand how past land use and contemporary canopy harvesting generate spatial variation in seed predation by modifying granivore identity and behavior, we monitored seed fate and rodent activity in a large-scale experiment in the longleaf pine (*Pinus palustris*) ecosystem in the southeastern USA. Agricultural history is pervasive in contemporary longleaf-pine woodlands, affecting plant communities, herbivory, and habitat structure (Veldman et al. 2014, Hahn and Orrock 2015, Stuhler and Orrock 2016). In these woodlands, seed limitation prevents the recovery of native plant species, and rodents are important seed predators (Orrock et al. 2003, 2006, Stuhler and Orrock 2016, Turley et al. 2017). Using replicated, large-scale experimental landscapes that combine a factorial manipulation of contemporary disturbance (canopy harvesting) across plots that differ in their historical land use, we used explicit tracking of seed fate and monitoring of rodent granivores to evaluate two hypotheses: 1) by modifying rodent habitat structure, past agriculture and present canopy harvesting affect rodent species activity, and 2) by modifying rodent species activity, past agriculture and present canopy harvesting affect seed predation rates.

Methods

Study area and design

We conducted our study at the Savannah River Site (SRS; Aiken, SC), an 80,125-ha National Environmental Research Park (NERP). SRS is within the historical range of the longleaf-pine woodland; and much of this ecosystem was converted to tillage agriculture between 1856 and 1950 (Frost 2006). These agricultural lands were small and dispersed, resulting in heterogeneous landscapes with plots of tilled farmland and untilled forests (Kilgo and Blake 2005). Agricultural fields were abandoned in 1951 and have henceforth been under management as longleaf and loblolly pine plantations (Kilgo and Blake 2005). Past research at SRS shows that agricultural land-use history has a strong effect on overstory communities such that post-agricultural areas are dominated by pine and nonagricultural areas are dominated by hardwoods, an artifact of historic fire suppression (Brudvig et al. 2013). We selected seven sites, spanning an 807-km^2 area, each straddling a land-use history boundary. Each site was relatively homogenous in soil type, slope, and fire frequency (see Brudvig et al. 2013 for further details). Since fire regime is an important driver of rodent population dynamics, habitat structure, and plant communities in this system (Frost 2006, Morris et al. 2011a, 2011b, Karmacharya et al. 2012), we selected sites that spanned a fire regime ranging from 0 to 12 years since the last prescribed burn to capture the range of variation typical in managed longleaf pine woodlands (Frost 2006). A primary obstacle to studying land-use history is that agricultural history can be confounded with other properties of the site that were favored for agriculture (Flinn and Vellend 2005). We minimized these confounding effects by using paired plots, split by land-use history (Brudvig et al. 2013). Land-use history classification was based on aerial photography taken prior to land abandonment in 1951. Plots that were farmland in 1951 were classified as "post-agricultural," and plots that were forested were classified as "nonagricultural." At each site, we established four 1-ha (100 m x 100 m) research plots that contained 2 pairs of plots on opposing sides of the land-use history boundary (Fig. 1), and we imposed a canopy harvesting treatment (8-10 mature trees remaining per ha) in 2011 to create a fully factorial manipulation of land-use history and canopy harvesting (Fig. 1).

Seed tracking experiment

To test how land-use history and canopy harvesting alters rodent activity and seed fate, we employed an acorn-tracking method that has been successfully used in past studies examining seed predation and seed dispersal (Sork 1984, Moore et al. 2007, Lichti et al. 2014, Guiden and Orrock 2017). We obtained *Quercus nigra* seeds from a commercial supplier (Louisiana Forest Seed Company, Lecompte, LA, USA), which we tagged with 12-mm brad nails (Sork 1984, Moore et al. 2007, Lichti et al. 2014, Guiden and Orrock 2017). *Quercus nigra* is a common oak species found in both post-agricultural and nonagricultural areas at our sites. We deployed 1,000 nail-tagged *Q. nigra* seeds in the center of every 1-ha plot at all seven sites for a period of four weeks in July 2017 (Fig. 1). Within a site, we painted the nails for each plot a unique fluorescent color to make it possible to determine between-plot movement events. To focus on seed foraging by rodents, we secured a 0.5 m x 0.5 m hardware-cloth box around tagged acorns to create a seed depot. The seed depot contained a 7 x 7 cm hole that allowed rodent access and prohibited seed foraging by larger, non-focal taxa (e.g., turkeys and deer). At the end of the deployment period, we used a metal detector (Bounty Hunter Platinum, First Texas Products, El Paso, TX, USA) to survey the area within a 30-m radius of each depot for the nails. Preliminary tests verified that our metal detector was able to detect a nail 15 cm below the surface, which greatly exceeds the published range of cache depths: 0.26 – 9 cm (Vander Wall 2003, Vander Wall et al. 2009, Lichti et al. 2014, Dittel et al. 2017). Once a tagged acorn or nail was recovered, we recorded the distance and compass bearing from the depot and whether or not the seed was consumed. By counting the number of seeds remaining in the depot, we were able to estimate the number of seeds removed and determine recovery rates. Because *Glaucomys volans* nest boxes and *Peromsycus polionotus* burrows in the southeastern US have been shown to contain the remains of consumed acorns and never intact acorns (Moore 1947, Gentry and Smith 1968, Goertz et al. 1975, Heidt 1977), we assume, consistent with other studies that follow acorn fate (Steele et al. 2001, Guiden and Orrock 2017), that unrecovered acorns are likely to be nonviable because they have been moved to arboreal or deep subterranean caches where they are likely to be consumed or are incapable of successful germination and emergence. Habitat structure was measured at each depot by using four 1-m^2 quadrats where percent cover for bare soil, leaf litter, woody debris, and vegetative cover (herbaceous and woody plants) was visually estimated. All data were collected by the same observer.

Rodent species activity

To examine how land-use history and canopy harvesting affected rodent activity and community composition, we positioned a motion-activated digital trail camera one meter from each depot for one week while nail-tagged seeds were deployed (Fig. 1). We recorded the date and time of each photo and the species captured in it. Since the identification of the two common *Peromyscus* species in our study area, *Peromyscus gossypinus* and *Peromyscus polionotus*, requires morphological measurements, we did not identify this genus to the species level. To create an estimate of rodent species activity from the camera-trap data that was relevant for seed predation and dispersal, we quantified the total number of foraging bouts per rodent species at each depot. Because our camera traps were positioned to capture rodents entering, exiting, and foraging inside of the depot, a bout was defined as a single visit to the depot.

Data analysis

We calculated the proportion of seeds removed from the depot and the average distance seeds were moved at each plot. All analyses were conducted in R ver. 3.5.1, and linear mixed models were constructed using the "lme4" package (Bates et al. 2015; see Appendix S1: Table S1 for list of hypotheses and models). To test the hypothesized effects of land-use history and canopy harvesting on habitat structure, we used multivariate analysis of variance (MANOVA) with percent ground cover variables (bare, litter, vegetation, and woody debris) as response variables and canopy harvesting and land-use history as fixed effects. If a significant result from MANOVA analysis was detected, we used univariate analysis of variance (ANOVA) to test the effects of land-use history and harvesting on specific ground cover variables (Scheiner 2001). To test the hypothesized effects of land-use history and canopy harvesting on the proportion of seeds removed, we used a binomial generalized linear mixed model (GLM) with a random intercept for site and varying slopes for land-use history. To test how land-use history and canopy harvesting affected the spatial extent of rodent foraging, we used linear mixed effects models with a random intercept for site and varying slopes for land-use history. To test how activity of individual rodent species was related to the proportion of seeds removed, we used separate binomial GLMs (Table 1) with a random intercept for site and different slopes for land-use history. For species that were only found in one harvesting treatment group, we had to subset the data by harvesting treatment for analyses. For rodent species whose activity had a significant effect on seed removal, we used linear mixed effect models to test how land-use history and canopy harvesting affected the activity with a random intercept for site.

Results

The average seed removal rate at each plot was 31.5 ± 5.6 (SE) percent seeds, and the average nail recovery rate was 66 ± 5 (SE) percent. Our average recovery rate was higher than that of other acorn metal-tagging studies (17 - 37 percent (Sork 1984, Steele et al. 2001, Lichti et al. 2014, Guiden and Orrock 2017)). The longest distance a nail was recovered was 10.3 m, and the average distance at which moved nails were recovered was 0.9 ± 0.2 (SE) m. A total of 49 (< 0.01%) seeds were removed from the depot and found intact. We did not find any intact seeds that had been cached (i.e., buried under litter or soil). The farthest distance an intact seed was moved was 7.5 m, and the average distance was 1.1 m. Camera traps captured 11,124 photos of animal activity, including 1,103 photos of *Peromyscus* spp., 2,476 of *Sigmodon hispidus,* 5,145 of *Sciurus niger,* and 1,936 of *Glaucomys volans* foraging in the seed depots.

Canopy harvesting had a significant effect on ground cover ($F_{4,21} = 21.23$, $p < 0.001$), and the interaction of harvesting and land-use history also significantly affected ground cover ($F_{4,21} = 4.66$, $p = 0.008$). Litter cover was significantly lower in harvested plots ($p < 0.001$; Fig. 2).

Vegetation cover was significantly higher in harvested plots ($p < 0.001$; Fig. 2). Land-use history and harvesting interacted to affect vegetation cover ($p < 0.034$; Fig. 2) such that land-use history only affected vegetation cover in harvested plots where nonagricultural plots had greater cover.

Land-use history and canopy harvesting interacted to affect seed-removal rates ($\chi^2 = 10.71$, $p = 0.001$). The lowest seed-removal rates were in harvested, post-agricultural plots, and the highest rates were in harvested, nonagricultural plots (Fig. 3a). Canopy harvesting altered rodent species activity such that *Sciurus niger* and *Glaucomys volans* were only observed in unharvested plots, and *Sigmodon hispidus* was largely observed in harvested plots (Fig. 2). Bouts by *S. niger* were positively correlated with seed removal in unharvested plots (Table 1), and there was no effect of land-use history on *S. niger* bouts in unharvested plots ($F_{1,6} = 2.25$, $p = 0.184$). Land-use history and canopy harvesting marginally interacted to affect *S. hispidus* bouts ($F_{1,27} = 3.53$, $p = 0.077$), and harvested post-agricultural plots had fewer bouts (Fig. 3b). Bouts by *S. hispidus* were positively correlated with seed removal in harvested plots (Table 1; Fig. 3c). Seed movement distances were not affected by land-use history ($F_{1,13} = 2.26$, $p = 0.184$), canopy harvesting ($F_{1,13} = 3.73$, $p = 0.077$), the interaction of land use and harvesting ($F_{1,27} = 0.51$, $p = 0.487$), or rodent species bouts (Table 1).

Discussion

Seed limitation structures plant populations in a wide array of terrestrial ecosystems (Clark et al. 1998, Turnbull et al. 2000, Zobel et al. 2000, Standish et al. 2007, Öster et al. 2009, Turley et al. 2017). Our study is the first to demonstrate that past agricultural land use, which is known to have lasting legacies on plant communities (Foster 1993, Flinn and Vellend 2005, Kopecký and Vojta 2009, Brudvig et al. 2014), may also interact with contemporary canopy harvesting to yield significant changes in an essential component of seed limitation, seed predation. Moreover, we find that the effect of past land use on seed predation is contingent upon contemporary disturbance, in the form of canopy harvesting (Fig. 3a). These significant changes in seed predation arise because of the varying effects of land-use history and canopy harvesting on different rodent species (Fig. 3b,c). Our findings have several implications. First, our results suggest that understanding seed predation may require knowledge of both past and present disturbance. Second, in finding a strong link between habitat characteristics that modify the activity of different rodent species and the magnitude of seed predation, our work suggests that studies relating rapid environmental changes to shifts in animal behavior may provide unappreciated insight into spatial patterns of seed fate.

Past and present disturbances modify the magnitude of seed predation

Agricultural land-use history decreased seed predation rates when canopy harvesting was imposed, but there was no effect of land-use history in unharvested plots. Harvesting amplified agricultural legacies on seed predation by shifting rodent species activity, such that species only found in harvested plots exhibited reduced activity with historic agriculture. A notable limitation to generalizing these results is that we tracked the fate of one, large-seeded species, *Q. nigra*. Since seed traits can modify rodent foraging decisions (Lichti et al. 2017), the fate of *Q. nigra* seeds may not represent the fate of all seeds handled by rodents. However, our results do illuminate a possible mechanism behind well-documented patterns of *Q. nigra* regeneration in restored post-agricultural areas (Shear et al. 1996, Allen 1997, Allen et al. 1998). *Quercus nigra* and related southeastern oaks are known to have low rates of natural establishment in post-agricultural areas with suitable abiotic conditions (Shear et al. 1996, Allen 1997, Allen et al. 1998), and our results from explicit tracking of *Q. nigra* seed fates supports the common assumption that these species are limited by infrequent dispersal events and high rates seed predation. In fact, guidelines for hardwood reforestation in the southeast often emphasize the necessity of actively planting *Q. nigra* (e.g., direct seeding or planting saplings) in order to enable its establishment (Allen 1997, Allen et al. 2001). In a Louisiana study investigating the cause of failed reforestation efforts involving oak direct seeding in the late-1980s, it was found that seed predation by rodents, particularly *S. hispidus*, was a primary limitation to oak establishment (Buchholz 1996). Our results provide further evidence of *S. hispidus*' role as an important seed predator of southeastern oaks and illuminate the effects of past land use on *S. hispidus* seed predation.

Environmental change that creates spatial variation in animal behavior may generate spatial patterns in seed predation

Our study suggests that contemporary disturbances that generate rapid environmental change can modify animal behavior and transform the strength of land-use legacies. Canopy harvesting increased the strength of post-agricultural effects on seed predation by driving a shift in rodent species activity (Fig. 2,3). There was no effect of land-use history in unharvested plots on seed predation or the activity of *S. niger*, the primary seed predator in unharvested plots (Table 1); however, canopy harvesting drove a shift in rodent species activity such that *S. hispidus* was the primary seed predator and was most active in nonagricultural plots, which had higher vegetation cover than post-agricultural plots (Table 1; Fig. 2). These results show that changes in habitat structure caused by canopy harvesting may modify the relationship between rodent seed removal and past land use. The effects of land-use history on *S. hispidus* foraging activity in harvested plots are likely driven by differences in vegetation cover in post-agricultural vs. nonagricultural habitats after harvesting because it is known to prefer dense understories to reduce predation risk (Fleharty and Mares 1973, Conner et al. 2013). Since herbaceous ground cover was lower in harvested post-agricultural plots, agricultural land-use history may enhance predation risk in harvested plots. In a separate experiment comparing seed removal by rodents in unharvested longleaf-pine woodlands of different land-use histories and fire regimes, Stuhler and Orrock (2016) found that seed predation by *P. gossypinus* increased with vegetation cover in nonagricultural sites with low fire frequencies, which were habitats with generally higher vegetation cover than high-fire nonagricultural sites and all post-agricultural sites. In the other habitat types with generally lower vegetation cover, *P. gossypinus* seed predation increased with woody debris cover. This contingency of habitat structure on the relationship between microhabitat characteristics and rodent seed removal reflects our study's findings that rodent seed predation was greater in habitats with higher vegetation cover (i.e., nonagricultural plots) in harvested plots, which had generally higher vegetation cover than unharvested plots. Alternatively, since harvesting increases seed production (Turley et al. 2017), it is possible that *S. hispidus* is responding to changes in food availability. Food supplementation in nonagricultural longleaf-pine woodlands can amplify *S. hispidus* populations (Morris et al. 2011a); however, *S. hispidus* space use is more strongly affected by perceived predation risk than food availability (Conner et al. 2013). Viewed in light of this past work, our results suggest that *S. hispidus* may generally prefer harvested sites for food availability, but they concentrate their foraging activity in nonagricultural harvested areas where there is greater herbaceous cover to reduce predation risk. Future studies quantifying *S. hispidus* anti-predator behavior in these habitats, e.g., via giving-up densities (Brown 1988), could help evaluate this hypothesis.

Rodent populations can vary both spatially and temporally, which is important for the generality of our results across space and time. Spatial variation in rodent populations in our study system is well-documented (Hinkelman and Loeb 2007, Morris et al. 2011a); and given our experimental design's large-scale replication, we are confident in the spatially-consistent patterns of rodent behavior and seed fate shown in our results. Furthermore, experiments conducted at our study site in habitats similar to our harvested and unharvested plots in previous years have shown similarly high levels of rodent seed predation and similar effects of past land use on seed predation for multiple years (Orrock et al. 2003, 2006, Orrock and Damschen 2005, Stuhler and Orrock 2016). Past work in our system has also found no variation in rodent seed predation across seasons (Orrock and Damschen 2005). These consistencies across multiple years and seasons indicate that the effects of past and present disturbance on seed predation in our results are unlikely to have significant temporal variation.

The timing of our experiment may also be important for rodent caching behavior. Secondary seed dispersal by rodents can help seeds of various sizes reach favorable microsites and most often occurs in the fall (Herrera 2002, Vander Wall et al. 2005, 2017). In North America, plants dispersed by scatter-hoarding rodents are most prevalent in the southeastern and southern part of the continent (Vander Wall et al. 2017); however, no research to our knowledge has investigated scatter-hoarding behavior in the southeastern US. The closest approximation to our knowledge was a seed-tracking study conducted in Kentucky in which fox squirrels were largely seed predators, dispersing only 0.02% of the acorns presented (Cilles et al. 2016). Less than 0.01% of the acorns we deployed were effectively "dispersed" in that they were both moved and not consumed. These generally high rates of seed predation and low rates of seed dispersal reflect patterns of acorn fate found in other seed-tracking experiments that more closely approximate the seasonal timing of acorn production (Sork 1984, Lichti et al. 2014, Guiden and Orrock 2017). Our dispersal rate, however, is lower than other experiments that have investigated dispersal by rodents using our nail-tagging methods with a search radius of 30 m (1-

10%; Sork 1984, Lichti et al. 2014, Guiden and Orrock 2017). Additionally, our study was unique in that we did not detect a single cache. While our recovery rate (66%) was nearly double that of other nail-tagging experiments that did detect caches in other ecosystems (17-37%; (Sork 1984, Steele et al. 2001, Lichti et al. 2014, Guiden and Orrock 2017), it is possible that some of the unrecovered seeds were cached. In our system, unrecovered seeds are likely to have been to be consumed in arboreal nests by *G. volans* or subterranean nests by *P. polionotus*. Consumed remains of acorns have been found in both settings while intact acorns were not found (Moore 1947, Gentry and Smith 1968, Goertz et al. 1975, Heidt 1977). It is possible that the uniquely low dispersal rates found in our experiment is due to its timing 2-4 weeks prior to natural *Q. nigra* maturation. Future studies on seed fate that capture a larger temporal range are needed to determine the frequency of seed dispersal by rodents in the southeastern US. It is worth noting, however, that despite the natural maturation of *Q. nigra* seeds occurring in September, direct seeding of oak species in the southeast occurs year-round and often during the summer (Buchholz 1996, Allen et al. 2001). Our findings that seed predation by *S. hispidus* is modified by past agricultural land use illustrates the potentially significant role of disturbance histories in determining the outcomes of these restoration efforts. Finally, while oak species in some ecosystems are able to overcome seed limitation by satiating predators through masting (Kelly 1994, Vander Wall 2001), vertebrate seed predation has been shown to limit oak recruitment in a variety of ecosystems (Santos and Telleria 1997, Gómez 2004, Sun et al. 2004, Pé Rez-Ramos and Marañon 2008, Cilles et al. 2016, Bogdziewicz et al. 2019). Our results indicate that past and present disturbances that affect granivore behavior could subsequently determine when oaks may overcome seed limitation through masting. Future research that explicitly links seed fate with oak recruitment in the southeastern US is exceedingly needed to understand these potential dynamics.

Conclusions

Land-use legacies and contemporary disturbances can interact to modify animal behavior and generate spatial patterns in seed predation. As agricultural land abandonment increases and management practices are implemented to restore these secondary lands (Hurtt et al. 2006, Turley et al. 2017), studying the ways in which these past and present disturbances transform species interactions is increasingly relevant. In this study we found that the effects of past agricultural land use on rodent seed predation was contingent upon a contemporary canopy harvesting whereby past land use only had an effect on the magnitude of seed predation in harvested plots. Our work highlights several areas of research that require further investigation. First, further investigation is needed to understand if past land use and contemporary disturbance changes the activity of predators, the effects of predators on rodent foraging under different habitat contexts, and the potential for predators to elicit cascading effects on seed predation and ecosystem recovery. Additionally, further research is needed to understand the breadth of species interactions (e.g., predator-prey interactions of large mammals) that show spatial variation in response to past and present disturbances.

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References

Allen, J. A. 1997. Reforestation of bottomland hardwoods and the issue of woody species diversity. Restoration Ecology 5:125–134.

Allen, J. A., B. D. Keeland, J. A. Stanturf, A. F. Clewell, and J. Kennedy, H.E. 2001. A guide to bottomland hardwood restoration: U.S. Geological Survey, Biological Resources Division Information and Technology Report USGS/BRD/ITR-2000-0011. USDA, Forest Service, Southern Research Station.

Allen, J. A., J. McCoy, and B. D. Keeland. 1998. Natural establishment of woody species on abandoned agricultural fields in the lower Mississippi Valley: first- and second-year results. Pages 263–268 *in* T. A. Waldrop, editor. Proceedings of the 9th Biennial Southern Silvicultural Research Conference. USDA Forest Service, Southern Research Station, Asheville, NC.

Barker, C. A., N. E. Turley, J. L. Orrock, J. A. Ledvina, and L. A. Brudvig. 2019. Agricultural land-use history does not reduce woodland understory herb establishment. Oecologia 189:1049–1060.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bellocq, M. I., C. Jones, D. C. Dey, and J. J. Turgeon. 2005. Does the shelterwood method to regenerate oak forests affect acorn production and predation? Forest Ecology and

Management 205:311–323.

Bermejo, T., A. Traveset, and M. Willson. 1998. Post-dispersal seed predation in the temperate rainforest of Southeast Alaska. The Canadian Field-Naturalist 112:510–512.

Bogdziewicz, M., E. E. Crone, and R. Zwolak. 2019. Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. Journal of Ecology 00:1–10.

Brehm, A. M., A. Mortelliti, G. A. Maynard, and J. Zydlewski. 2019. Land-use change and the ecological consequences of personality in small mammals. Ecology Letters 22:1387–1395.

Bricker, M., D. Pearson, and J. Maron. 2010. Small-mammal seed predation limits the recruitment and abundance of two perennial grassland forbs. Ecology 91:85–92.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37–47.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

Brudvig, L. A., and E. I. Damschen. 2011. Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. Ecography 34:257–266.

Brudvig, L. A., E. Grman, C. W. Habeck, J. L. Orrock, and J. A. Ledvina. 2013. Strong legacy of agricultural land use on soils and understory plant communities in longleaf pine woodlands. Forest Ecology and Management 310:944–955.

Brudvig, L. A., J. L. Orrock, E. I. Damschen, C. D. Collins, P. G. Hahn, W. B. Mattingly, J. W. Veldman, and J. L. Walker. 2014. Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities.

PLoS ONE 9:e86604.

Buchholz, R. 1996. Rodent damage to direct seeded willow oak in Louisiana. Pages 340–349 *in* A. G. Eversole, editor. Proceedings of the Fiftieth Annual Conference of the Southeastern Association of Fish and Wildlife Agencies. Southeastern Association of Fish and Wildlife Agencies, Hot Springs, Arkansas.

Chen, W., J. Zhong, S. Sun, Z. Xie, and Y. Zhou. 2017. Fuelwood collection depresses the seed-dispersal service provided by rodents. Forest Ecology and Management 406:53–60.

Cilles, S. E., G. Coy, C. R. Stieha, J. J. Cox, P. H. Crowley, and D. S. Maehr. 2016. A comparison of seed predation, seed dispersal, and seedling herbivory in oak and hickory. Northeastern Naturalist 23:466–481.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in Southern Appalachian forests. Ecological Monographs 68:213–235.

Conner, L. M., G. Morris, B. Karmacharya, M. K. Oli, and J. A. Hostetler. 2013. The influence of mammalian predator exclusion, food supplementation, and prescribed fire on survival of *Glaucomys volans*. Journal of Mammalogy 94:672–682.

Corlett, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. Global Ecology and Conservation 73:413–448.

Crawley, M. J. 2000. Seed predators and plant population dynamics. Pages 167–182 *in* M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. Second edition. CABI, Wallingford, UK.

Culbert, P. D., I. Dorresteijn, J. Loos, M. K. Clayton, J. Fischer, and T. Kuemmerle. 2017. Legacy effects of past land use on current biodiversity in a low-intensity farming landscape in Transylvania (Romania). Landscape Ecology 32:429–444.

Culot, L., C. Bello, J. L. F. Batista, H. T. Z. do Couto, and M. Galetti. 2017. Synergistic effects of seed disperser and predator loss on recruitment success and long-term consequences for carbon stocks in tropical rainforests. Scientific Reports 7:7662.

Dittel, J. W., R. Perea, and S. B. Vander Wall. 2017. Reciprocal pilfering in a seed-caching rodent community: implications for species coexistence. Behavioral Ecology and Sociobiology 71.

Drever, C. R., G. Peterson, C. Messier, Y. Bergeron, and M. Flannigan. 2006. Can forest management based on natural disturbances maintain ecological resilience? Canadian Journal of Forest Research 36:2285–2299.

Dueser, R. D., and H. H. Shugart. 1978. Microhabitats in a forest-floor small mammal fauna. Ecology 59:89–98.

Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review 35:51–81.

Fleharty, E. D., and M. A. Mares. 1973. Habitat preference and spatial relations of Sigmodon hispidus on a remnant prairie in West-Central Kansas. The Southwestern Naturalist 18:21.

Flinn, K. M., and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3:243–250.

Foster, D. R. 1993. Land-use History and Forest Transformations in Central New England. Pages 91–110 Humans as Components of Ecosystems. Springer New York, New York, NY.

Frost, C. 2006. History and Future of the Longleaf Pine Ecosystem. Pages 9–48 *in* S. Jose, E. J. Jokela, and D. L. Miller, editors. The Longleaf Pine Ecosystem. Springer-Verlag New York, New York, NY.

Gentry, J. B., and M. H. Smith. 1968. Food habits and burrow associates of *Peromyscus* *polionotus*. Journal of Mammalogy 49:562–565.

Goertz, J. W., R. M. Dawson, and E. E. Mowbray. 1975. Response to nest boxes and reproduction by *Glaucomys volans* in Northern Louisiana. Journal of Mammalogy 56:933–939.

Gómez, J. M. 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: Non-additive effects on multiple demographic processes. Ecology 172:287–297.

Gómez, J. M., E. W. Schupp, and P. Jordano. 2019. Synzoochory: the ecological and evolutionary relevance of a dual interaction. Biological Reviews 94:874–902.

Guiden, P. W., and J. L. Orrock. 2017. Invasive exotic shrub modifies a classic animal-habitat relationship and alters patterns of vertebrate seed predation. Ecology 98:321–327.

Hahn, P. G., and J. L. Orrock. 2015. Spatial arrangement of canopy structure and land-use history alter the effect that herbivores have on plant growth. Ecosphere 6:Article 193.

Hahn, P. G., and J. L. Orrock. 2016. Ontogenetic responses of four plant species to additive and interactive effects of land-use history, canopy structure and herbivory. Journal of Ecology 104:1518–1526.

Heidt, G. A. 1977. Utilization of nest boxes by the Southern Flying Squirrel, *Glaucomys volans*, in Central Arkansas. Journal of the Arkansas Academy of Science 31:55–57.

Herrera, C. M. 2002. Seed Dispersal by Vertebrates. Pages 185–208 *in* C. M. Herrera and O. Pellmyr, editors. Plant–Animal Interactions: An Evolutionary Approach. Wiley-Blackwell, Hoboken, NJ.

Hinkelman, T. M., and S. C. Loeb. 2007. Effect of woody debris abundance on daytime refuge use by cotton mice. Southeastern Naturalist 6:393–406.

Hulme, P. E. 1994. Post-dispersal seed predation in grassland: Its magnitude and sources of variation. Journal of Ecology 82:645–652.

Hurtt, G. C., S. Frolking, M. G. Fearon, B. Moore, E. Shevliakovas, S. Malyshev, S. W. Pacala, and R. A. Houghton. 2006. The underpinnings of land-use history: three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. Global Change Biology 12:1208–1229.

Jacques, M.-E., S. W. Hallgren, and D. S. Wilson. 2017. Low-basal area treatment and prescribed fire to restore oak-pine savannas alter small mammal communities. Forest Ecology and Management 400:353–362.

Jansen, P. A., B. T. Hirsch, W.-J. Emsens, V. Zamora-Gutierrez, M. Wikelski, and R. Kays. 2012. Thieving rodents as substitute dispersers of megafaunal seeds. Proceedings of the National Academy of Sciences 109:12610–12615.

Ji-Qi, L., and Z. Zhi-Bin. 2004. Effects of habitat and season on removal and hoarding of seeds of wild apricot (*Prunus armeniaca*) by small rodents. Acta Oecologica 26:247–254.

Kappler, R. H., H. J. Michaels, and K. V Root. 2012. Impact of seed predation by mice on Wild lupine in and near oak savannas. American Midland Naturalist 168:18–29.

Karmacharya, B., J. A. Hostetler, L. Mike Conner, G. Morris, and M. K. Oli. 2012. Longleaf pine management practices and their impact on small mammal populations. Forest Ecology and Management 271:140–146.

Kelly, D. 1994. The evolutionary ecology of mast seeding. Trends in Ecology & Evolution 9:465–470.

Kelt, D. A., E. J. Heske, X. Lambin, M. K. Oli, J. L. Orrock, A. Ozgul, J. N. Pauli, L. R. Prugh, R. Sollmann, and S. Sommer. 2019. Advances in population ecology and species interactions in mammals. Journal of Mammalogy 100:965–1007.

Kilgo, J., and J. I. Blake, editors. 2005. Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site. Island Press, Washington, DC, USA.

Kopecký, M., and J. Vojta. 2009. Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. Applied Vegetation Science 12:251–260.

Lambert, T. D., J. R. Malcolm, and B. L. Zimmerman. 2005. Effects of mahogany (*Swietenia macrophylla*) logging on small mammal communities, habitat structure, and seed predation in the southeastern Amazon Basin. Forest Ecology and Management 206:381–398.

Lichti, N. I., M. A. Steele, and R. K. Swihart. 2017. Seed fate and decision-making processes in scatter-hoarding rodents. Biological Reviews 92:474–504.

Lichti, N. I., M. A. Steele, H. Zhang, and R. K. Swihart. 2014. Mast species composition alters seed fate in North American rodent-dispersed hardwoods. Ecology 95:1746–1758.

Louda, S. M. 1982. Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower-and seed-feeding insects. Journal of Ecology 70:43–53.

Maron, J. L., and E. L. Simms. 1997. Effect of seed predation on seed bank size and seedling recruitment of Bush lupine. Oecologia 111:76–83.

Mattingly, W. B., J. L. Orrock, C. D. Collins, L. A. Brudvig, E. I. Damschen, J. W. Veldman, and J. L. Walker. 2015. Historical agriculture alters the effects of fire on understory plant beta diversity. Oecologia 177:507–518.

Moore, J. C. 1947. Nests of the Florida flying squirrel. The American Midland Naturalist 38:248–253.

Moore, J. E., A. B. McEuen, R. K. Swihart, T. A. Contreras, and M. A. Steele. 2007. Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests.

Ecology 88:2529–2540.

Morris, G., J. A. Hostetler, L. M. Conner, and M. K. Oli. 2011a. Effects of prescribed fire, supplemental feeding, and mammalian predator exclusion on hispid cotton rat populations. Oecologia 167:1005–1016.

Morris, G., J. A. Hostetler, M. K. Oli, and L. M. Conner. 2011b. Effects of predation, fire, and supplemental feeding on populations of two species of *Peromyscus* mice. Journal of Mammalogy 92:934–944.

Orrock, J. L., and E. I. Damschen. 2005. Corridors Cause Differential Seed Predation. Ecological Applications 15:793–798.

Orrock, J. L., B. J. Danielson, and R. J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behavioral Ecology 15:433–437.

Orrock, J. L., B. J. Danielson, M. J. Burns, and D. J. Levey. 2003. Spatial ecology of predator-prey interactions: Corridors and patch shape influence seed predation. Ecology 84:2589–2599.

Orrock, J. L., R. D. Holt, and M. L. Baskett. 2010. Refuge-mediated apparent competition in plant–consumer interactions. Ecology Letters 13:11–20.

Orrock, J. L., D. J. Levey, B. J. Danielson, and E. I. Damschen. 2006. Seed predation, not seed dispersal, explains the landscape-level abundance of an early successional plant. Journal of Ecology 94:838–845.

Öster, M., K. Ask, S. A. O. Cousins, and O. Eriksson. 2009. Dispersal and establishment limitation reduces the potential for successful restoration of semi-natural grassland communities on former arable fields. Journal of Applied Ecology 46:1266–1274.

Pé Rez-Ramos, I. M., and T. Marañon. 2008. Factors affecting post-dispersal seed predation in two coexisting oak species: Microhabitat, burial and exclusion of large herbivores. Forest Ecology and Management 255:3506–3514.

Santos, T., and J. L. Telleria. 1997. Vertebrate predation on Holm Oak, *Quercus ibex*, acorns in a fragmented habitat: effects on seedling recruitment. Forest Ecology and Management 98:18–187.

Scheiner, M. 2001. MANOVA: Multiple Response Variables and Multispecies Interactions. Pages 99–115 *in* M. Scheiner and J. Gurevitch, editors. Design and Analysis of Ecological Experiments. 2nd edition. Oxford University Press, New York, NY.

Shear, T. H., T. J. Lent, and S. Fraver. 1996. Comparison of restored and mature bottomland hardwood rorests of Southwestern Kentucky. Restoration Ecology 4:111–123.

Simberloff, D. 1999. The role of science in the preservation of forest biodiversity. Forest Ecology and Management 115:101–111.

Sork, V. L. 1984. Examination of seed dispersal and survival in Red oak, *Quercus rubra* (Fagaceae), using metal-tagged acorns. Ecology 65:1020–1022.

Standish, R. J., V. A. Cramer, S. L. Wild, and R. J. Hobbs. 2007. Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in Western Australia. Journal of Applied Ecology 44:435–445.

Steele, M. A., G. Turner, P. D. Smallwood, J. O. Wolff, and J. Radillo. 2001. Cache management by small mammals: Experimental evidence for the significance of acorn-embryo excision. Journal of Mammalogy 82:35–42.

Stuhler, J. D., and J. L. Orrock. 2016. Past agricultural land use and present-day fire regimes can interact to determine the nature of seed predation. Oecologia 181:463–473.

Sullivan, T. P., and D. S. Sullivan. 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and Population Dynamics of Small Mammals. Journal of Applied Ecology 38:1234–1252.

Sun, S., X. Gao, and L. Chen. 2004. High acorn predation prevents the regeneration of Quercus liaotungensis in the Dongling Mountain region of North China. Restoration Ecology 12:335–342.

Toman, M. A., P. Mark, and S. Ashton. 1996. Sustainable forest ecosystems and management: A review article. Forest Science 42:366–377.

Turley, N. E., J. L. Orrock, J. A. Ledvina, and L. A. Brudvig. 2017. Dispersal and establishment limitation slows plant community recovery in post-agricultural longleaf pine savannas. Journal of Applied Ecology 54:1100–1109.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225–238.

Veldman, J. W., L. A. Brudvig, E. I. Damschen, J. L. Orrock, W. B. Mattingly, and J. L. Walker. 2014. Fire frequency, agricultural history and the multivariate control of pine savanna understorey plant diversity. Journal of Vegetation Science 25:1438–1449.

Vander Wall, S. B. 2001. The evolutionary ecology of nut dispersal. Botanical Review 67:74–117.

Vander Wall, S. B. 2003. Effects of seed size of wind-dispersed pines (Pinus) on secondary seed dispersal and the caching behavior of rodents. Oikos 100:25–34.

Vander Wall, S. B., S. C. Barga, A. E. Seaman, and A. Org. 2017. The geographic distribution of seed-dispersal mutualisms in North America. Evolutionary Ecology 31:725–740.

Vander Wall, S. B., M. S. Enders, and B. A. Waitman. 2009. Asymmetrical cache pilfering between yellow pine chipmunks and golden-mantled ground squirrels. Animal Behaviour

78:555–561.

Vander Wall, S. B., K. M. Kuhn, and M. J. Beck. 2005. Seed removal, seed predation, and secondary dispersal. Ecology 86:801–806.

Zobel, M., M. Otsus, J. Liira, M. Moora, and T. Mols. 2000. Is small-scale species richness limited by Sseed availability or microsite availability? Ecology 81:3274–3282.

Zwolak, R. 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. Forest Ecology and Management 258:539–545.

Tables and figures

Table 1. Coefficients, test statistics, and p-values for our eight single-species models evaluating the effects of each rodent species' foraging activity on the proportion of seeds removed (binomial GLM models) and the average distance seeds were moved (linear mixed effects models). Levels of significance are expressed as *P < 0.05, **P < 0.01.

	Binomial GLMs				Linear Mixed Effects Models			
	Seeds Foraged				Average Distance			
Effect	β	χ^2	AIC	*P*	β	*F*	AIC	*P*
G. volans bouts[†]	0.04	0.91	173.8	0.340	0.00	0.11	38.9	0.749
Peromysucs spp. bouts	0.01	0.03	365.2	0.869	0.03	1.27	101.0	0.271
S. niger bouts[†]	0.14	5.28	170.1	0.022*	-0.01	0.38	37.5	0.548
S. hispidus bouts[†]	0.05	9.08	187.8	0.003**	-0.01	0.59	64.9	0.458

[†] Models in which a subset of the data was analyzed due to the absence of bout data across a canopy harvesting treatment for the rodent species. Only data from the canopy harvesting treatment that contained bout data for the species was analyzed in these models.

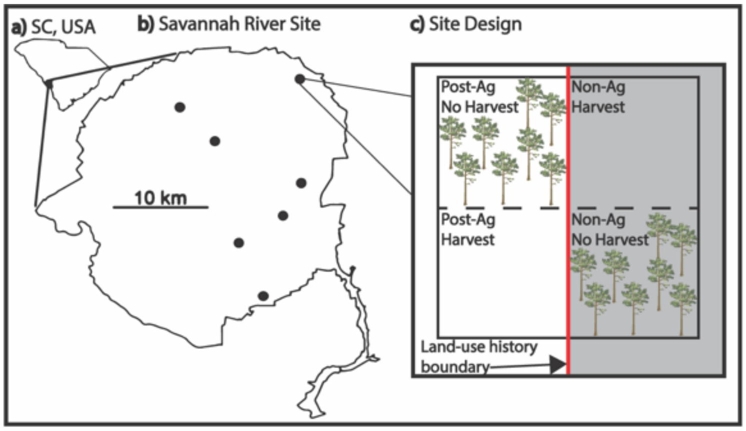

Figure 1. We conducted this experiment in South Carolina **(a)** at the Savannah River Site (b). The location of the seven sites utilized in this study at SRS are depicted as black dots on the SRS map (b). Each of our seven sites straddled a land-use history boundary, on top of which we imposed a fully factorial manipulation of canopy harvesting **(c)**. Each site contained four 1-ha plots.

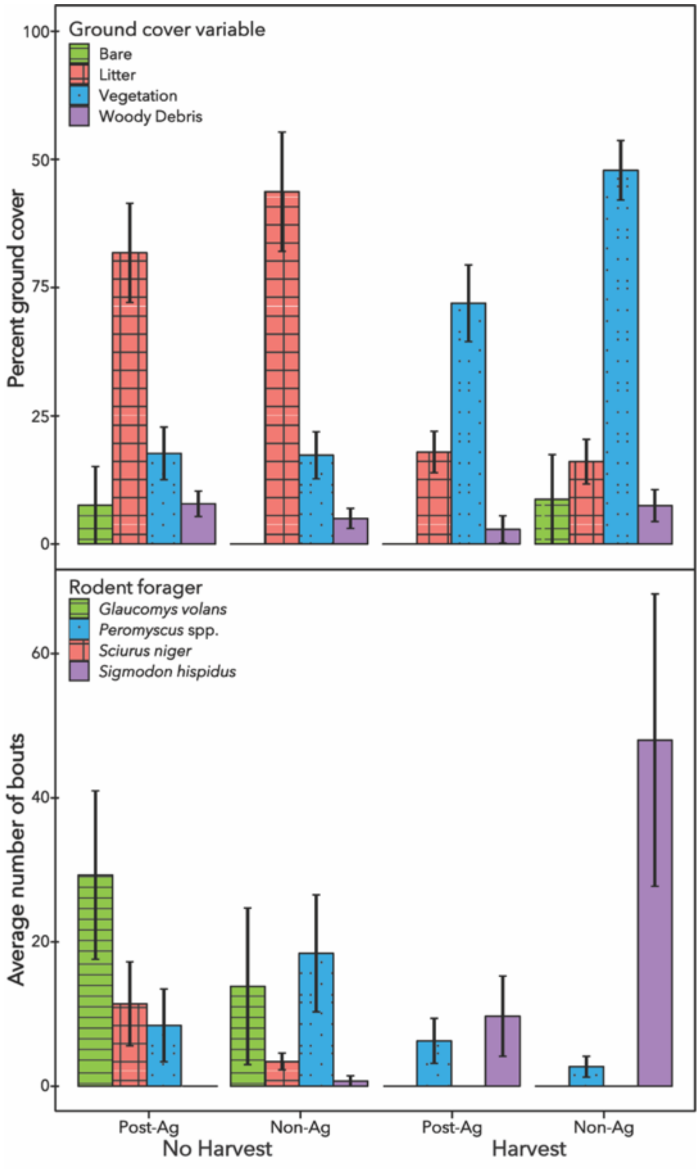

Figure 2. Canopy harvesting and past land use caused shifts in percent ground cover and rodents species activity. Litter cover was significantly lower in harvested plots ($p < 0.001$). Vegetation cover was significantly higher in harvested plots ($p < 0.001$). Land-use history and harvesting interacted to affect vegetation cover ($p = 0.034$) such that land-use history only affected vegetation cover in harvested plots where nonagricultural plots had greater cover. *Sciurus niger* and *Glaucomys volans* were only active in unharvested plots and were not affected by land-use history. *Sigmodon hispidus* was almost exclusively active in harvested plots. *Peromyscus* spp. activity did not change with harvesting or land-use history. Error bars represent one standard error.

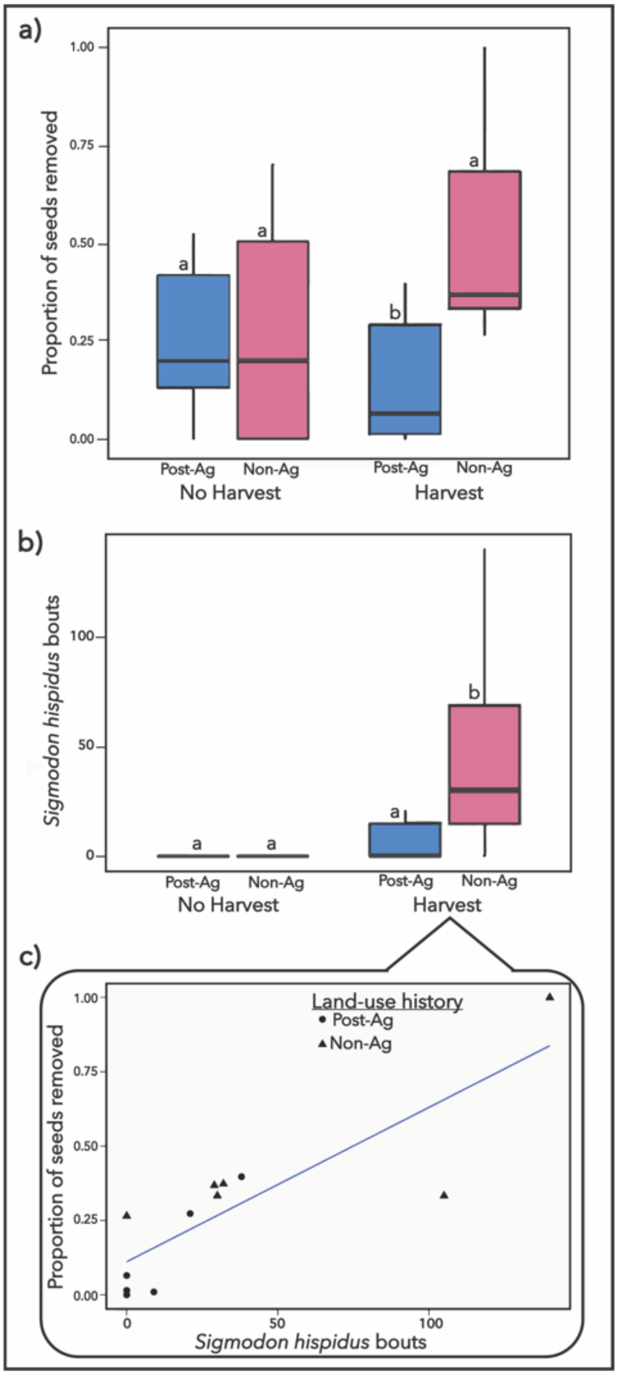

Figure 3. a) The interaction of land-use history and canopy harvesting had a significant effect on seed removal rates (p = 0.001). Land-use history did not affect seed removal in unharvested plots. With canopy harvesting, post-agricultural plots had significantly lower seed removal rates than nonagricultural plots. **b)** The interaction of land-use history and canopy harvesting had a marginally significant effect on *S. hispidus* activity (p = 0.069), and *S. hispidus* was significantly more active in harvested post-agricultural sites than harvested nonagricultural sites (p = 0.015). **c)** The proportion of seeds removed from depots in harvested sites increased with *S. hispidus* activity (p = 0.003). We therefore expect that the negative effect of agricultural history on seed removal in harvested sites is driven by a reduction in *S. hispidus* activity.

Appendix S1. Hypotheses and models used to statistically test them.

Table S1. Summary of the mechanisms, predictions, and models of our specified hypotheses.

Hypothesis	Mechanism	Prediction	Model Type
Land-use history and canopy harvesting affect habitat structure	Canopy harvesting reduces canopy cover, increasing light availability for understory growth. Past agricultural land use limits understory growth.	Canopy harvesting leads to an increase in herbaceous and shrubby ground cover and a decrease in woody debris. Post-agricultural plots will have lower herbaceous and shrubby ground cover than non-agricultural plots both with and without canopy harvesting.	MANOVA
Land-use history and canopy harvesting affect rates of seed predation	Rodents forage more frequently in areas with high vegetation cover.	Seed predation will be higher in harvested plots. Seed predation will be higher in non-agricultural plots both with and without canopy harvesting.	Binomial generalized linear mixed-effects model
Land-use history and canopy harvesting affect seed movement distance	Rodents move seeds further in habitats with higher vegetation cover.	Seed movement distances will be higher in harvested plots. Seed movement distances will be higher in non-agricultural plots both with and without canopy harvesting .	Linear mixed-effects model
S. hispidus activity drives seed predation rates in harvested patches	Harvested sites have more vegetation cover than unharvested sites, and *Sigmodon hispidus* selects for habitats with high vegetation cover.	*Sigmodon hispidus* will be most active in harvested patches, and seed predation in harvested patches will increase with the number of *S. hispidus* bouts.	Binomial generalized linear mixed-effects model
S. niger activity drives seed predation rates in unharvested patches	Unharvested sites contain more mature canopy trees than harvested sites, and *Sciurus niger* selects for habitats containing mature canopy trees.	*Sciurus niger* will be most active in unharvested patches, and seed predation in harvested patches will increase with the number of *S. niger* bouts.	Binomial generalized linear mixed-effects model
Land-use history affects *S. hispidus* activity in harvested patches	Harvested post-agricultural plots have less vegetation cover than harvested non-agricultural plots, and *Sigmodon hispidus* prefers to forage in areas with high vegetation cover.	*Sigmodon hispidus* will be more active in non-agricultural harvested plots than in post-agricultural harvested plots.	Linear mixed-effects model
Land-use history affects *S. niger* activity in unharvested patches	Harvested post-agricultural plots have less vegetation cover than harvested non-agricultural plots, and *Sciurus niger* prefers to forage in areas with high vegetation cover.	*Sciurus niger* will be more active in non-agricultural unharvested plots than in post-agricultural unharvested plots in response to higher vegetation cover in non-agricultural plots.	Linear mixed-effects model

CHAPTER 2

Past agricultural land use affects multiple facets of ungulate antipredator behavior

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Abstract: Antipredator behavior affects prey fitness, prey demography, and the strength of ecological interactions. Although predator-prey interactions increasingly occur in habitats that experience multiple forms of human-generated disturbance, it is unclear how different forms of disturbance might affect antipredator behavior. Fire is a contemporary disturbance that has dramatic effects on terrestrial habitats. Such habitats may have also experienced past disturbances, like agricultural land use, that leave lasting legacies on habitat structure (e.g., overstory and understory composition). It is unclear how these past and present disturbances affect the use of different antipredator behaviors, like temporal avoidance and vigilance. We examined whether variation in disturbance regimes generates differences in ungulate antipredator behavior by using cameras to measure white-tailed deer vigilance and activity time across 24 longleaf pine woodlands that vary in past land use and contemporary fire regime. Regardless of land-use history, woodlands with high fire frequencies had 4 times less vegetation cover than low-fire woodlands, generating riskier habitats for deer; however, deer responded to fire with different antipredator strategies depending on land-use history. In nonagricultural woodlands,

fire affected deer activity time such that activity was nocturnal in low-fire woodlands and crepuscular in high-fire woodlands. In post-agricultural woodlands, fire affected vigilance and not activity time such that deer were more vigilant in high-fire woodlands than in low-fire woodlands. These results suggest that ungulate antipredator behavior may vary spatially depending upon past land use and contemporary fire regime, and such disturbances may generate "landscapes of fear" that persist for decades after agricultural use.

Introduction

Behaviors that mitigate the risk of predation are ubiquitous (Lima & Dill 1990; Caro 2005; Preisser *et al.* 2005). Understanding variation in antipredator behavior is important because it can provide insight into the factors that shape prey fitness, the strength of intra- and interspecific interactions, as well as community-level processes, such as disease transmission and trophic cascades (reviewed in Pace et al. 1999; Schmitz et al. 2004; Peckarsky et al. 2008; Preisser and Bolnick 2008; Terborgh and Estes 2010; Estes et al. 2011). The characteristics of the habitat in which predator-prey interactions occur can play a fundamental role in shaping antipredator behavior (Guiden *et al.* 2019) by altering the likelihood of an encounter between predators and prey, the likelihood that prey detect predators before an attack is initiated, and the likelihood that prey can escape an attack once initiated (Lima & Dill 1990; Lima & Bednekoff 1999; Sheriff *et al.* 2020). Understanding how environmental variation shapes antipredator behavior may be particularly important given that anthropogenic activities are leading to rapid changes in habitats throughout the globe (Haddad et al. 2015; IPBES 2018).

Disturbances, such as fire, forest harvest, and drought, are common in terrestrial habitats (Sousa 1984; Pickett & White 1985) and can lead to profound changes in habitat characteristics. Disturbances vary not only in form, but also in the possible duration of their effects (Dobson *et* *al.* 1997; Buma 2015). Human disturbances, in particular, can lead to rapid and persistent changes to habitats and the species they contain. For example, human conversion of natural habitats to agriculture, leading to degraded land after agricultural abandonment, is one of the biggest factors contributing to the current biodiversity crisis (Sisk *et al.* 1994; Pimm *et al.* 1995; Dobson *et al.* 1997; Dirzo & Raven 2003; Dudley & Alexander 2017). Degraded lands once used for agriculture have increased by 10-44x10^6 km^2 since 1700 CE (Hurtt *et al.* 2006); and agricultural legacies can persist in these lands for decades and sometimes centuries (Foster 1993; Flinn & Vellend 2005), reflected in lasting effects on the diversity and structure of plant communities (Foster 1993; Flinn & Vellend 2005; Kopecký & Vojta 2009; Mattingly *et al.* 2015; Culbert *et al.* 2017). In contrast, disturbances caused by fire (e.g., prescribed burns or wildfire) are often dramatic and rapid, which can lead to significant differences in habitats on shorter time scales that affect predation risk and behavior of a broad range of animal prey, including arthropods (Karpestam *et al.* 2012), birds (Morris & Conner 2016), rodents (Fordyce *et al.* 2016), and ungulates (Eisenberg *et al.* 2015; Cherry *et al.* 2017; Kymmell 2019; Jorge *et al.* 2020). Animals in many terrestrial areas may be subject to both of these disturbance types, and the legacies of past disturbances, such as agricultural land use, can determine the outcomes of contemporary disturbances, such as fire (Buma 2015). For example, evidence is accumulating that agricultural legacies can modify animal foraging responses to contemporary disturbances (Hahn & Orrock 2015c, b; Stuhler & Orrock 2016; Bartel & Orrock 2020). Contemporary fire and past agricultural land use may often co-occur, and evidence suggests that they interact to affect both plant and animal communities (Brudvig *et al.* 2014; Veldman *et al.* 2014; Hahn & Orrock 2015a; Mattingly *et al.* 2015) as well as important trophic interactions (e.g., herbivory and granivory; Hahn & Orrock, 2015b; Stuhler & Orrock, 2016). However, despite the importance of understanding the various components of antipredator behavior and the widespread modification of habitats via past and present disturbance, large-scale studies examining the interface of these processes are rare.

Ungulates provide an optimal study system to evaluate how past and present disturbances modify antipredator behavior across large spatial scales. Ungulates are known to utilize multiple strategies to mitigate predation risk (Lima 1995; Bednekoff & Lima 1998; Hunter & Skinner 1998; Ripple & Beschta 2003; Creel & Winnie 2005; Winnie & Creel 2007; Valeix *et al.* 2009; Kohl *et al.* 2018; Prugh *et al.* 2019; Smith *et al.* 2019); they may exhibit different forms of antipredator behavior (e.g., vigilance or spatiotemporal avoidance); and they range over large areas where they may encounter a variety of human-modified habitats. Ungulates respond to contemporary disturbances that modify habitat structure, such as fire (Eby *et al.* 2014; Cherry *et al.* 2016, 2017; Kymmell 2019); however, it is unknown if past land use generates persistent changes in habitat structure that may influence ungulate antipredator behavior and if this effect is modified by fire regime. For example, while it has been shown that fire alters vegetation structure and leads to changes in the antipredator behavior of deer in longleaf pine ecosystems (Cherry *et al.* 2017), habitats with a history of agriculture also have significantly different vegetation structure (Duguy & Ramón 2007; Veldman *et al.* 2014; Hahn & Orrock 2015b; Stuhler & Orrock 2016; Bartel & Orrock 2020) and may thus be areas that give rise to unappreciated shifts in deer antipredator behavior. This current lacuna is likely due to the logistical challenges of conducting large-scale, replicated experiments in landscapes containing habitat patches with known land-use histories and variable fire regimes that have no other environmental differences (e.g., steep slopes or soil series due to non-random land-use decisions; Flinn & Vellend 2005).

In order to understand how past agricultural land use and contemporary fire regime affect multiple ungulate antipredator behaviors, we monitored white-tailed deer (*Odocoileus virginianus*) in a large-scale experiment in the longleaf pine ecosystem in southeastern USA. In longleaf pine woodlands, coyotes (*Canis latrans*) are the primary predators of deer, and predation by coyotes affects deer behavior and population dynamics (Kilgo *et al.* 2010; Cherry *et al.* 2015, 2016, 2017; Gulsby *et al.* 2017). Agricultural legacies and fire regime have well-documented effects on habitat structure in longleaf pine woodlands. In our study site, nonagricultural woodlands have a mixture of hardwood and pine while post-agricultural woodlands are dominated by pine (Brudvig *et al.* 2013). Post-agricultural woodlands have greater vine cover (Hahn & Orrock 2015a). Frequently burned post-agricultural woodlands have greater visible sky than frequently burned nonagricultural woodlands or infrequently burned woodlands of either land-use history (Stuhler & Orrock 2016). Across sites varying in both land-use history and fire regime, we deployed motion-activated cameras to measure deer vigilance and activity timing, evaluating two hypotheses: 1) deer are most vigilant in post-agricultural woodlands with frequent fires and least vigilant in nonagricultural woodlands with infrequent fires corresponding to the effects of land-use history and fire frequency on vegetation cover, and 2) deer show crepuscular activity in lower-risk sites (i.e., low-fire, nonagricultural woodlands) and nocturnal activity in higher-risk sites (i.e., high-fire, post-agricultural woodlands).

Methods

Study area and design

This study was conducted at the Savannah River Site (SRS; Aiken, SC), an 80,125-ha National Environmental Research Park (NERP). SRS is within the historical range of the longleaf pine woodland ecosystem, much of which was converted to tillage agriculture from

1856 to 1950 (Frost 2006). Since these agricultural lands were small and dispersed, heterogeneous landscapes resulted containing patches of tilled farmland and intact forests (Kilgo & Blake 2005). Agricultural fields were abandoned in 1951 when SRS was established and have henceforth been under management as longleaf and loblolly pine plantations by the US Forest Service (Kilgo and Blake 2005). We selected 24 sites, spanning an 807-km^2 area, that differed in land-use history and fire frequency (Fig. 1). Land-use history classification was based on aerial photography taken prior to land abandonment in 1951. Sites that were farmland in 1951 were classified as "post-agricultural woodlands," and sites that were forested were classified as "nonagricultural woodlands." Sites did not differ in other environmental variables that may be associated with non-random agricultural land use (e.g., topography or soil texture; see Appendix S1 for details). The number of fires since 1991 was determined from annual fire records, and sites were characterized as low (five or less burns) or high (more than five burns) fire frequency, a metric previously used to classify these sites based on plant-community characteristics (Brudvig et al. 2014; see Appendix S2 for site fire histories). Sites were not burned the year of the study. The resulting site classification by land-use history and fire frequency generated four distinct habitat types distributed across the study area.

Deer behavior and habitat structure

At each of our 24 sites, we deployed an unbaited, motion-activated camera trap (Bushnell 16MP Trophy Cam HD; Bushnell Corporation, Overland Park, KS) between June 8 and July 9 in 2018 for a total trapping period of 33 days. Camera traps were set to take photos at 1-second intervals while motion was detected, enabling us to capture individual foraging behavior at a fine scale. All photos were subsequently sorted and analyzed by a single observer, who was blind to site-level disturbance treatments, to control for possible variation in species, sex, and behavioral classifications. For every photo capturing deer activity during an independent foraging bout, the observer recorded the date and time, the sex of the individual, whether or not it was in a group, group size, and if the individual was foraging (1) or being vigilant (0) as a binomial variable. If the individual's head was up in a non-feeding posture, then the photo was classified as vigilant, and if the individual's head was down in a feeding posture, then the photo was classified as foraging (1; Lashley et al. 2014; Cherry et al. 2017). Photos in which an individual's behavior did not clearly fall under one of these two categories (e.g., rapid movement across the camera) were not evaluated. We characterized independent foraging bouts as any sequence of deer photos of the same sex captured within 30 minutes at a site; a common threshold for characterizing independent detections of large mammals (Kelly 2003; Kelly & Holub 2008; Wang *et al.* 2015; O'Connor & Rittenhouse 2017).

To test the hypothesis that habitat characteristics relevant to perceived predation risk for deer varied with land-use history and fire frequency, we measured vertical vegetation cover at every site. Vertical vegetation cover was measured by a single observer using a density board that estimated percent visibility across 1 x 1 foot quadrats (Griffith & Youtie 1988; Nudds 2018). The density board was placed 15-m from the observer standing at the camera-trap station. The observer took four measurements (one in each cardinal direction from the station) at each site. In order to account for potential effects of forage quality on deer vigilance, we measured the presence of plant species preferred by deer in the southeast (Appendix S3) within 8 x 8 m vegetation plots used for long-term vegetation monitoring at 18 of our sites. We estimated forage species richness at these sites by calculating the number of species present in each plot.

Data Analysis

To test how land-use history and fire frequency affects vegetation cover, we employed a linear model with land-use history, fire frequency, and the interaction of land-use history and fire as fixed effects and proportion of vegetation cover as a response variable. To test how land-use history and fire frequency affects spatial patterns of deer activity, we used a linear model with land-use history, fire frequency, the interaction of land-use history and fire as fixed effects and the log-transformed total number of foraging bouts at each site as a response variable. To test how land-use history and fire frequency affects deer antipredator behavior during foraging bouts, we used a binomial generalized linear mixed effects model (GLMM) with land-use history and fire frequency, the interaction of land-use history and fire frequency, the presence of conspecifics, and the individual's sex as fixed effects; site as a random intercept; and proportion of vigilant photos for each individual bout as a response variable. To test how forage quality affects deer antipredator behavior during foraging bouts, we used a binomial GLMM with forage species richness as a fixed effect, site as a random intercept, and proportion of vigilant photos as a response variable.

We measured the temporal patterns of deer foraging bouts using the *activity* package (Rowcliffe 2019) in R (R Core Development Team 2019) following the methods of Rowcliffe et al. (2014) and Ridout and Linkie (2009). The time of individual bouts was converted to radians to fit circular kernel densities of deer activity for each land-use history and fire-regime treatment combination. Temporal patterns of deer activity were plotted using a von Mises kernel (Ridout & Linkie 2009; Rowcliffe *et al.* 2014) and 95% confidence intervals for the distributions were obtained from 999 smoothed bootstrap samples. We measured the overlap of circular distributions using the *compareCkern* function in the *activity* package (Rowcliffe 2019). This function calculates an overlap index (Δ; Ridout and Linkie 2009) of two fitted distributions, generates a null distribution of overlap indices using randomly sampled data from the combined dataset, and estimates the probability that the observed overlap arose by chance (Rowcliffe 2019). We conducted pairwise comparisons to measure overlap of circular distributions across the four land-use history and fire-regime treatment combinations.

Results

We captured 158 independent white-tailed deer foraging bouts across 22 of the 24 sites in our study. The majority of foraging bouts (80% of 158) were from individuals detected alone and not in a group. A total of 32 individuals were detected in groups of two, and groups with more than two individuals were never observed. We detected 122 bouts by female individuals, 28 bouts by male individuals, and 8 individuals could not be confidently classified by sex. There was a significant effect of fire frequency on vegetation cover ($F_{1,20} = 8.17$, $p = 0.009$), and land-use history and fire frequency did not interact to affect vegetation cover ($F_{1,20} = 0.44$, $p = 0.516$; Fig. 2A). For both post-agricultural and nonagricultural woodlands, vegetation cover was significantly higher in frequently burned sites. There was not a significant interaction of land-use history and fire frequency on the frequency of deer activity ($F_{1,20} = 0.47$, $p = 0.502$; Fig. 2B). Additional analyses confirmed that there were no sex-specific effects of land-use history and fire on deer activity (Appendix S4). Because we did not observe deer foraging activity at two of the sites in our study, we did not include these sites in analyses of vigilance or activity timing patterns. Deer activity timing patterns depended upon the interaction of past land use and contemporary fire regime. While activity was generally crepuscular and nocturnal (Fig. 2C), the frequency of crepuscular activity depended upon fire frequency, but only in nonagricultural woodlands (Fig. 2C). This shift in activity was not observed in post-agricultural woodlands (Fig. 2C). These shifts in activity are also reflected in patterns of overlap in activity timing (Fig. 3).

There was a significant lack of overlap in the temporal distribution of deer activity between nonagricultural woodlands with low fire frequencies and nonagricultural woodlands with high fire frequencies ($\Delta = 0.68 \pm 0.05$, $p = 0.012$; Fig. 3B), but not between high- and low-fire sites in post-agricultural woodlands ($\Delta = 0.82 \pm 0.06$, $p = 0.401$; Fig. 3A).

There was a significant effect of fire frequency ($X^2 = 4.58$, $p = 0.032$) and the interaction of land-use history and fire frequency ($X^2 = 4.70$, $p = 0.030$) on deer vigilance such that fire only affected deer in post-agricultural woodlands. In post-agricultural woodlands, deer were significantly more vigilant in frequently burned sites (Fig. 2D). Additional analyses confirmed that vigilance did not change as a function of activity timing (Appendix S5). There was no effect of forage species richness on deer vigilance ($X^2 = 0.37$ $p = 0.546$).

Discussion

Spatial and temporal variation in predation risk across heterogeneous landscapes can generate predictable patterns in prey behavior (Lima & Bednekoff 1999; Sih & Ziemba 2000; Laundré *et al.* 2001; Fortin *et al.* 2005; Hernández & Laundré 2005; Kohl *et al.* 2018). This study demonstrates that past disturbances can lead to long-lasting changes in the present-day antipredator behaviors employed by animals and also highlights how the effect of past disturbance on contemporary antipredator behavior depends substantially upon recent disturbance by fire (Fig. 2). We found that deer responded to fire-mediated changes in perceived predation risk by shifting activity timing in nonagricultural woodlands (Fig. 2C); conversely, deer responded to fire-mediated changes in risk through vigilance behavior in post-agricultural woodlands (Fig. 2D). These findings have multiple implications that we discuss below. First, past land use may affect the utilization of different antipredator strategies by ungulates. Second, agricultural legacies and contemporary fire regimes may elicit landscapes of fear by generating spatiotemporal variation in antipredator behaviors.

Utilization of different antipredator strategies is conditioned upon agricultural legacies

The characteristics of the habitat in which predator-prey interactions occur can influence antipredator behavior of prey species by affecting the probability of encountering a predator, the probability of detecting a predator before an attack is initiated, or the probability of escaping an attack once initiated (Lima & Dill 1990; Lima & Bednekoff 1999; Guiden *et al.* 2019; Sheriff *et al.* 2020). Our results suggest that past land use influences the utilization of different antipredator behaviors that either reduce the probability of encountering a predator (activity timing) or increase the probability of detecting a predator (vigilance). By reducing vegetation cover, frequent fires increase white-tailed deer visibility to cursorial predators, and our results confirm past research finding that white-tailed deer vigilance responds to fire-mediated changes in perceived risk (Cherry *et al.* 2017). While these parallel results suggest that the effects of fire regime on deer perceived risk are generalizable beyond our study system, our findings illuminate the role of land-use history in mediating behavioral responses to fire regime and perceived risk.

In nonagricultural woodlands, deer exhibited crepuscular activity in sites with high fire frequencies (i.e., riskier sites) and primarily nocturnal activity in sites with low fire frequencies (i.e., safer sites). Coyotes are primarily nocturnal in areas where populations are persecuted by humans (Kitchen *et al.* 2000; Gallo *et al.* 2019), which is incentivized in South Carolina. Since coyotes in our study area are likely nocturnal, we expect that deer are mitigating risk in nonagricultural woodlands by limiting nocturnal activity to safer, infrequently burned sites. Interestingly, these findings of deer using risky habitats at safe times and safe habitats at risky times parallel the results of spatiotemporal habitat partitioning in a classic predator-prey system, elk and wolves in Yellowstone National Park (Kohl *et al.* 2018). Elk activity in risky locations was greatest at night, when wolf activity is at its lowest (Kohl *et al.* 2018). Similar patterns were also documented among white-tailed deer within the Florida panther's range: deer were more likely to use risky habitats during panther downtimes (Crawford *et al.* 2019). In finding that deer modified activity timing in response to perceived risk only under specific habitat contexts (nonagricultural woodlands), our study contributes to the growing body of literature documenting habitat-specific activity timing among mammals as an antipredator strategy (Connolly & Orrock 2018; Gaynor *et al.* 2018; Kohl *et al.* 2018; Crawford *et al.* 2019; Higdon *et al.* 2019; Smith *et al.* 2019). Moreover, our study provides further evidence of the role of fire in mediating ungulate activity time as demonstrated in Oregon elk populations by Spitz et al. (2018), while also revealing that the effects of fire on ungulate activity time may depend on past land use.

Our finding that deer modified vigilance, not activity time, in post-agricultural woodlands suggests that habitat context may play an important role in affecting the costs or benefits of behaviors that either decrease the probability of a predator encounter (activity time) or increase the probability of detecting a predator (vigilance; Fig. 2D). Changing activity timing in nonagricultural woodlands may be beneficial because increased density of predators in those habitats makes vigilance too costly or ineffective (Illius & Fitzgibbon 1994; Fortin *et al.* 2004). In our study site, nonagricultural woodlands have a mixture of hardwood and pine while post-agricultural woodlands are dominated by pine (Brudvig *et al.* 2013). Nonagricultural woodlands may be areas of higher coyote activity because habitats characterized by hardwoods are preferred denning sites for coyotes (Hickman *et al.* 2015) and exhibit greater coyote densities (Jorge *et al.* 2020). In post-agricultural woodlands, deer vigilance was greater in sites with high fire frequencies (Fig. 2D). This suggests that in habitats where the probability of an encounter might be generally low, vigilance may become the optimal strategy for reducing predation risk while also allowing deer to access food resources. Alternatively, the foraging trade-offs associated with vigilance (Illius & Fitzgibbon 1994; Fortin *et al.* 2004) may vary with land-use history, modifying the utility of this strategy. For example, while we did not find an effect of forage species richness on deer vigilance, land-use history does effect plant community composition in this system (Brudvig & Damschen 2011; Brudvig *et al.* 2014). It is possible that deer foraging efficiency may be greater in post-agricultural woodlands (e.g., more nutritious species available), permitting deer to sacrifice foraging time for vigilance in risky conditions. We also note the possibility that plant nutritional quality could change after fire; therefore, deer may need less foraging time (i.e., fewer bites and more time being vigilant) in frequently burned sites to acquire the same amount of nutrients as in infrequently burned sites. Since most sites in our study had at least two full years of recovery since the last fire (Appendix S2), we expect that potential differences in forage quality would be the result of plant community composition, not changes in plant nutritional quality soon after fire.

Vegetation cover is one of the most common metrics employed in studies predicting ungulate demography and behavior (Myserud & Østbye 1999), including in ecosystems of high conservation concern (e.g., Bro-Jørgensen et al. 2008; Creel et al. 2014). Our results show that agricultural legacies may have important implications for ungulate conservation efforts by altering the relationship between vegetation cover and important ungulate behaviors. In finding that deer responses to fire differed with land-use history despite the consistent effects of fire on vegetation cover across land-use histories (Fig. 2), our results highlight that habitats with similar vegetation cover - a frequently used metric for predation risk – may still vary substantially from the prey's perspective. Recent work has shown that predictive models of antipredator behavior may benefit from including not only vegetation cover but also information regarding predator activity (see Moll et al., 2017) and habitat characteristics that modify the potential of escape during an attack (see Sheriff et al., 2020). In addition to these suggestions, our results indicate that agricultural legacies can alter habitats in a way that may compromise model predictions of ungulate behavior and predator-prey dynamics when land-use history is not taken into account.

Agricultural legacies and contemporary fire regimes may generate landscapes of fear

Contemporary landscapes are mosaics affected by multiple disturbances that operate at different spatial and temporal scales (Pickett & White 1985; Vitousek *et al.* 1997; Buma 2015). In revealing that deer antipredator behavior is contingent upon both past and present disturbances, our work provides two means to further refine behavioral models that characterize the nature and extent of the "landscape of fear." First, our results show that understanding how multiple forms of disturbance interact may elucidate spatial patterns in antipredator behavior. It is appreciated that the legacies of past disturbances can alter the likelihood, severity, and outcome of contemporary disturbances (Buma 2015), and our study demonstrates how the interaction of multiple disturbances may give rise to dynamic landscapes of fear in animal populations. Second, landscapes of fear are often quantified by measuring spatial variance in a single antipredator behavior (Laundré *et al.* 2001; Moll *et al.* 2017; Gaynor *et al.* 2019); however, recent work has revealed spatiotemporal variability in antipredator strategies (Kohl *et al.* 2018). Our results show that ungulates may employ multiple antipredator strategies in different environmental contexts across a landscape. Consequently, accurately detecting landscapes of fear may hinge upon the measurement of a suite of antipredator behaviors and accounting for multiple disturbance regimes. In finding that agricultural legacies change the antipredator strategies of deer, this study demonstrates the value of evaluating landscapes of fear in degraded habitats. While protected areas provide invaluable ecological baselines for understanding large-scale patterns in predator-prey dynamics (Boyce 2018), as much as 75% of the earth's land cover is considered degraded (IPBES 2018). The ubiquity of human disturbances necessitates research that applies basic principles of predator-prey dynamics to human-modified landscapes (Guiden *et al.* 2019). Since as much as 80% of forest cover in North America and Europe is on post-agricultural land (Flinn & Vellend 2005), restoration of degraded forests may benefit from knowledge of how agricultural legacies affect ungulate behavior, particularly when efforts include the reintroduction of predators. Our results show that ungulates may not exhibit the same behavioral responses to predation risk in restored habitats as they do in remnant habitats, necessitating the measurement of multiple antipredator behaviors to accurately detect the effects of predator reintroduction.

Variation in the employment of different antipredator strategies across a landscape may have important ecosystem consequences since different behaviors may have different ecological effects. Changes in vigilance can determine herbivory pressure on plant communities (Schmitz *et al.* 2004; Creel & Winnie 2005; Cherry *et al.* 2016) whereas increased ungulate nocturnality may increase metabolic costs, decrease visual acuity, and increase overlap with competitors (Gaynor *et al.* 2018). Importantly, frequent fires can reduce tick abundance (Gleim *et al.* 2014), and increased nocturnality among white-tailed deer in high-fire sites may affect temporal overlap with ectoparasites during times of day when environmental conditions are optimal for parasites to seek hosts (e.g., ticks; Orr et al. 2013; Dubie et al. 2018). Hence, fire-mediated shifts in activity timing in nonagricultural woodlands may modify ectoparasite load and disease transmission by altering spatiotemporal overlap with ectoparasites. Since vigilance and activity timing yield different costs to deer and modify different ecological interactions (e.g., herbivory vs. parasitism), it is possible that the nature and strength of behaviorally-mediated trophic cascades may differ across habitats with different land-use histories. Past work has found evidence of behaviorally-mediated trophic cascades driven by deer antipredator behavior in longleaf pine woodlands (Cherry *et al.* 2016), and our findings suggest the interesting possibility that differences in past land use found throughout the range of this ecosystem (e.g., 50% of longleaf pine acreage contains stands <50 years old; Oswalt et al., 2012) could be a significant, but unappreciated factor contributing to variation in trophic cascades.

Conclusions and future directions

Land-use legacies and contemporary fire regimes can interact to modify deer vigilance and activity time, potentially generating dynamic landscapes of fear in longleaf pine woodlands. The historic diversity of understory plant communities in longleaf pine woodlands has made this ecosystem a global biodiversity hotspot (Frost 2006). Since shifts in ungulate foraging behavior in response to perceived risk can generate cascading effects on plant communities (Schmitz *et al.* 2000; Winnie 2012; Kauffman *et al.* 2013; Cherry *et al.* 2016), it is possible that the effects of past land use and contemporary fire regime on deer foraging behavior could have unappreciated consequences for the restoration and maintenance of understory plant diversity in longleaf pine woodlands. Variation in the employment of different antipredator strategies may also have important ecosystem consequences since different behaviors have different ecological effects. Future studies that employ herbivore exclosures to measure the effects of herbivory on understory plants across different land-use histories and fire regimes are necessary to understand the ultimate consequences of deer behavioral responses to past and present disturbances detected in our study.

References

Bartel, S.L. & Orrock, J.L. (2020). Past and present disturbances generate spatial variation in seed predation. *Ecosphere*, 11, e03116.

Bednekoff, P.A. & Lima, S.L. (1998). Randomness, chaos and confusion in the study of antipredator vigilance. *Trends Ecol. Evol.*, 13, 284–287.

Boyce, M.S. (2018). Wolves for Yellowstone: dynamics in time and space. *J. Mammal.*, 99, 1021–1031.

Bro-Jørgensen, J., Brown, M.E. & Pettorelli, N. (2008). Using the satellite-derived normalized difference vegetation Index (NDVI) to explain ranging patterns in a lek-breeding antelope: The importance of scale. *Oecologia*, 158, 177–182.

Brudvig, L.A. & Damschen, E.I. (2011). Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. *Ecography (Cop.)*., 34, 257–266.

Brudvig, L.A., Grman, E., Habeck, C.W., Orrock, J.L. & Ledvina, J.A. (2013). Strong legacy of agricultural land use on soils and understory plant communities in longleaf pine woodlands. *For. Ecol. Manage.*, 310, 944–955.

Brudvig, L.A., Orrock, J.L., Damschen, E.I., Collins, C.D., Hahn, P.G., Mattingly, W.B., *et al.* (2014). Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities. *PLoS One*, 9, e86604.

Buma, B. (2015). Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere*, 6, 1–15.

Caro, T. (2005). *Antipredator Defenses in Mammals and Birds*. University of Chicago Press, Chicago, IL.

Cherry, M.J., Conner, L.M. & Warren, R.J. (2015). Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. *Behav. Ecol.*, 26, 1091–1099.

Cherry, M.J., Warren, R.J. & Conner, L.M. (2016). Fear, fire, and behaviorally mediated trophic cascades in a frequently burned savanna. *For. Ecol. Manage.*, 368, 133–139.

Cherry, M.J., Warren, R.J. & Conner, L.M. (2017). Fire-mediated foraging tradeoffs in white-tailed deer. *Ecosphere*, 8, e01784.

Connolly, B.M. & Orrock, J.L. (2018). Habitat-specific capture timing of deer mice (*Peromyscus maniculatus*) suggests that predators structure temporal activity of prey. *Ethology*, 124, 105–112.

Crawford, D.A., Cherry, M.J., Kelly, B.D., Garrison, E.P., Shindle, D.B., Conner, L.M., *et al.* (2019). Chronology of reproductive investment determines predation risk aversion in a felid-ungulate system. *Ecol. Evol.*, 9, 3264–3275.

Creel, S., Schuette, P. & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behav. Ecol.*, 25, 773–784.

Creel, S. & Winnie, J.A. (2005). Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Anim. Behav.*, 69, 1181–1189.

Culbert, P.D., Dorresteijn, I., Loos, J., Clayton, M.K., Fischer, J. & Kuemmerle, T. (2017). Legacy effects of past land use on current biodiversity in a low-intensity farming landscape in Transylvania (Romania). *Landsc. Ecol.*, 32, 429–444.

Dirzo, R. & Raven, P.H. (2003). Global state of biodiversity and loss. *Annu. Rev. Environ.*

Resour., 28, 137–67.

Dobson, A.P., Bradshaw, A.D. & Baker, A.J.M. (1997). Hopes for the future: Restoration ecology and conservation biology. *Science (80-.).*, 277, 515–522.

Dubie, T.R., Turner, J. & Noden, B.H. (2018). Questing behavior and analysis of tick-borne bacteria in *Ixodes scapularis* (Acari: Ixodidae) in Oklahoma. *J. Med. Entomol.*, 55, 1569–1574.

Dudley, N. & Alexander, S. (2017). Agriculture and biodiversity: a review. *Biodiversity*, 18, 45–49.

Duguy, B. & Ramón, V. V. (2007). Land-use and fire history effects on post-fire vegetation dynamics in eastern Spain. *J. Veg. Sci.*, 19, 97–108.

Eby, S.L., Anderson, T.M., Mayemba, E.P. & Ritchie, M.E. (2014). The effect of fire on habitat selection of mammalian herbivores: The role of body size and vegetation characteristics. *J. Anim. Ecol.*, 83, 1196–1205.

Eisenberg, C., Hibbs, D.E. & Ripple, W.J. (2015). Effects of predation risk on elk (*Cervus elaphus*) landscape use in a wolf (*Canis lupus*) dominated system. *Can. J. Zool.*, 93, 99–111.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., *et al.* (2011). Trophic downgrading of planet earth. *Science (80-.).*, 333, 301–306.

Flinn, K.M. & Vellend, M. (2005). Recovery of forest plant communities in post-agricultural landscapes. *Front. Ecol. Environ.*, 3, 243–250.

Fordyce, A., Hradsky, B.A., Ritchie, E.G. & Di Stefano, J. (2016). Fire affects microhabitat selection, movement patterns, and body condition of an Australian rodent (*Rattus fuscipes*). *J. Mammal.*, 97, 102–111.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86, 1320–1330.

Fortin, D., Boyce, M.S., Merrill, E.H. & Fryxell, J.M. (2004). Foraging costs of vigilance in large mammalian herbivores. *Oikos*, 107, 172–180.

Foster, D.R. (1993). Land-use History and Forest Transformations in Central New England. In: *Humans as Components of Ecosystems*. Springer New York, New York, NY, pp. 91–110.

Frost, C. (2006). History and Future of the Longleaf Pine Ecosystem. In: *The Longleaf Pine Ecosystem* (eds. Jose, S., Jokela, E.J. & Miller, D.L.). Springer-Verlag New York, New York, NY, pp. 9–48.

Gallo, T., Fidino, M., Lehrer, E.W. & Magle, S. (2019). Urbanization alters predator-avoidance behaviours. *J. Anim. Ecol.*, 88, 793–803.

Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E. & Brashares, J.S. (2019). Landscapes of fear: Spatial patterns of risk perception and response. *Trends Ecol. Evol.*, 34.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H. & Brashares, J.S. (2018). The influence of human disturbance on wildlife nocturnality. *Science (80-.).*, 360, 1232–1235.

Gleim, E.R., Conner, L.M., Berghaus, R.D., Levin, M.L. & Zemtsova, G.E. (2014). The phenology of ticks and the effects of long-term prescribed burning on tick population dynamics in southwestern Georgia and northwestern Florida. *PLoS One*, 9, 112174.

Griffith, B. & Youtie, B.A. (1988). Two devices for estimating foliage density and deer hiding cover. *Wildl. Soc. Bull.*, 16, 206–210.

Guiden, P.W., Bartel, S.L., Byer, N.W., Shipley, A.A. & Orrock, J.L. (2019). Predator-prey interactions in the Anthropocene: Reconciling multiple aspects of novelty. *Trends Ecol.*

Evol., 34, 616–627.

Gulsby, W.D., Kilgo, J.C., Vukovich, M. & Martin, J.A. (2017). Landscape heterogeneity reduces coyote predation on white-tailed deer fawns. *J. Wildl. Manage.*, 81, 601–609.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., *et al.* (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.*, 1, e1500052.

Hahn, P.G. & Orrock, J.L. (2015a). Land-use history alters contemporary insect herbivore community composition and decouples plant-herbivore relationships. *J. Anim. Ecol.*, 84, 745–754.

Hahn, P.G. & Orrock, J.L. (2015b). Land-use legacies and present fire regimes interact to mediate herbivory by altering the neighboring plant community. *Oikos*, 124, 497–506.

Hahn, P.G. & Orrock, J.L. (2015c). Spatial arrangement of canopy structure and land-use history alter the effect that herbivores have on plant growth. *Ecosphere*, 6, Article 193.

Hernández, L. & Laundré, J.W. (2005). Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biol.*, 11, 215–220.

Hickman, J.E., Gulsby, W.D., Killmaster, C.H., Bowers, J.W., Byrne, M.E., Chamberlain, M.J., *et al.* (2015). Home range, habitat use, and movement patterns of female coyotes in Georgia: implications for fawn predation. *J. Southeast. Assoc. Fish Wildl. Agencies*, 2, 144–150.

Higdon, S.D., Diggins, C.A., Cherry, M.J. & Ford, M.W. (2019). Activity patterns and temporal predator avoidance of white-tailed deer (*Odocoileus virginianus*) during the fawning season. *J. Ethol.*, 37, 283–290.

Hunter, L.T.B. & Skinner, J.D. (1998). Vigilance behaviour in African ungulates: The role of predation pressure. *Behaviour*, 135, 195–211.

Hurtt, G.C., Frolking, S., Fearon, M.G., Moore, B., Shevliakovas, E., Malyshev, S., *et al.* (2006). The underpinnings of land-use history: Three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. *Glob. Chang. Biol.*, 12, 1208–1229.

Illius, A.W. & Fitzgibbon, C. (1994). Costs of vigilance in foraging ungulates. *Anim. Behav.*, 47, 481–484.

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, I. (2018). *The IPBES assessment report on land degradation and restoration.*

Jorge, M.H., Garrison, E.P., Conner, L.M. & Cherry, M.J. (2020). Fire and land cover drive predator abundances in a pyric landscape. *For. Ecol. Manage.*, 461, 117939.

Karpestam, E., Merilaita, S. & Forsman, A. (2012). Reduced predation risk for melanistic pygmy grasshoppers in post-fire environments. *Ecol. Evol.*, 2, 2204–2212.

Kauffman, M.J., Brodie, J.F. & Jules, E.S. (2013). Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade: reply. *Ecology*, 94, 1425–1431.

Kelly, M.J. (2003). Jaguar monitoring in the Chiquibul Forest, Belize. *Caribb. Geogr.*, 13, 19–32.

Kelly, M.J. & Holub, E.L. (2008). Camera trapping of carnivores: Trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. *Northeast. Nat.*, 15, 249–262.

Kilgo, J. & Blake, J.I. (Eds.). (2005). *Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site*. Island Press, Washington, DC, USA.

Kilgo, J.C., Ray, H.S., Ruth, C. & Miller, K. V. (2010). Can coyotes affect deer populations in southeastern North America? *J. Wildl. Manage.*, 74, 929–933.

Kitchen, A.M., Gese, E.M. & Schauster, E.R. (2000). Changes in coyote activity patterns due to reduced exposure to human persecution human persecution. *Can. J. Zool.*, 78, 853–857.

Kohl, M.T., Stahler, D.R., Metz, M.C., Forester, J.D., Kauffman, M.J., Varley, N., *et al.* (2018). Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.*, 88, 638–652.

Kopecký, M. & Vojta, J. (2009). Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. *Appl. Veg. Sci.*, 12, 251–260.

Kymmell, D. (2019). Fire effects in a landscape of fear – food availability and perceived predation risk as potential determinants of patch utilization by herbivore prey. Swedish University of Agricultural Sciences.

Lashley, M.A., Chitwood, C.C., Biggerstaff, M.T., Morina, D.L. & Moorman, C.E. (2014). White-tailed deer vigilance: The influence of social and environmental factors. *PLoS One*, 9, 90652.

Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001). Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Can. J. Zool.*, 79, 1401–1409.

Lima, S.L. (1995). Back to the basics of anti-predatory vigilance: The group-size effect. *Anim. Behav.*, 49, 11–20.

Lima, S.L. & Bednekoff, P.A. (1999). Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *Am. Nat.*, 153, 649–659.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Can. J. Zool.*, 68, 619–640.

Mattingly, W.B., Orrock, J.L., Collins, C.D., Brudvig, L.A., Damschen, E.I., Veldman, J.W., *et* *al.* (2015). Historical agriculture alters the effects of fire on understory plant beta diversity. *Oecologia*, 177, 507–518.

Moll, R.J., Redilla, K.M., Mudumba, T., Muneza, A.B., Gray, S.M., Abade, L., *et al.* (2017). The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. *J. Anim. Ecol.*, 86, 749–765.

Morris, G. & Conner, L.M. (2016). Effects of forest management practices, weather, and indices of nest predator abundance on nest predation: A 12-year artificial nest study. *For. Ecol. Manage.*, 366, 23–31.

Myserud, A. & Østbye, E. (1999). Cover as a habitat element for temperate ungulates: Effects on habitat selection and demography. *Wildl. Soc. Bull.*, 27, 385–394.

Nudds, T.D. (2018). Quantifying the vegetative structure of wildlife cover. *Wildl. Soc. Bull.*, 5, 113–117.

O'Connor, K.M. & Rittenhouse, T.A.G. (2017). Temporal activity levels of mammals in patches of early successional and mature forest habitat in eastern Connecticut. *Am. Midl. Nat.*, 177, 15–28.

Orr, J.M., Smith, J.D., Zawada, S.G. & Arias, J.R. (2013). Diel and seasonal activity and trapping of ticks (Acari: Ixodidae) in Northern Virginia, U.S.A. *Syst. Appl. Acarol.*, 18, 111.

Oswalt, C.M., Cooper, J.A., Brockway, D.G., Brooks, H.W., Walker, J.L., Connor, K.F., *et al.* (2012). *History and current condition of longleaf pine in the Southern United States*. *United States Dep. Agric. For. Serv. South. Res. Station. Gen. Tech. Rep. SRS-166.*

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.*, 14.

Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbeg, B., *et al.*

(2008). Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology*, 89, 2416–2425.

Pickett, S.T.A. & White, P.S. (Eds.). (1985). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press.

Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995). The future of biodiversity. *Science (80-.).*, 269, 347–350.

Preisser, E.L. & Bolnick, D.I. (2008). The many faces of fear: Comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS One*, 3, e2465.

Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501–509.

Prugh, L.R., Sivy, K.J., Mahoney, P.J., Ganz, T.R., Ditmer, M.A., van de Kerk, M., *et al.* (2019). Designing studies of predation risk for improved inference in carnivore-ungulate systems. *Biol. Conserv.*, 232, 194–207.

R Core Development Team. (2019). R.

Ridout, M.S. & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *J. Agric. Biol. Environ. Stat.*, 14, 322–337.

Ripple, W.J. & Beschta, R.L. (2003). Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *For. Ecol. Manage.*, 184, 299–313.

Rowcliffe, J.M., Kays, R., Kranstauber, B., Carbone, C. & Jansen, P.A. (2014). Quantifying levels of animal activity using camera trap data. *Methods Ecol. Evol.*, 5, 1170–1179.

Rowcliffe, M. (2019). Activity: Animal Activity Statistics.

Schmitz, O.J., Hambäck, P.A. & Beckerman, A.P. (2000). Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.*, 155, 141–153.

Schmitz, O.J., Krivan, V. & Ovadia, O. (2004). Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecol. Lett.*, 7, 153–163.

Sheriff, M.J., Orrock, J.L., Ferrari, M.C.O.O., Karban, R., Preisser, E.L., Sih, A., *et al.* (2020). Proportional fitness loss and the timing of defensive investment: A cohesive framework across animals and plants. *Oecologia*, 193, 273–283.

Sih, A. & Ziemba, R. (2000). New insights on how temporal variation in predation risk shapes prey behavior. *Trends Ecol. Evol.*, 15, 3–4.

Sisk, T.D., Launer, A., Switky, K.R. & Ehrlich, P.R. (1994). Identifying extinction threats. *Bioscience*, 44, 592–604.

Smith, J.A., Donadio, E., Pauli, J.N., Sheriff, M.J. & Middleton, A.D. (2019). Integrating temporal refugia into landscapes of fear: Prey exploit predator downtimes to forage in risky places. *Oecologia*, 189, 883–890.

Sousa, W.P. (1984). The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.*, 15, 353–391.

Spitz, D.B., Clark, D.A., Wisdom, M.J., Rowland, M.M., Johnson, B.K., Long, R.A., *et al.* (2018). Fire history influences large-herbivore behavior at circadian, seasonal, and successional scales. *Ecol. Appl.*, 28, 2082–2091.

Stuhler, J.D. & Orrock, J.L. (2016). Past agricultural land use and present-day fire regimes can interact to determine the nature of seed predation. *Oecologia*, 181, 463–473.

Terborgh, J. & Estes, J.A. (Eds.). (2010). *Trophic cascades: predators, prey, and the changing dynamics of nature*. Island Press, Washington, DC.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., *et al.* (2009). Behavioral adjustments of African herbivores to predation risk by lions:

Spatiotemporal variations influence habitat use. *Ecology*, 90, 23–30.

Veldman, J.W., Brudvig, L.A., Damschen, E.I., Orrock, J.L., Mattingly, W.B. & Walker, J.L. (2014). Fire frequency, agricultural history and the multivariate control of pine savanna understorey plant diversity. *J. Veg. Sci.*, 25, 1438–1449.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997). Human domination of Earth's ecosystems. *Science (80-.).*, 277, 3–13.

Wang, Y., Allen, M.L. & Wilmers, C.C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biol. Conserv.*, 190, 23–33.

Winnie, J. & Creel, S. (2007). Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Anim. Behav.*, 73, 215–225.

Winnie, J.A. (2012). Predation risk, elk, and aspen: Tests of a behaviorally mediated trophic cascade in the Greater Yellowstone Ecosystem. *Ecology*, 93, 2600–2614.

Figures

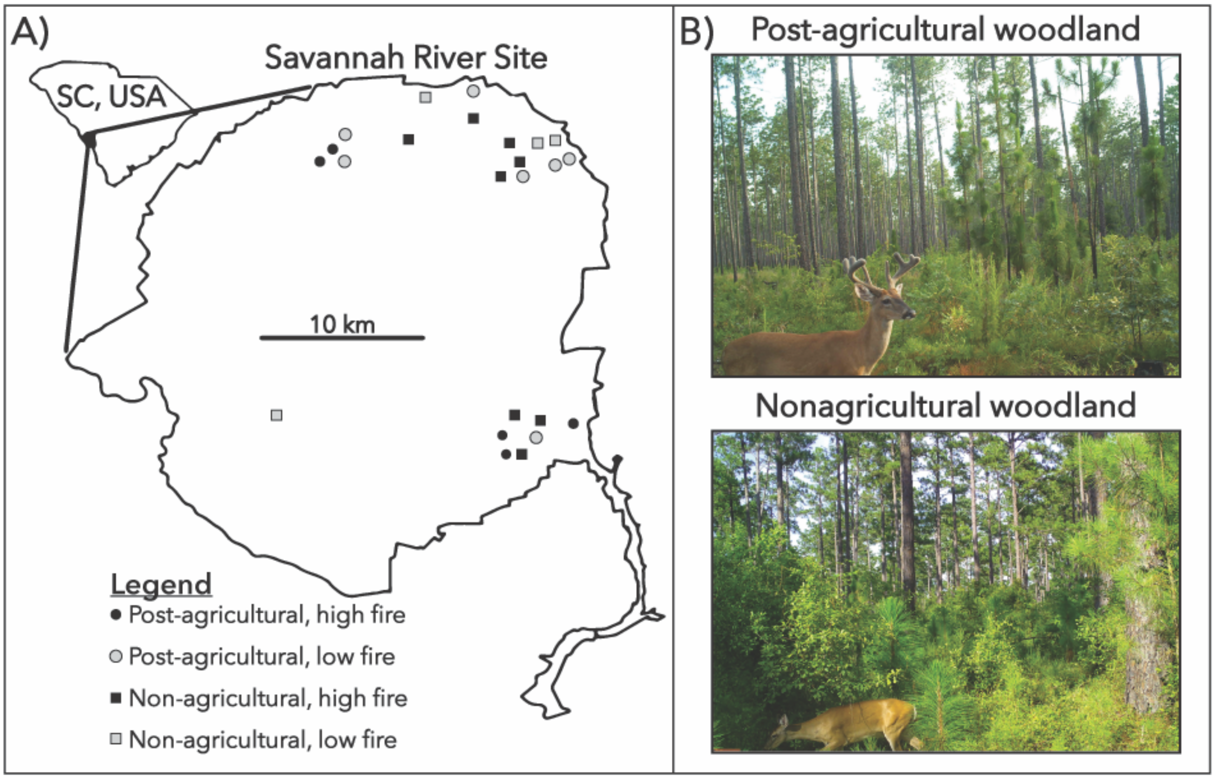

Figure 1. A) We conducted our study in South Carolina, USA, at the Savannah River Site, an 80,000-ha area containing longleaf pine woodlands varying in agricultural legacies and fire frequencies. Circles and squares on the map indicate the locations of our 24 sites where camera traps were deployed to measure deer behavior. Sites were all located in flat uplands and were more than 250 m apart. **B)** Agricultural legacies can affect habitat structure that is relevant for deer perceptions of risk. At SRS, post-agricultural woodlands are dominated by mature pine with depauperate understories, and nonagricultural woodlands contain mixed hardwood-pine canopies with denser understories.

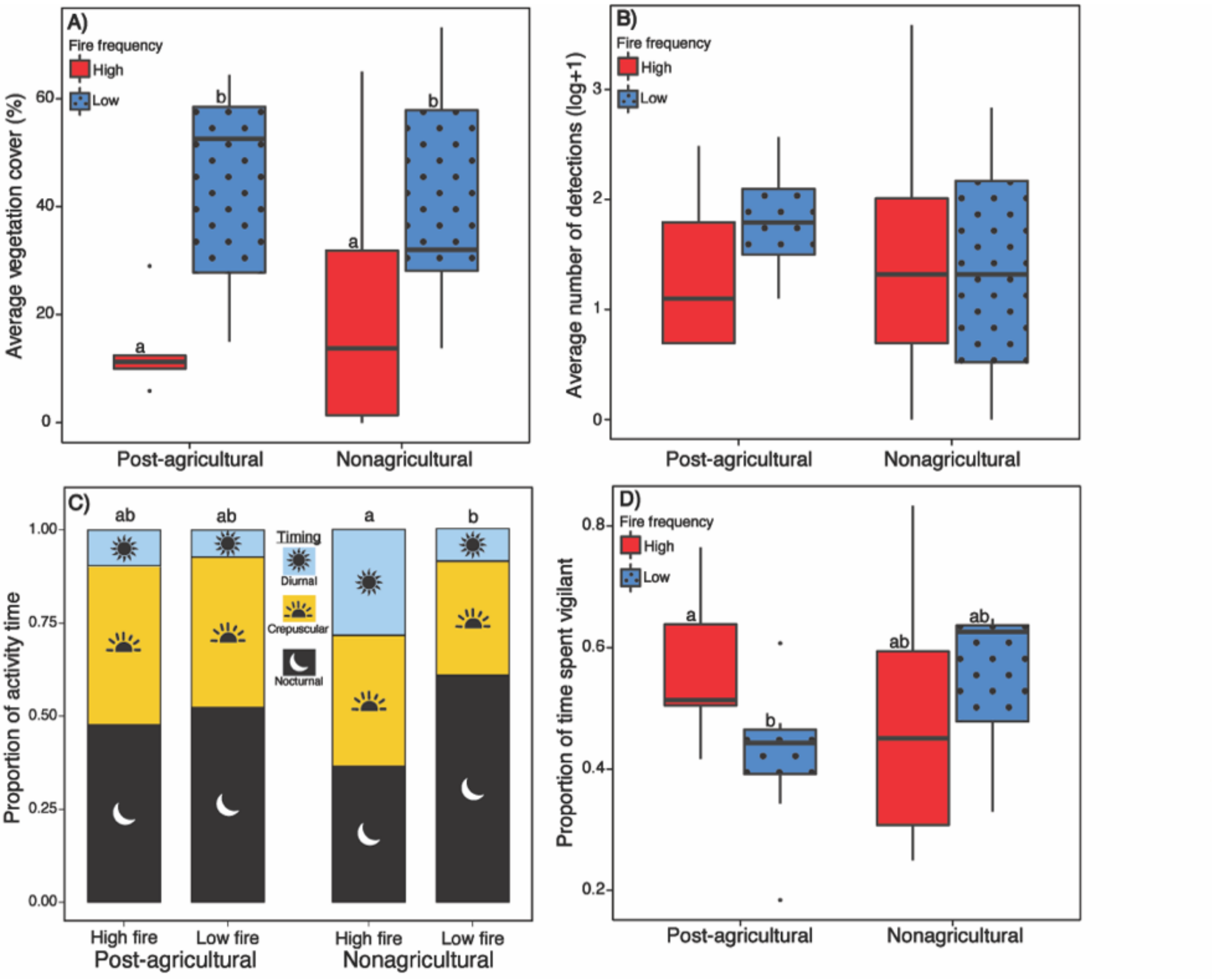

Figure 2. Past land use and contemporary fire frequency significantly affected vegetation cover, deer activity timing, and deer vigilance. **A)** Sites with frequent fire regimes had significantly lower vertical vegetation cover in both post-agricultural and nonagricultural woodlands. **B)** The frequency of deer foraging activity across sites did not differ with land-use history or fire frequency. **C)** Independent deer detections were categorized as crepuscular, diurnal, or nocturnal using daily sunrise and sunset times. We calculated the proportion of total deer detections occurring within each timing category for each land-use history and fire frequency category. There was no difference in activity timing between post-agricultural woodlands of different fire frequencies. In nonagricultural woodlands, deer exhibited greater nocturnal activity and less

crepuscular or diurnal activity in woodlands with low fire frequencies than in woodlands high fire frequencies. **D)** The effect of fire frequency on deer vigilance was contingent upon land-use history. In post-agricultural woodlands, deer allocated a higher proportion of their time to vigilance in sites with frequent fire regimes, but there was no effect of fire on deer vigilance in nonagricultural woodlands. Lowercase letters indicate significant differences between group means at an alpha level of 0.05.

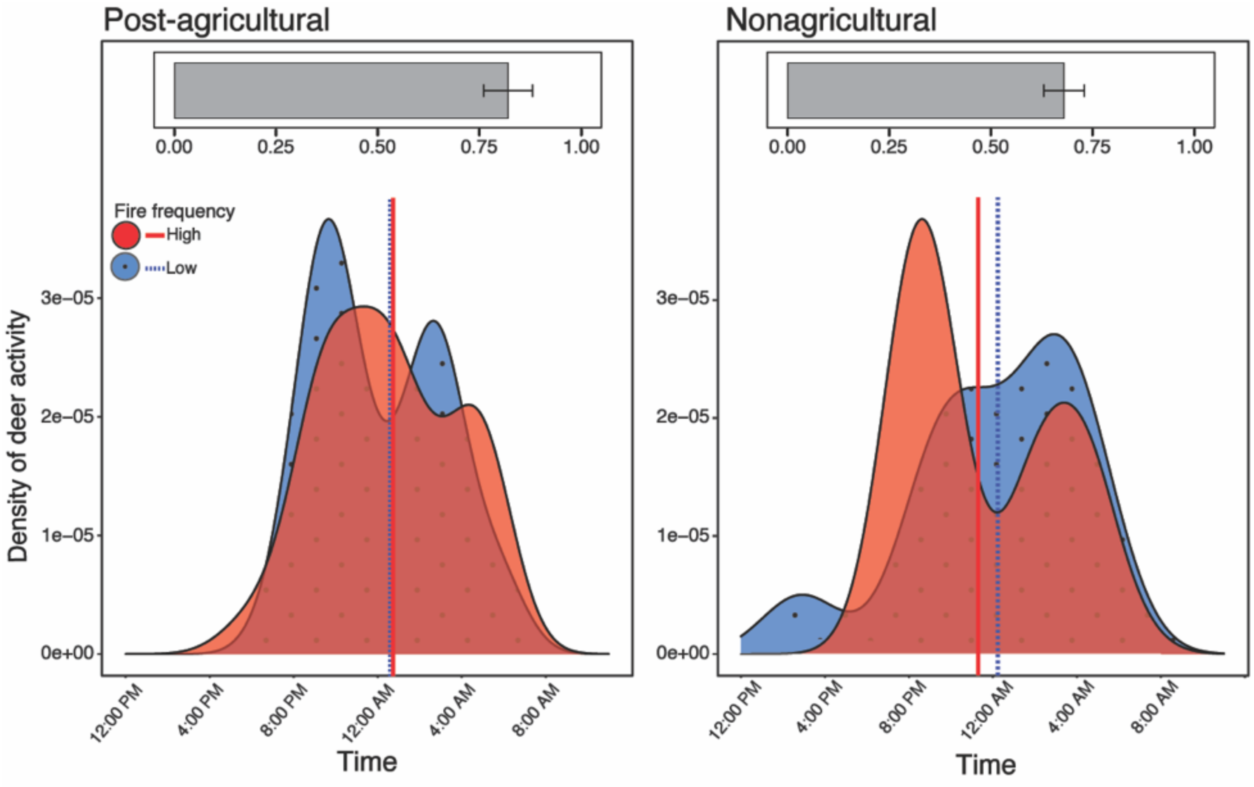

Figure 3. Deer activity patterns were significantly affected by fire frequency in nonagricultural woodlands but not in post-agricultural woodlands. In post-agricultural woodlands, the distribution of foraging bouts showed a range of activity from the evening (~9:00PM) through the early morning (~5:00PM). In nonagricultural woodlands, deer were primarily crepuscular in sites with high fire frequencies showing activity peaks primarily in the evening (~8:00-9:00 PM) and secondarily in the early morning (~5:00 AM). Deer were primarily nocturnal in sites with low fire frequencies, showing activity peaks only at nighttime (~2:00-3:00 AM). Vertical lines represent group means. Bars within each panel represent coefficient of overlap in distributions between fire treatments, and error bars represent bootstrapped 95% confidence intervals.

Appendix S1. Longleaf pine woodland site selection.

The 24 sites sampled in this study were randomly selected from 36 longleaf pine woodland sites at the Savannah River Site used for a long-term study investigating how differences in land-use history and contemporary fire regime affect ecological processes and biodiversity restoration efforts (see Orrock et al. 2015 for full details). All sites were at least 250 m apart. Each site covered ≥ 1 ha of uniform habitat that did not cross topographical or hydrological boundaries, contained overstory longleaf pines, and lacked features causing abrupt changes in understory vegetation (e.g., firebreaks or drainages). All study sites were located on flat uplands and contained well-drained sandy soils, which serve as the primary substrate for longleaf pine (Orrock et al. 2015). Soil texture did not differ between post-agricultural and nonagricultural sites (Mattingly et al. 2015). This site selection scheme ensured that sites did not differ in other environmental variables that may be associated with non-random agricultural land use (e.g., topography, hydrology, or soil texture; Orrock et al. 2015).

Mattingly WB, Orrock JL, Collins CD, Brudvig LA, Damschen EI, Veldman JW, Walker JL. 2015. Historical agriculture alters the effects of fire on understory plant beta diversity. Oecologia. 177(2):507–518.

Orrock J, Damschen E, Brudvig L, Walker J. 2015. Developing and Testing a Robust , Multi-scale Framework for the Recovery of Longleaf Pine Understory Communities.

Appendix S2. Fire history of each study site.

Table 1. The number of fires since 1991 was determined from annual fire records, and sites were characterized as low (five or less burns) or high (more than five burns) fire frequency. In the case where a site had had five burns but was also recently burned (e.g., S72), the site was classified as high fire frequency. For the majority of sites, sites that were frequently burned since 1991 were also recently burned, and sites that were infrequently burned had not been recently burned.

Site	Land-use history	Fires since 1991	Years since last fire	Fire regime categorization
S64	Non-agricultural	0	20	Low
S22	Non-agricultural	2	17	Low
S35	Agricultural	3	6	Low
S12*	Agricultural	4	6	Low
S103	Non-agricultural	4	6	Low
S109	Non-agricultural	4	3	Low
S15	Agricultural	5	5	Low
S50	Agricultural	5	4	Low
S51	Agricultural	5	4	Low
S57	Agricultural	5	4	Low
S77	Agricultural	5	4	Low
S72	Agricultural	5	3	High
S11	Agricultural	6	3	High
S34	Non-agricultural	6	2	High
S59	Non-agricultural	6	4	High
S62	Non-agricultural	6	1	High
S113	Non-agricultural	6	4	High
S101	Non-agricultural	7	2	High
S102	Agricultural	7	3	High
S105	Non-agricultural	7	3	High
S110	Non-agricultural	7	1	High
S84	Agricultural	8	3	High
S106	Agricultural	8	3	High
S104*	Non-agricultural	9	1	High

*Sites where no deer activity was detected during camera deployment

Appendix S3. Forage quality assessments.

Methods: Within 18 of our sites, we recorded the presence of plant species that are preferred forage for deer in the southeast to estimate forage quality at each site through a species richness metric. A species list for deer forage in the southeastern US was constructed referencing both understory plant identification manuals (John et al. 1961; Miller and Miller 2005; Norden and Kirkman 2006) and published literature of past research on deer foraging (Lashley et al. 2015; Cherry et al. 2016). We present only the species on this list that were found in our plots (Table 1).

Table S1. Deer forage species that were detected at the 18 sites measured at the Savannah River Site, SC, USA.

Forage Species	Family	Form	Life Cycle
Centrosema virginianum	Fabacaea	Forb, legume	Perennial
Chamaechrista fasciculata	Fabacaea	Forb, legume	Annual
Chamaechrista nictitans	Fabacaea	Forb, legume	Annual
Cnidoscolus stimulosus	Euphorbiacea	Forb, nettle	Perennial
Desmodium spp.	Fabacaea	Forb, legume	Perennial
Galactia spp.	Fabacaea	Forb, legume	Perennial
Lespedeza spp.	Fabacaea	Forb, legume	Perennial
Prunus spp.	Rosaceae	Hardwood, fleshy fruit	Perennial
Quercus spp.	Fagaceae	Hardwood, hard mast	Perennial
Rhyncosia reniformus	Fabacaea	Forb, legume	Perennial
Rubus spp.	Rosaceae	Shrub, fleshy fruit	Perennial
Smilax spp.*	Smilaceae	Vine	Perennial
Tephrosia virginiana	Fabacaea	Forb, legume	Perennial
Vitis spp.*	Vitaceae	Vine	Perennial

*Dominant vines removed from richness calculations

Appendix S4. Sex-specific deer activity responses to land-use history and fire regime.

Methods: To evaluate if land-use history and fire frequency had sex-specific effects on spatial patterns of deer activity, we used a linear mixed effects model with land-use history, fire frequency, sex, and the interaction of land-use, fire, and sex as fixed effects; site as a random effect; and the log-transformed total number of foraging bouts for each sex at each site as a response variable.

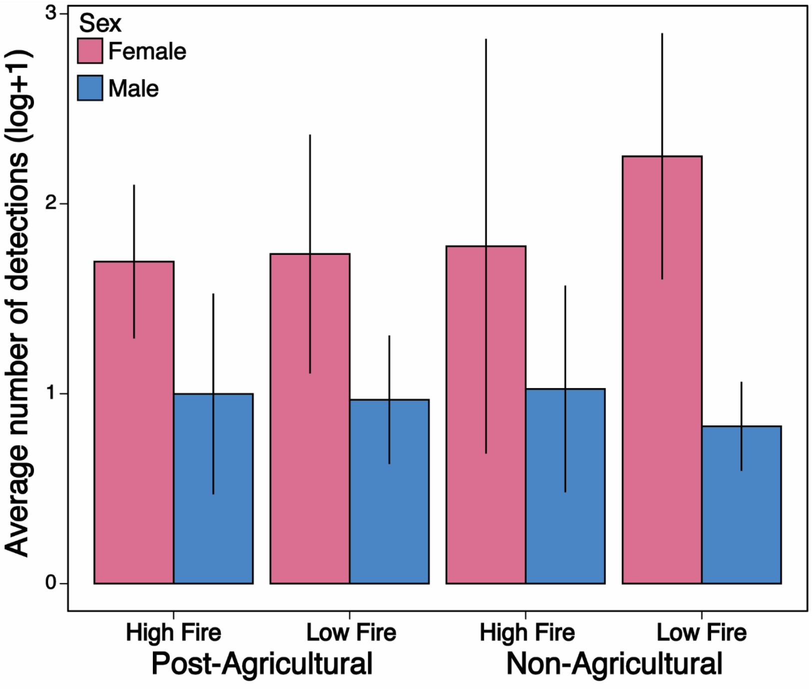

Figure 2. While the majority of deer foraging activity that we captured was conducted by female individuals, there was not a significant interaction of land-use history, fire frequency, and individual sex on the frequency of deer foraging activity ($F_{1,40} = 0.10$, $p = 0.752$).

Appendix S5. The effect of activity timing on deer vigilance.

Methods: In order to assess if deer activity timing affects deer vigilance behavior, we used a generalized linear mixed effects model with land-use history, fire frequency, time of detection, and the interaction of history, fire, and time as fixed effects; site as a random effect; and proportion of "vigilant" photos as a response variable. Time of detection was quantified numerically as hours since noon.

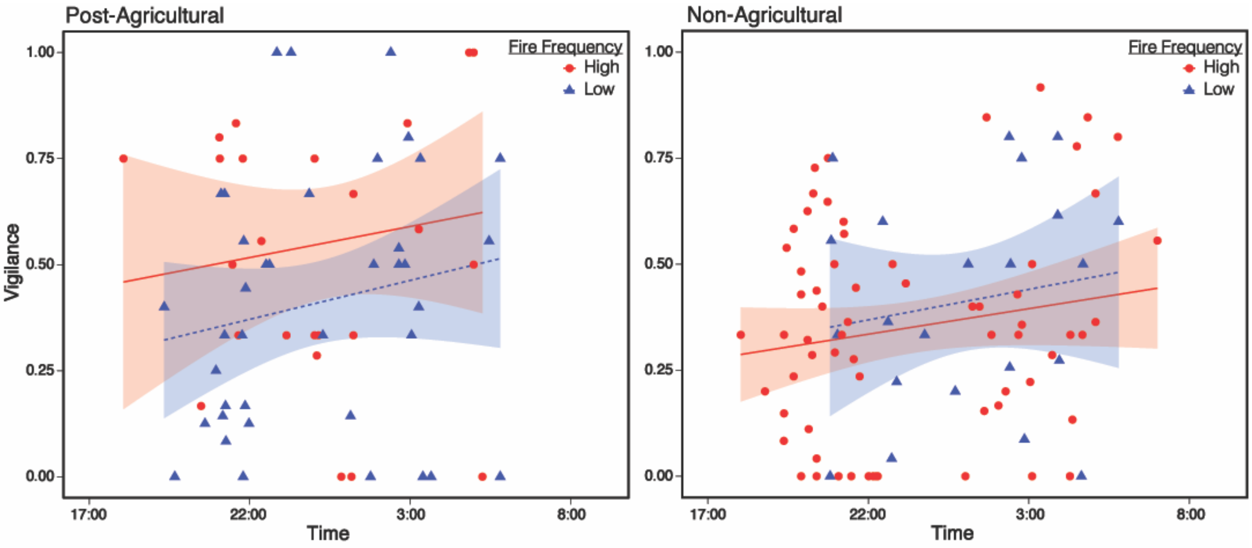

Figure S3. There was not a significant effect of activity time or the interaction of activity time and land-use history on vigilance. There was a significant effect of the interaction of land-use history and fire frequency ($X^2 = 8.16$, $p = 0.004$), the interaction of fire and activity time ($X^2 = 5.12$, $p = 0.024$), and the interaction of history, fire, and time on vigilance ($X^2 = 5.06$, $p = 0.024$).

CHAPTER 3

Land-use history, fire regime, and large-mammal herbivory affect deer-preferred plant diversity in longleaf pine woodlands

Savannah L. Bartel and John L. Orrock

Bartel, S. L., J. L. Orrock. Land-use history, fire regime, and large-mammal herbivory affect deer-preferred plant diversity in longleaf pine woodlands. In review.

Abstract: Since ecological systems often experience multiple disturbances, understanding changes in important ecological interactions, such as plant-herbivore interactions, may require studies capable of disentangling the unique and interactive effects of multiple forms of disturbance. For example, understanding how mammalian herbivores affect plant communities may require understanding how widespread past disturbances, such as agricultural land use, interact with contemporary disturbances, such as prescribed fire. We tested if past agricultural land use and contemporary fire regime modified the effects of mammalian herbivory on focal plant communities by measuring the richness of plant species preferred by deer at 26 longleaf pine woodlands containing paired open and mammal-exclusion plots. Land-use history significantly affected the community composition of deer-preferred species, and post-agricultural sites had greater focal species richness than nonagricultural sites. Large-mammal herbivory only affected plant species richness in woodlands with low fire frequencies. These results suggest that past and present disturbances may mediate contemporary plant-animal interactions and may

explain spatial patterns in the intensity of large-mammal herbivory. Since past work suggests that the primary large-mammal herbivores in this system, white-tailed deer, perceive the lowest risk of predation in woodlands with low fire frequencies, these results indicate that our ability to anticipate and predict local changes in animal foraging behavior may provide a powerful means to explain large-scale, long-term patterns in plant communities across multiple disturbance contexts.

Introduction

Global environmental change has become so pervasive that many ecological systems typically experience multiple forms of disturbance (Vitousek et al. 1997, Wilcove et al. 1998, Foley et al. 2005, Hobbs et al. 2009, Buma 2015), such as shifts in the occurrence and severity of wildfires and prescribed burns, a history of agricultural land use, and changes in precipitation and storm regime. Indeed, recent work across a variety of systems clearly demonstrates the importance of evaluating multiple disturbances for understanding how species and ecosystems may respond to global change (e.g., Hansen et al. 2018, Lucash et al. 2018, Brudvig et al. 2021; see Buma 2015, Kleinman et al. 2019 for reviews). However, since ecosystems (and disturbances) are dynamic and ecological systems may take years to respond to disturbance, understanding how multiple disturbances might interact to affect ecological systems requires measuring ecological processes over sufficiently long time periods. For example, long-term studies demonstrate that plant-herbivore interactions shape diversity and function in plant communities over multiple years (Brown and Heske 1990, Huntly 1991, Belsky 1992, Milchunas and Lauenroth 1993, Virtanen et al. 1997, Augustine and McNaughton 1998, Olff and Ritchie 1998, Maron and Crone 2006, Agrawal et al. 2012). As a result, long-term studies may be essential for understanding how multiple disturbances that affect plant-herbivore interactions might ultimately affect plant communities. Moreover, studies are rarely able to experimentally evaluate ecological processes involving large-bodied organisms, which may have large effects on ecological communities (McNaughton 1979, Belsky 1992, Milchunas and Lauenroth 1993, Augustine and McNaughton 1998, Pringle et al. 2007, Ford et al. 2014), due to the challenges of consistently manipulating large-animal presence or activity at sites spanning different disturbance regimes over many years.

Among the many types of global change that affect plant communities, changes in fire regime and past agricultural land use are two of the most globally pervasive disturbances. For example, changes in the frequency, size, and severity of fires have been documented across the globe both in temperate and tropical regions (Cochrane et al. 1999, Flannigan A et al. 2009, Harvey et al. 2016, Prichard et al. 2017), and the global area burned was estimated to have increased from 500 Mha year^{-1} to 608 Mha year^{-1} over the second half of the 20th century (Mouillot and Field 2005, Flannigan A et al. 2009). Legacies of past agricultural land-use are also widespread: 10 to 44 million km^2 of global land cover is recovering from agricultural land use since 1700 (Hurtt et al. 2006). Fire and agricultural legacies are two types of disturbance that have profound impacts on plant communities. Changes in fire regime can lead to regeneration failure of forest trees (Harvey et al. 2016) and declines in plant diversity (Prichard et al. 2017). Agricultural legacies can have persistent effects on plant community structure and diversity for decades and sometimes centuries following agricultural land abandonment (Foster 1993, Flinn and Vellend 2005, Kopecký and Vojta 2009, Mattingly et al. 2015, Culbert et al. 2017). Moreover, while it is known that agricultural legacies can interact with contemporary fire regime to determine plant community structure in restored habitats (Brudvig and Damschen 2011, Veldman et al. 2014, Mattingly et al. 2015), the degree to which these differences in plant communities reflect underlying changes in plant-consumer interactions remains unclear. This is an important gap in our knowledge because community composition and optimal approaches for conservation and restoration may be fundamentally different for plant communities limited by consumers compared to those limited by other processes (e.g., dispersal limitation).

Large-mammal herbivores have the potential to generate large-scale and long-term impacts on habitats through top-down control of plant communities (Rooney and Waller 2003, Côté et al. 2004, Holdo et al. 2009, Winnie 2012, Daskin et al. 2016, Goheen et al. 2018); however, these impacts can be highly variable across heterogeneous landscapes due to variation in large-mammal abundance and foraging behavior among habitats (Schütz et al. 2003, Prendeville et al. 2015, Burkepile et al. 2016, Loughnan and Williams 2019). Since agricultural legacies and fire regime modify large-mammal foraging behavior (Bartel and Orrock 2021), it is possible that these past and present disturbances may interact to generate significant spatial variation in the impact of large-mammal herbivory on plant communities. Moreover, agricultural legacies and fire may alter soil nutrient availability (Brudvig et al. 2013), and soil nutrient availability can mediate the effects of herbivory on vegetation (Connolly et al. 2016, Borer et al. 2020). While past land use and contemporary disturbances have been shown to modify arthropod herbivory in multiple ecosystems (Donihue et al. 2013, Hahn and Orrock 2015a, 2015b), no research has investigated if past and present disturbances interactively modify large-mammal herbivory. Importantly, most studies that manipulate large-mammal herbivory to understand its impact on plant communities are of relatively short duration (e.g., a systematic review by Bernes et al. (2018) found a median duration of 6 years). Since the effects of large-mammal herbivory on understory plant communities may only become apparent after long time periods (Augustine and McNaughton 1998, Gómez 2005, Bernes et al. 2018), long-term manipulations of large-mammal access to understory communities replicated across large spatial scales are necessary for understanding how past and present disturbances might modify large-mammal herbivory and resultant patterns in plant communities.

Longleaf pine woodlands can contain some of the most diverse understory plant communities in North America and are ecosystems characterized by contemporary fire as well as past agricultural land use (Frost 2006, Brudvig et al. 2014). White-tailed deer (*Odocoileus virginianus*) are common in these ecosystems, and fire (Cherry et al. 2017) as well as the overlap of fire and land-use history (Bartel and Orrock 2021) can affect deer foraging behavior. For example, deer spend less time foraging when frequent fire removes vegetative cover that protects deer from predators (Cherry et al. 2016, 2017). Moreover, evidence suggests that deer foraging behavior may strongly respond to the interaction of fire regime and past land-use as deer exhibit the greatest vigilance behavior in frequently burned post-agricultural woodlands but exhibit shifts in activity timing (i.e., avoiding risky times of day) in frequently burned nonagricultural woodlands (Bartel and Orrock 2021). While recent work in longleaf pine woodlands suggests that strong shifts in deer foraging behavior may lead to significant changes in deer herbivory and its effects on plant diversity in systems without a known history of agricultural use (Cherry et al. 2016), it is not known whether past agricultural land use modifies the role of fire in affecting deer herbivory or if this results in long-term changes in plant communities.

We used a large-scale, long-term herbivore-exclusion experiment to evaluate the effects of past agricultural land use and contemporary fire regime on herbivory by deer. We quantify herbivore effects by measuring the presence or absence of 12 plant species preferred by deer at 26 sites in longleaf pine woodlands. We focus on deer-preferred species because these species often serve important ecological roles (e.g., many are nitrogen-fixing plants), and they are often species that are targets for restoration (Brudvig et al. 2014, 2021). Past research has also indicated that these deer-preferred plant species may respond strongly to changes in deer foraging behavior (Cherry et al. 2016). We hypothesized that herbivory would have the strongest effect in woodlands with infrequent fire regimes because these are habitats with thicker woody shrub layers that provide more protective concealment for deer (i.e., safe foraging habitat), leading to greater deer herbivory. We also hypothesized that herbivory would have a stronger effect on the presence of plant species in post-agricultural woodlands than in nonagricultural woodlands because past work indicates that deer may be more fearful of predation in nonagricultural woodlands (Bartel and Orrock 2021), suggesting that deer herbivory may be less intense in nonagricultural woodlands.

Materials and Methods

Study area and design

This study was conducted at the Department of Energy (DOE) Savannah River Site (SRS; Aiken, SC), an 80,125-ha National Environmental Research Park (NERP). Established by the DOE in 1951, the USDA Forest Service manages the site on behalf of DOE. SRS is within the historical range of the longleaf-pine woodland ecosystem, much of which was converted to tillage agriculture from 1856 to 1950 (Frost 2006). Since these agricultural lands were small and dispersed, heterogeneous landscapes resulted containing patches of tilled farmland and intact forests (Kilgo and Blake 2005). Agricultural fields were abandoned in 1951 and have henceforth been under management as longleaf and loblolly pine plantations (Kilgo and Blake 2005). We selected 26 sites, spanning an 807-km^2 area, that differed in land-use history and fire frequency. Land-use history classification was based on aerial photography taken prior to land abandonment in 1951. Sites that were farmland in 1951 were classified as “post-agricultural woodlands,” and sites that were forested were classified as “nonagricultural woodlands.” The number of fires since 1991 was determined from annual fire records and sites were characterized as high (five or more burns) or low (fewer than five burns) fire frequency, a metric previously used to classify these sites based on plant-community characteristics (Brudvig et al. 2014). The resulting site classification by land-use history and fire frequency generated four distinct habitat types distributed across the study area.

Within each site, four 7 x 7 m plots were established to factorially manipulate large-herbivore access in 2010, and the experimental treatments were implemented in 2011. Large-mammal herbivore access was manipulated by building exclosure fences (~2.4 m tall) around 2 of the four plots. Fences allow access for small-mammal and invertebrate herbivores, so paired plots within a site can be assumed to experience equal herbivory and granivory pressure from these groups. White-tailed deer (*Odocoileus virginianus*) are the primary large-mammal herbivores at SRS (Cothran et al. 1991); however, feral hogs (*Sus scrofa*) are common large-mammal omnivores at SRS that can cause significant destruction to plants through rooting behavior (Barrios-Garcia and Ballari 2012). Since feral hog destruction of plant species is likely to be random while deer herbivory is expected to be greatest on palatable plant species (Edwards et al. 1961, Lashley et al. 2015), we only measured the presence and absence of plant species commonly consumed by deer. A list of plant species preferred by deer in the southeastern US was constructed referencing both understory plant identification manuals (Edwards et al. 1961, Miller and Miller 2005, Norden and Kirkman 2006) and published literature of past research on plant preferences by deer (Appendix S1; Lashley et al. 2015, Cherry et al. 2016). We present only the species on this list that were found in our plots and used in our analyses (Table 1). At each site, one of the two paired plots was given a seed-addition treatment at the center 5 x 5 m of each plot as part of a separate experiment (Orrock et al. 2015). Of the 22 seed species added, only two (*Tephrosia virginiana* and *Lespedeza hirta*) are preferred by deer (Appendix S1), and these two species were not included our analyses (Table 1). While past work has shown that plant species richness is positively correlated with plant abundance in this experimental system (Orrock et al. 2015), we also verified that this positive correlation existed for plant species preferred by deer that we examined using pre-treatment data on plant communities at our 26 sites (Appendix S2). We therefore assume that species richness of plants preferred by deer provides a reliable metric for the cover of these species at our study sites. In order to account for the potential that soil nutrient conditions may moderate the effects of herbivory, we measured phosphorus and nitrogen from soil samples taken at each site in spring 2011. We collected soil cores (2.5 cm diameter by 15cm deep) at 10 m intervals along the center line of each plot. Soil was composited by site and analyzed by Brookside Laboratories, Inc. (New Knoxville, OH) for Mehlich III-extractable phosphorus (P; Mehlich 2008) and inorganic nitrogen (N; sum of 1 N KCl cadmium reduction NO3 and NH4; Dahnke and Johnson 2018). In July 2018, we measured presence of deer-preferred plant species within each plot at the 7 x 7 m plot level. Thirteen of our 26 sites only had 1 intact herbivore exclosure (totaling 18 intact seed-addition paired plots, 21 intact no-addition paired plots) due to random fence damage that was stratified across all fire-frequency and land-use history treatments.

Data analysis

We used a multilevel model (MLM) described by Jackson *et al.* (2012) for analyses of focal plant species (i.e., the plants in the community preferred by deer) to estimate both species-level and community-level responses to land-use history, fire frequency, and herbivore access. MLMs allow us to estimate both changes in focal plant species richness and community composition. MLMs analyze the presence/absence of individual plant species in response to predictor variables as random-effect slopes. Significant variation in species-specific responses to land-use history, fire frequency, and herbivore access implies shifts in the composition of the focal plant community (Jackson et al. 2012). The fixed-effect parameter estimates report the mean response of all plant species to a predictor variable and can be interpreted as the mean probability of plant species presence (i.e., higher mean probability indicates higher number of species present). We constructed this model using the *glmer* function in the "lme4" package (Bates et al. 2015) in R ver. 3.6.1.

To test how land-use history, fire frequency, herbivore access, soil N, and soil P affected species richness and community composition for focal deer-preferred plant species 2018, we constructed an MLM with a binomial distribution including species presence/absence as the response variable; land-use history, fire frequency, herbivore access, soil N, soil P, the interaction of soil N and herbivore access, the interaction of soil P and herbivore access, and the interaction of land-use history x fire x herbivore access as fixed effects; random intercepts for site and species; and random slope terms (i.e., fixed effect x species) for land-use history, fire frequency, and herbivore access. We also evaluated if land-use history and fire regime affected soil N or soil P in follow-up analyses (see Appendix S3 for methods and results). To measure the effects of land-use history, fire frequency, and herbivore access on the composition of the focal plant community, we used likelihood ratio tests (LRTs) comparing the full model to models without the random effects of a land-use history, fire frequency, or herbivore access slope wherein a significant random effect of the slope indicates that species vary significantly in their responses to land-use history or fire frequency (Jackson et al. 2012, McCormick et al. 2019).

Results

Across our 26 sites, the average species richness of deer-preferred plant species in plots with herbivore access (i.e., open plots) was 3.82 ± 0.32, and the average species richness of deer-preferred plants in exclosure plots was 4.67 ± 0.34. In the MLM model, community composition was significantly affected by land-use history (LRT: $\chi^2 = 42.16$, $p < 0.001$) but not fire frequency (LRT: $\chi^2 = 3.72$, $p = 0.054$) or herbivore access (LRT: $\chi^2 = 0.00$, $p = 1.00$; Table 1). Land-use history had a significant effect on the average probability of species presence ($\beta = -2.62$, SE = 0.87, $\chi^2 = 9.06$ $p = 0.003$) in that most species had a higher probability of being present in post-agricultural sites (Fig. 2). The average probability of species presence was also positively affected by soil N ($\beta = 0.05$, SE = 0.02, $\chi^2 = 4.36$, $p = 0.037$) and negatively affected by soil P ($\beta = -0.07$, SE = 0.02, $\chi^2 = 8.01$, $p = 0.005$). The interaction of fire and herbivore access significantly affected the average probability of species presence ($\beta = -1.15$, SE = 0.56, $\chi^2 = 4.19$, $p = 0.041$) such that herbivore exclosures only increased species presence when fire frequency was low, particularly in post-agricultural woodlands (Fig. 2). The interaction of soil N and access, the interaction of soil P and access, and the interaction of land-use history, fire, and access had no effect on average focal species presence (Appendix S4).

Discussion

In this study, we found that communities of deer-preferred plant species were impacted by both land-use history and herbivory, and the effects of herbivory on these plant species were contingent upon contemporary fire regime and land-use history. These findings have two broad implications for our understanding of trophic dynamics in the context of disturbance. First, our results demonstrate that agricultural legacies can lead to lasting patterns in contemporary deer-preferred plant communities. Second, contemporary disturbances, such as fire, can mediate the impacts of deer herbivory on plant communities. Finally, deer foraging behavior may provide a profitable means to understand large-scale variation in the strength of herbivory in shaping plant communities.

Past agricultural land use affects deer-preferred plant communities

We found that post-agricultural woodlands had more deer-preferred plant species present (i.e., greater species richness) than nonagricultural woodlands, regardless of fire frequency (Fig. 2). Land-use history also had a significant effect on focal plant community composition (Table 1). Long-term herbivore exclosures confirmed that the effects of past land use on focal species richness in frequently burned woodlands were not due to deer herbivory (Fig. 2). The importance of resource availability in modifying southeastern plant communities in post-agricultural woodlands is evidenced in past structural equation modeling (Veldman et al. 2014), and we found a significantly positive effect of soil N and P on focal plant species richness. We also found that soil P, but not soil N, was greater in post-agricultural woodlands (Appendix S3), indicating that soil P availability may mediate the effects of past land use on deer-preferred plant species. Past work in our study system has also shown that dispersal limitation is an important process contributing to differences in plant communities among post-agricultural and nonagricultural woodlands (Turley et al. 2017). While it is possible that differential invertebrate herbivory may explain these effects of past land use, past work in this ecosystem indicates that invertebrate herbivory of a suite of species different from those we measured (*Carphephorus bellidifolius, Sericocarpus tortifolius, Solidago nemoralis,* and *Solidago odora*) is greater in post-agricultural woodlands (Hahn and Orrock 2015a, 2016). If the effects of land-use history on species richness in frequently burned woodlands were produced by invertebrate herbivory, then we would have found greater forage richness in nonagricultural woodlands. As such, we posit that the effects of land-use history on the richness and community composition of focal plant species are a result of non-trophic mechanisms, such as nutrient availability and dispersal limitation. We also note that while we found increased deer-preferred species richness in post-agricultural woodlands, overall plant richness (Veldman et al. 2014), phylogenetic diversity (Turley and Brudvig 2016), and beta diversity (Grman et al. 2015) are all generally lower in post-agricultural woodlands in the southeast. These contrasting results in diversity likely arise due to our focus on deer-preferred plant species, many of which (e.g., *Desmodium* spp. and *Prunus* spp.) are associated with past agricultural land use (Turley and Brudvig 2016). As such, our results demonstrate a valuable role for post-agricultural woodlands: while these woodlands contain low-diversity plant communities, they are disproportionately rich in species that provide important forage for deer. These effects of land-use history on deer-preferred plant species richness may be of particular importance in the southeastern US where deer population declines are of concern to wildlife managers (Kilgo et al. 2010).

Effects of large-mammal herbivory are contingent upon disturbance regime

Our results also illustrate the important role of a contemporary disturbance, fire, in mediating the impacts of deer herbivory on deer-preferred plant species richness. While deer herbivory did not affect richness in frequently burned woodlands, herbivory significantly reduced the richness of deer-preferred plant species in with low fire frequencies (Fig. 2). Variation in the strength of top-down effects is sometimes attributed to variation in the ability of plants to tolerate herbivory (Hilbert et al. 1981, Maschinski and Whitham 1989, Pringle et al. 2007). Since we did not find a significant interaction between soil nutrients and herbivore access on the richness of deer-preferred species, we did not find evidence that differences in nutrient availability across habitat contexts mediated plant resistance to herbivory. Similar fire-contingent effects of large-mammal herbivory have been found in other systems (Royo et al. 2010, Burkepile et al. 2016, Crowther et al. 2016). Our study confirms the importance of contemporary fire in generating spatial variance in large-mammal herbivory while illuminating the important role of past land use in determining the community composition of plants preferred by large mammals. Importantly, our results indicate that the effects of fire frequency on deer herbivory are not consistent across woodlands with different land-use histories (Fig. 2): deer herbivory had largest effect on focal species richness in post-agricultural woodlands. This suggests that the effects of contemporary fire regime on herbivory may be predictably variable across landscapes containing habitats with different land-use histories. Hence, in order to understand contemporary patterns in plant communities and herbivory by large mammals, studies must consider how contemporary disturbance regimes overlap with the history of human activities across a landscape.

We hypothesize that a likely mechanism by which fire mediates the effects of deer herbivory on the richness of deer-preferred species is through deer behavioral responses to fire. Past work in this system has shown that frequent fire regimes increase deer visibility to predators (i.e., coyotes; Bartel and Orrock 2021) and that deer antipredator behavior responds accordingly to this fire-mediated change in predation risk (Bartel and Orrock 2021). Research at a nearby (~400 km) site found that deer vigilance (i.e., the proportion of time spent vigilant versus foraging) was greater in recently burned longleaf-pine woodlands with no documented agricultural legacies to our knowledge (Cherry et al. 2017). Work at our study site evaluating deer behavior across longleaf-pine woodlands with varying land-use histories found that deer vigilance increased with fire frequency in post-agricultural sites and found that deer used a more proactive antipredator behavior (avoiding risky high-fire sites at risky times) in nonagricultural woodlands, suggesting that deer may be most fearful of encountering a predator in frequently burned nonagricultural woodlands (Bartel and Orrock 2021). In finding that large-mammal herbivory is less impactful when fire is frequent, particularly in post-agricultural woodlands (Fig. 2), our results indicate that deer herbivory is most pronounced in habitats where deer perceive lower predation risk. Past work suggests that deer behavioral responses to predation risk can generate cascading effects of deer-preferred plant species in recently burned longleaf-pine woodlands (Cherry et al. 2016). Our implementation of long-term herbivore exclosures across sites with varying fire regimes provide some preliminary empirical support for the potential of behaviorally-mediated trophic cascades to occur in frequently-burned woodlands because we found no effect of deer herbivory in these woodlands.

Conclusions and Future Directions

As agricultural land abandonment increases and management practices that prescribe natural disturbance regimes are implemented to restore secondary lands (Hurtt et al. 2006, Brudvig et al. 2014, Veldman et al. 2014), studying the ways in which past and present disturbances transform trophic dynamics is increasingly relevant. In this study, we found that explaining contemporary patterns in plant communities requires an understanding of past land use, contemporary fire regime, and large-mammal foraging behavior. These findings highlight several areas of research that are profitable for further investigation. First, our findings show that deer herbivory only affects deer-preferred plant species richness when fire frequency is low, but it is unclear how fire regimes mediate the ability for plants to compensate for deer herbivory. While we did not find a significant effect of the interaction between soil nutrients and herbivore access on species richness, it is possible that other abiotic factors associated fire frequency may mediate plant susceptibility to herbivory. For example, light availability has been shown to mediate the susceptibility of other plant species consumed by grasshoppers (*Solidago nemoralis* and *S. odora*) in our study area (Hahn and Orrock 2015b), but no work has evaluated how changes in light availability due to fire might affect plant susceptibility to large-mammal herbivory in our system. Experiments that simulate herbivory on plants inside large-mammal exclosures across a gradient of fire regimes are needed to evaluate how disturbance mediates trophic dynamics in this context. Second, while our results show that six years of large-mammal exclusion can lead to significant increases in deer-preferred species richness, long-term herbivory by large mammals can have much broader effects on plant communities as a whole (Augustine and McNaughton 1998, Gómez 2005, Bernes et al. 2018). Future studies that manipulate large-mammal access for longer periods with frequent sampling throughout the experimental period may reveal new insights into how past land use, contemporary fire regime, and large-mammal herbivory affect plant communities over large timescales. Finally, while our results indicate that deer-preferred plant species are released from deer herbivory in frequently burned sites, the potential for this to be a consequence of a behaviorally-mediated trophic cascade requires further investigation. Experiments that manipulate herbivore access and predator presence (or predator cues) across sites varying in fire frequency and land-use history will elucidate the roles of predation risk and historic disturbance in generating trophic cascades.

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References

Agrawal, A. A., A. P. Hastings, M. T. J. Johnson, J. L. Maron, and J. P. Salminen. 2012. Insect herbivores drive real-time ecological and evolutionary change in plant populations. Science 338:113–116.

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. The Journal of Wildlife Management 62:1165–1183.

Barrios-Garcia, M. N., and S. A. Ballari. 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biological Invasions 14:2283–2300.

Bartel, S. L., and J. L. Orrock. 2021. Past agricultural land use affects multiple facets of ungulate antipredator behavior. Behavioral Ecology 32:961–969.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Belsky, A. J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. Journal of Vegetation Science 3:187–200.

Bernes, C., B. Macura, B. Gunnar Jonsson, K. Junninen, J. Müller, J. Sandström, A. Lõhmus, and E. Macdonald. 2018. Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review. Environmental Evidence 7.

Borer, E. T., W. S. Harpole, P. B. Adler, C. A. Arnillas, M. N. Bugalho, M. W. Cadotte, M. C.

Caldeira, S. Campana, C. R. Dickman, T. L. Dickson, I. Donohue, A. Eskelinen, J. L. Firn, P. Graff, D. S. Gruner, R. W. Heckman, A. M. Koltz, K. J. Komatsu, L. S. Lannes, A. S. MacDougall, J. P. Martina, J. L. Moore, B. Mortensen, R. Ochoa-Hueso, H. Olde Venterink, S. A. Power, J. N. Price, A. C. Risch, M. Sankaran, M. Schütz, J. Sitters, C. J. Stevens, R. Virtanen, P. A. Wilfahrt, and E. W. Seabloom. 2020. Nutrients cause grassland biomass to outpace herbivory. Nature Communications 2020 11:1 11:1–8.

Brown, J. H., and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. Science 250:1705–1707.

Brudvig, L. A., and E. I. Damschen. 2011. Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. Ecography 34:257–266.

Brudvig, L. A., E. Grman, C. W. Habeck, J. L. Orrock, and J. A. Ledvina. 2013. Strong legacy of agricultural land use on soils and understory plant communities in longleaf pine woodlands. Forest Ecology and Management 310:944–955.

Brudvig, L. A., J. L. Orrock, E. I. Damschen, C. D. Collins, P. G. Hahn, W. B. Mattingly, J. W. Veldman, and J. L. Walker. 2014. Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities. PLoS ONE 9:e86604.

Brudvig, L. A., N. E. Turley, S. L. Bartel, L. Bell-Dereske, S. Breland, E. I. Damschen, S. E. Evans, J. Gibbs, P. G. Hahn, R. Isaacs, J. A. Ledvina, J. L. Orrock, Q. M. Sorenson, and J. D. Stuhler. 2021. Large ecosystem-scale effects of restoration fail to mitigate impacts of land-use legacies in longleaf pine savannas. Proceedings of the National Academy of Sciences 118.

Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6:1–15.

Burkepile, D. E., D. I. Thompson, R. W. S. Fynn, S. E. Koerner, S. Eby, N. Govender, N. Hagenah, N. P. Lemoine, K. J. Matchett, K. R. Wilcox, S. L. Collins, K. P. Kirkman, A. K. Knapp, and M. D. Smith. 2016. Fire frequency drives habitat selection by a diverse herbivore guild impacting top–down control of plant communities in an African savanna. Oikos 125:1636–1646.

Cherry, M. J., R. J. Warren, and L. M. Conner. 2016. Fear, fire, and behaviorally mediated trophic cascades in a frequently burned savanna. Forest Ecology and Management 368:133–139.

Cherry, M. J., R. J. Warren, and L. M. Conner. 2017. Fire-mediated foraging tradeoffs in white-tailed deer. Ecosphere 8:e01784.

Cochrane, M. A., A. Alencar, M. D. Schulze, C. M. Souza, D. C. Nepstad, P. Lefebvre, and E. A. Davidson. 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science 284:1832–1835.

Connolly, B. M., J. L. Orrock, and M. S. Witter. 2016. Soil conditions moderate the effects of herbivores, but not mycorrhizae, on a native bunchgrass. Acta Oecologica 77:100–108.

Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113–147.

Cothran, E. G., M. H. Smith, J. O. Wolff, and J. B. Gentry. 1991. Mammals of the Savannah River Site. SRO-NERP-21, Aiken, SC: Savannah River Site.

Crowther, M. S., G. Ortac, S. Pedersen, and C. Mcarthur. 2016. Interactions between fire and introduced deer herbivory on coastal heath vegetation. Austral Ecology 41:604–612.

Culbert, P. D., I. Dorresteijn, J. Loos, M. K. Clayton, J. Fischer, and T. Kuemmerle. 2017. Legacy effects of past land use on current biodiversity in a low-intensity farming landscape in Transylvania (Romania). Landscape Ecology 32:429–444.

Dahnke, W. C., and G. V. Johnson. 2018. Testing soils for available nitrogen. Pages 127–139 *in* R. L. Westerman, editor. Soil Testing and Plant Analysis. John Wiley & Sons, Ltd, Hoboken, NJ, US.

Daskin, J. H., M. Stalmans, and R. M. Pringle. 2016. Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. Journal of Ecology 104:79–89.

Donihue, C. M., L. M. Porensky, J. Foufopoulos, C. Riginos, and R. M. Pringle. 2013. Glade cascades: indirect legacy effects of pastoralism enhance the abundance and spatial structuring of arboreal fauna. Ecology 94:827–837.

Edwards, J., M. Ford, and D. Guynn. 1961. American Wildlife & Plants: A Guide to Wildlife Food Habits : the Use of Trees, Shrubs, Weeds, and Herbs by Birds and Mammals of the United States. Reprint Ed. Dover Publications, Mineola, NY.

Flannigan A, M. D., M. A. Krawchuk B, W. J. de Groot A, B. A. Mike Wotton, and L. M. Gowman A. 2009. Implications of changing climate for global wildland fire. International Journal of Wildland Fire 18:483–507.

Flinn, K. M., and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3:243–250.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J.

Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science 309:570–574.

Ford, A. T., J. R. Goheen, T. O. Otieno, L. Bidner, L. A. Isbell, T. M. Palmer, D. Ward, R. Woodroffe, and R. M. Pringle. 2014. Large carnivores make savanna tree communities less thorny. Science 346:346–9.

Foster, D. R. 1993. Land-use History and Forest Transformations in Central New England. Pages 91–110 Humans as Components of Ecosystems. Springer New York, New York, NY.

Frost, C. 2006. History and Future of the Longleaf Pine Ecosystem. Pages 9–48 *in* S. Jose, E. J. Jokela, and D. L. Miller, editors. The Longleaf Pine Ecosystem. Springer-Verlag New York, New York, NY.

Goheen, J. R., D. J. Augustine, K. E. Veblen, D. M. Kimuyu, T. M. Palmer, L. M. Porensky, R. M. Pringle, J. Ratnam, C. Riginos, M. Sankaran, A. T. Ford, A. A. Hassan, R. Jakopak, T. R. Kartzinel, S. Kurukura, A. M. Louthan, W. O. Odadi, T. O. Otieno, A. M. Wambua, H. S. Young, and T. P. Young. 2018. Conservation lessons from large-mammal manipulations in East African savannas: the KLEE, UHURU, and GLADE experiments Large mammal manipulations in Laikipia, Kenya. Annals of the New York Academy of Sciences 1429:31–49.

Gómez, J. M. 2005. Long-term effects of ungulates on performance, abundance, and spatial distribution of two montane herbs. Ecological Monographs 75:231–258.

Grman, E., J. L. Orrock, C. W. Habeck, J. A. Ledvina, L. A. Brudvig, E. Grman, C. W. Habeck, J. A. Ledvina, and L. A. Brudvig. 2015. Altered beta diversity in post-agricultural woodlands: two hypotheses and the role of scale. Ecography 38:614–621.

Hahn, P. G., and J. L. Orrock. 2015a. Land-use legacies and present fire regimes interact to mediate herbivory by altering the neighboring plant community. Oikos 124:497–506.

Hahn, P. G., and J. L. Orrock. 2015b. Spatial arrangement of canopy structure and land-use history alter the effect that herbivores have on plant growth. Ecosphere 6:Article 193.

Hahn, P. G., and J. L. Orrock. 2016. Neighbor palatability generates associational effects by altering herbivore foraging behavior. Ecology 97:2103–2111.

Hansen, W. D., K. H. Braziunas, W. Rammer, R. Seidl, and M. G. Turner. 2018. It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99:966–977.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984–2010). Landscape Ecology 31:2367–2383.

Hilbert, D. W., D. M. Swift, J. K. Detling, and M. I. Dyer. 1981. Relative growth rates and the grazing optimization hypothesis. Oecologia 51:14–18.

Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution 24:599–605.

Holdo, R. M., A. R. E. Sinclair, A. P. Dobson, K. L. Metzger, B. M. Bolker, M. E. Ritchie, and R. D. Holt. 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. PLoS Biology 7:e1000210.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics 22:477–503.

Hurtt, G. C., S. Frolking, M. G. Fearon, B. Moore, E. Shevliakovas, S. Malyshev, S. W. Pacala, and R. A. Houghton. 2006. The underpinnings of land-use history: Three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. Global

Change Biology 12:1208–1229.

Jackson, M. M., M. G. Turner, S. M. Pearson, and A. R. Ives. 2012. Seeing the forest and the trees: multilevel models reveal both species and community patterns. Ecosphere 3:art79.

Kilgo, J., and J. I. Blake, editors. 2005. Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site. Island Press, Washington, DC, USA.

Kilgo, J. C., H. S. Ray, C. Ruth, and K. V. Miller. 2010. Can coyotes affect deer populations in southeastern North America? Journal of Wildlife Management 74:929–933.

Kleinman, J. S., J. D. Goode, A. C. Fries, and J. L. Hart. 2019. Ecological consequences of compound disturbances in forest ecosystems: a systematic review. Ecosphere 10:e02962.

Kopecký, M., and J. Vojta. 2009. Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. Applied Vegetation Science 12:251–260.

Lashley, M. A., M. Colter Chitwood, C. A. Harper, C. S. Deperno, and C. E. Moorman. 2015. Variability in fire prescriptions to promote wildlife foods in the longleaf pine ecosystem. Fire Ecology 11.

Loughnan, D., and J. L. Williams. 2019. Climate and leaf traits, not latitude, explain variation in plant-herbivore interactions across a species' range. Journal of Ecology 107:913–922.

Lucash, M. S., R. M. Scheller, B. R. Sturtevant, E. J. Gustafson, A. M. Kretchun, and J. R. Foster. 2018. More than the sum of its parts: how disturbance interactions shape forest dynamics under climate change. Ecosphere 9:e02293.

Maron, J. L., and E. Crone. 2006. Herbivory: effects on plant abundance, distribution and population growth. Proceedings of the Royal Society B 273:2575–2584.

Maschinski, J., and T. G. Whitham. 1989. The continuum of plant responses to herbivory: The influence of plant association, nutrient availability, and timing. The American Naturalist

134.

Mattingly, W. B., J. L. Orrock, C. D. Collins, L. A. Brudvig, E. I. Damschen, J. W. Veldman, and J. L. Walker. 2015. Historical agriculture alters the effects of fire on understory plant beta diversity. Oecologia 177:507–518.

McCormick, A. R., J. S. Phillips, and A. R. Ives. 2019. Responses of benthic algae to nutrient enrichment in a shallow lake: Linking community production, biomass, and composition. Freshwater Biology 64:1833–1847.

McNaughton, S. J. 1979. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. The American Naturalist 113:691–703.

Mehlich, A. 2008. Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. Communications in Soil Science and Plant Analysis 15:1409–1416.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327–366.

Miller, J. H., and K. V. Miller. 2005. Forest Plants of the Southeast and Their Wildlife Uses. Revised Ed. University of Georgia Press, Athens, GA.

Mouillot, F., and C. B. Field. 2005. Fire history and the global carbon budget: a 1°× 1° fire history reconstruction for the 20th century. Global Change Biology 11:398–420.

Norden, H., and K. Kirkman. 2006. Field Guide to Common Legume Species of the Longleaf Pine Ecosystem. Joseph W. Jones Ecological Research Center.

Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology & Evolution 13:261–265.

Orrock, J., E. Damschen, L. Brudvig, and J. Walker. 2015. Developing and Testing a Robust, Multi-scale Framework for the Recovery of Longleaf Pine Understory Communities

SERDP Project RC-1695.

Prendeville, H. R., J. C. Steven, and L. F. Galloway. 2015. Spatiotemporal variation in deer browse and tolerance in a woodland herb. Ecology 96:471–478.

Prichard, S. J., C. S. Stevens-Rumann, and P. F. Hessburg. 2017. Tamm review: Shifting global fire regimes: Lessons from reburns and research needs. Forest Ecology and Management 396:217–233.

Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. Mccauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. Proceedings of the National Academy of Sciences 104:193–197.

Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181:165–176.

Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology 91:93–105.

Schütz, M., A. C. Risch, E. Leuzinger, B. O. Krüsi, and G. Achermann. 2003. Impact of herbivory by red deer (*Cervus elaphus* L.) on patterns and processes in subalpine grasslands in the Swiss National Park. Forest Ecology and Management 181:177–178.

Turley, N. E., and L. A. Brudvig. 2016. Agricultural land-use history causes persistent loss of plant phylogenetic diversity. Ecology 97:2240–2247.

Turley, N. E., J. L. Orrock, J. A. Ledvina, and L. A. Brudvig. 2017. Dispersal and establishment limitation slows plant community recovery in post-agricultural longleaf pine savannas. Journal of Applied Ecology 54:1100–1109.

Veldman, J. W., L. A. Brudvig, E. I. Damschen, J. L. Orrock, W. B. Mattingly, and J. L. Walker.

2014. Fire frequency, agricultural history and the multivariate control of pine savanna understorey plant diversity. Journal of Vegetation Science 25:1438–1449.

Virtanen, R., H. Henttonen, and K. Laine. 1997. Lemming grazing and structure of a snowbed plant community: A long-term experiment at Kilpisjärvi, Finnish Lapland. Oikos 79:155–166.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science 277:3–13.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48:607–615.

Winnie, J. A. 2012. Predation risk, elk, and aspen: Tests of a behaviorally mediated trophic cascade in the Greater Yellowstone Ecosystem. Ecology 93:2600–2614.

Tables and figures

Table 1. Random effect coefficients by plant species from the MLM. Coefficients are the random effect plus the fixed effect estimate in order to account for the mean slope. For each species, the predictor variable with the largest effect is bolded.

				Fire frequency		Land-use history		Herbivore access	
Forage species	Family	Form	Life cycle	High	Low	Post-ag	Non-ag	Exclosure	Open
Centrosema virginianum	Fabacaea	Forb, legume	Perennial	0.62343	-0.26463	0.39609	**-2.10535**	0.00067	-0.00068
Chamaechrista fasciculata	Fabacaea	Forb, legume	Annual	0.05010	-0.02127	0.17728	**-0.94227**	0.00001	-0.00001
Chamaechrista nictitans	Fabacaea	Forb, legume	Annual	-0.36446	0.15470	0.15981	**-0.84945**	-0.00028	0.00028
Cnidoscolus stimulosus	Euphorbiac	Forb, nettle	Perennial	0.19312	-0.08198	-0.16051	**0.85317**	0.00006	-0.00006
Desmodium spp.	Fabacaea	Forb, legume	Perennial	0.54577	-0.23167	0.43252	**-2.29898**	-0.00069	0.00071
Galactia spp.	Fabacaea	Forb, legume	Perennial	0.33721	-0.14314	-0.21604	**1.14829**	-0.00026	0.00027
Prunus spp.	Rosaceae	Hardwood, fleshy fruit	Perennial	-0.01597	0.00678	-0.32864	**1.74683**	0.00107	-0.00109
Quercus spp.	Fagaceae	Hardwood, hard mast	Perennial	-0.75538	0.32064	-0.62381	**3.31569**	0.00003	-0.00003
Rhyncosia reniformis	Fabacaea	Forb, legume	Perennial	-0.12137	0.05152	0.16340	**-0.86853**	-0.00011	0.00012
Rubus spp.	Rosaceae	Shrub, fleshy fruit	Perennial	0.14661	-0.06223	0.15975	**-0.84910**	0.00019	-0.00019
Smilax spp.	Smilacacea	Vine	Perennial	**-0.35267**	0.14970	-0.04603	0.24465	-0.00033	0.00033
Vitis spp.	Vitaceae	Vine	Perennial	-0.28638	0.12156	-0.11384	**0.60507**	-0.00035	0.00035

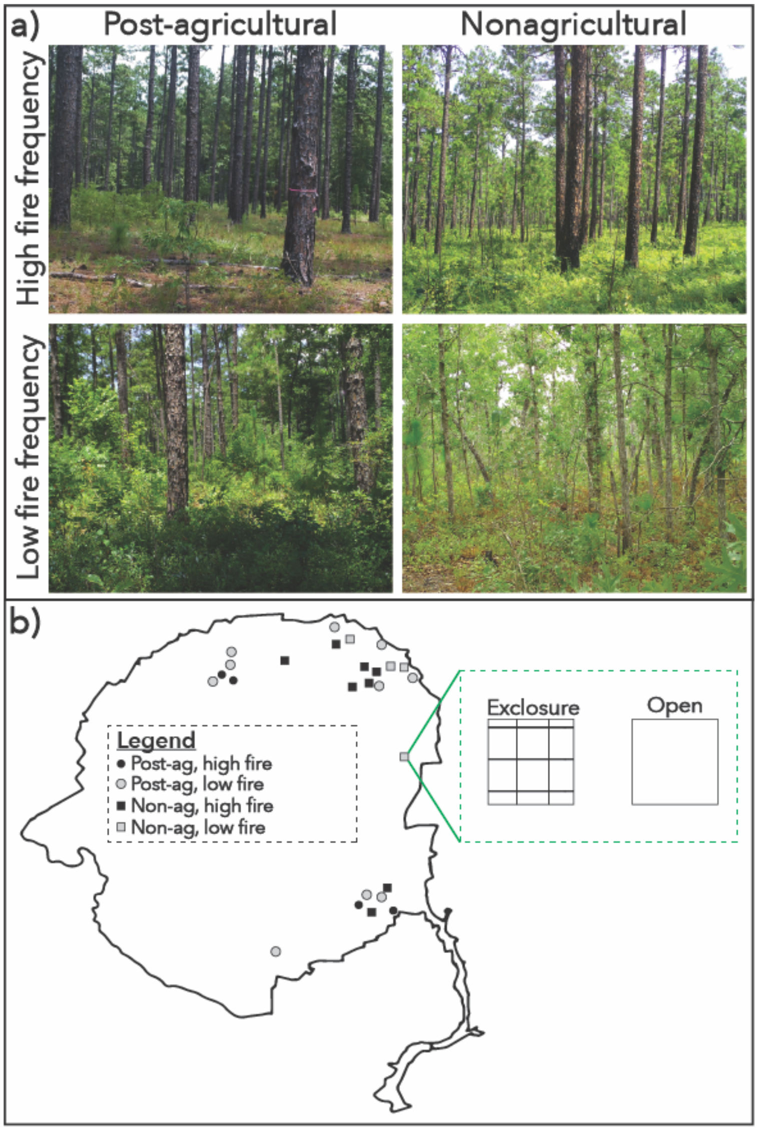

Figure 1. We conducted our experiment at 26 longleaf pine woodlands within the Savannah River Site (SRS) near Aiken, SC, USA. **a)** Woodlands were classified by past land use and contemporary fire frequency. The images above were captured within our sites during the experimental period and are representative of the variation in habitat across the different disturbance contexts. **b)** SRS is an ~80,000-ha area, and sites were stratified across SRS. At each site, paired plots were established to manipulate large-mammal herbivore access.

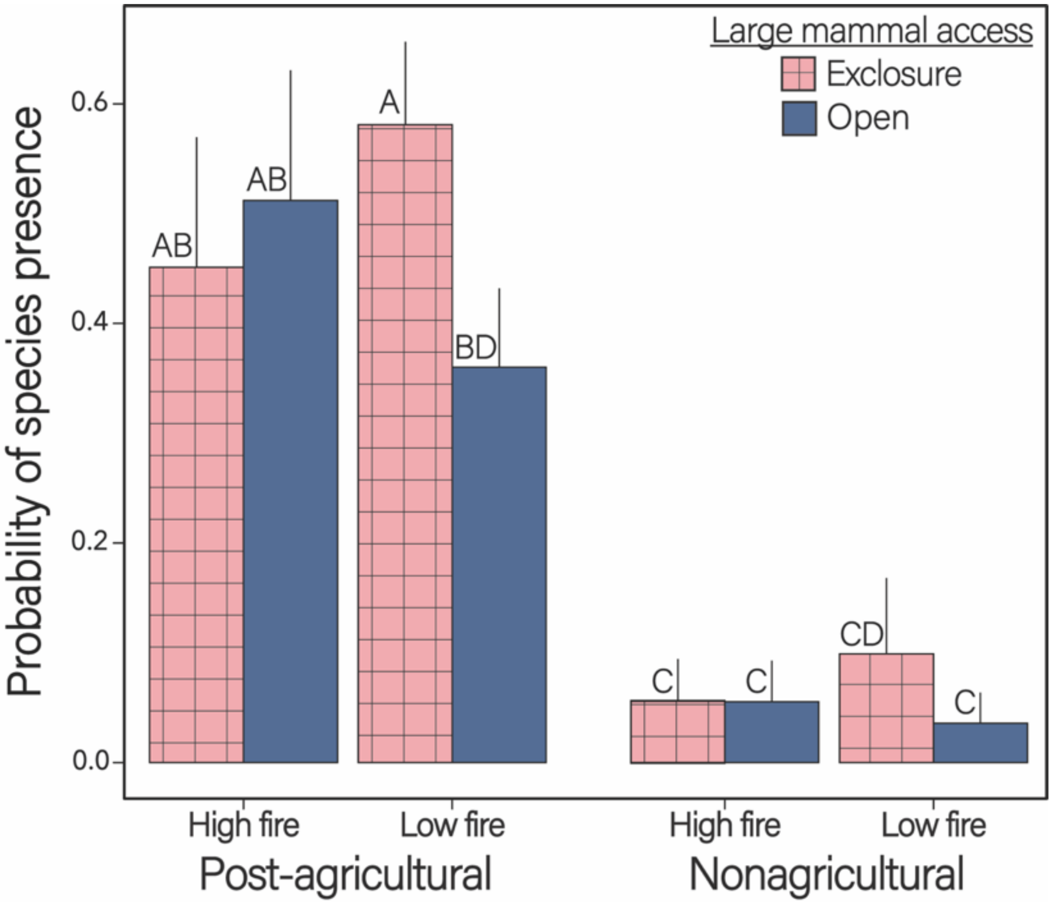

Figure 2. Land-use history and the interaction of fire frequency and herbivore exclusion had significant effects on the mean probability of deer-preferred species presence. The probability of species presence was greater in post-agricultural woodlands than in nonagricultural woodlands. Large-mammal herbivore access only significantly decreased the probability of species presence in post-agricultural woodlands with low fire frequencies. There was no effect of herbivore access in woodlands with high fire frequencies. Different letters represent group means that are significantly different ($P < 0.05$ using sequential Benjamini-Hochberg correction; Benjamini & Hochberg 1995). Error bars represent standard error.

Appendix S1. Deer-preferred plant species list.

We constructed a list of deer-preferred plant species in the southeastern US by referencing both understory plant identification manuals (Edwards et al. 1961, Miller and Miller 2005, Norden and Kirkman 2006) and peer-reviewed literature (Lashley et al. 2015, Cherry et al. 2016).

Acalypha rhomboidei
Acer spp.
Ambrosia spp.
Callicarpa spp.
Centrosema virginiana
Chamaechrista fasciculata
Chamaechrista nictitans
Clitoria mariana
Cnidosculus stimulosus
Desmodium spp.
Galactia spp.
Gleditsia spp.
Lespedeza spp.
Lupinus spp.
Magnolia spp.
Phytolacca americana
Prunus spp.
Rhynchosia reniformis
Rubus spp.
Smilax spp.
Tephrosia virginiana
Vitis spp.

References

Cherry, M. J., R. J. Warren, and L. M. Conner. 2016. Fear, fire, and behaviorally mediated trophic cascades in a frequently burned savanna. Forest Ecology and Management 368:133–139.

Edwards, J., M. Ford, and D. Guynn. 1961. American Wildlife & Plants: A Guide to Wildlife Food Habits : the Use of Trees, Shrubs, Weeds, and Herbs by Birds and Mammals of the United States. Reprint Ed. Dover Publications, Mineola, NY.

Lashley, M. A., M. Colter Chitwood, C. A. Harper, C. S. Deperno, and C. E. Moorman. 2015. Variability in fire prescriptions to promote wildlife foods in the longleaf pine ecosystem. Fire Ecology 11.

Miller, J. H., and K. V. Miller. 2005. Forest Plants of the Southeast and Their Wildlife Uses. Revised Ed. University of Georgia Press, Athens, GA.

Norden, H., and K. Kirkman. 2006. Field Guide to Common Legume Species of the Longleaf Pine Ecosystem. Joseph W. Jones Ecological Research Center.

Appendix S2. Relationship between deer-preferred species richness and species abundance.

Methods: In June 2010, we collected pre-treatment data on baseline plant communities at all 4 plots within each of our 26 sites (Orrock et al. 2015). Within the 3.16 x 3.16 m center of each plot, we recorded the presence and percent cover of plant species. In order to test if deer-preferred plant species richness was positively correlated with species abundance, we constructed a linear mixed-effects model with total percent ground cover of deer-preferred species as a response variable; species richness, land-use history, fire frequency, and the interaction of land-use history and fire as fixed effects; and site as a random intercept.

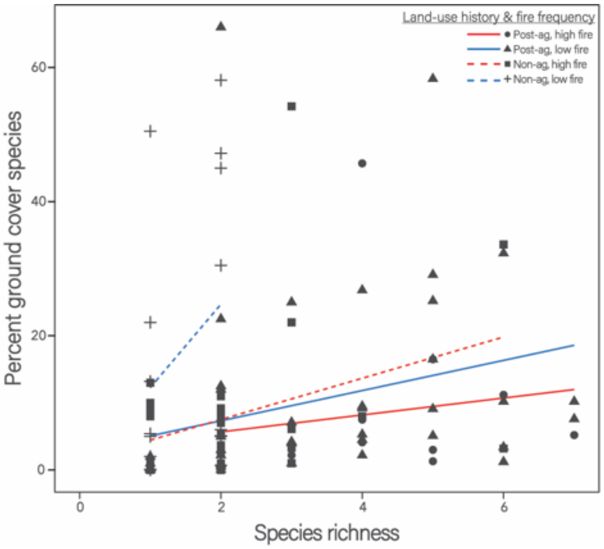

Figure S2. Species richness of deer-preferred plants had a significantly positive relationship with percent ground cover of deer-preferred plants ($F_{1,103} = 4.78$, $p = 0.03$). We did not detect an effect of land-use history, fire frequency, or the interaction of land-use history and fire on percent ground cover of deer-preferred species.

References

Orrock, J., E. Damschen, L. Brudvig, and J. Walker. 2015. Developing and Testing a Robust, Multi-scale Framework for the Recovery of Longleaf Pine Understory Communities SERDP Project RC-1695.

Appendix S3. The effects of land-use history and fire on soil nutrients.

Methods: We evaluated the effects of land-use history and fire frequency on soil N and soil P at the site level using two separate linear models for N and P. For each model, land-use history, fire frequency, and the interaction of land-use history and fire were fixed effects. Soil N and soil P were used as response variables.

Table S1. Results from the two linear models evaluating the effects of land-use history and fire frequency on soil N and soil P.

	Soil N				Soil P			
	β	SE	F	P-value	β	SE	F	P-value
Land-use history	1.17	5.56	0.04	0.836	-11.33	5.33	4.53	0.045
Fire frequency	-8.52	5.35	2.53	0.126	-1.97	5.13	0.15	0.704
Land-use x fire	0.02	7.34	0.00	0.998	-1.28	7.03	0.03	0.857

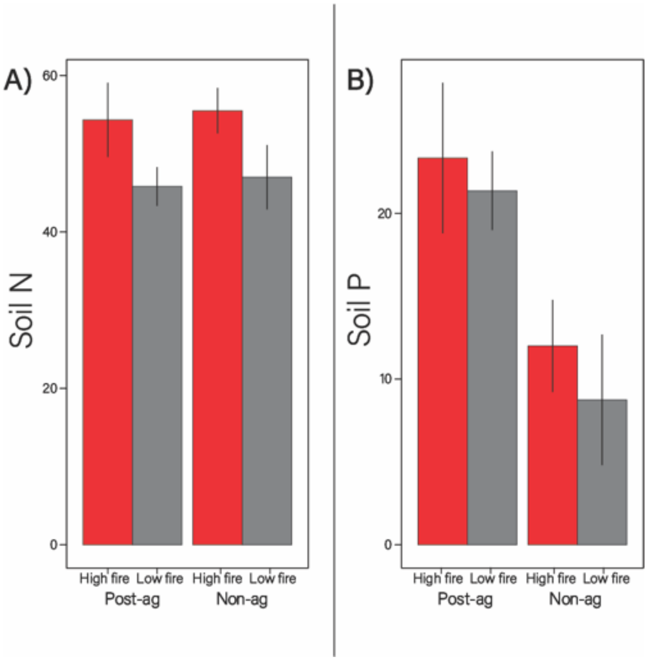

Figure S2. We did not detect an effect of land-use history or fire frequency on soil N. Soil P was significantly higher in post-agricultural woodlands than in nonagricultural woodlands, and there was no effect of fire frequency.

Appendix S4. The effects of land-use history, fire, herbivore access, and soil nutrients on the average probability of focal species presence.

Table S2. Results from the MLM evaluating the effects of land-use history, fire frequency, herbivore access, soil N, and soil P on focal species presence. Significant fixed effects ($p < 0.05$) are marked with asterisks.

	β	SE	X^2	P-value	
Land-use history	-2.62	0.87	9.06	0.003	*
Fire frequency	0.52	0.58	0.82	0.365	
Herbivore access	0.90	1.66	0.29	0.590	
N	0.05	0.02	4.36	0.037	*
P	-0.07	0.02	8.01	0.005	*
Land-use x fire	0.09	0.78	0.01	0.911	
Land-use x access	-0.26	0.63	0.18	0.675	
Fire x access	-1.15	0.56	4.19	0.041	*
Access x N	-0.02	0.03	0.65	0.419	
Access x P	0.03	0.03	1.22	0.270	
Land-use x fire x access	0.08	0.90	0.01	0.929	

CHAPTER 4

White-tailed deer responses to acoustic predator cues are contingent upon past land use and contemporary fire regime

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Abstract: Prey can assess immediate risk of predation by detecting cues of predator presence, and it is expected that prey should invest in costly antipredator behaviors when a cue of predator presence is detected. Features of the habitat in which the cue is detected, such as vegetative concealment, serve as indirect cues of risk and can mediate how prey respond to direct cues of predator presence. Past agricultural land use and contemporary fire regime are common disturbances that may modify prey perceptions of risk and could therefore alter prey responses to direct cues of predator presence. We examined whether variation in these two disturbance regimes generates predictable variation in white-tailed deer (*Odocoileus virginianus*) responses to cues of predator presence by using cameras to measure deer vigilance and foraging bout duration in response to coyote (*Canis latrans*) vocalizations across 20 longleaf pine woodlands that vary in past land use and contemporary fire regime. Frequent fire regimes consistently increased deer visibility to predators across both land-use history contexts. Deer exhibited no

behavioral response to the predator cue in habitats containing infrequent fire regimes or agricultural legacies and only responded to the cue in frequently burned woodlands without agricultural legacies through increased vigilance and duration spent at a foraging location. These findings not only reveal that land-use legacies and contemporary fire regimes can mediate how prey respond to direct cues of risk, but they also show how prey may balance the urgency with the uncertainty of a potential predator encounter through vigilance and remaining in place to acquire adequate information to launch an appropriate defense.

Introduction

Predation is among the strongest selection pressures that determine animal behavior (Lima 1998); consequently, many prey species exhibit a suite of adaptive antipredator behaviors to mitigate predation risk (Lima and Dill 1990, Caro 2005). Since antipredator behaviors entail costs (e.g., time, energy, or missed opportunities; Lind and Cresswell 2005, Preisser et al. 2005, Verdolin 2006, Zanette et al. 2011, LaManna and Martin 2016), prey may use cues from the environment to determine when to engage in potentially costly antipredator behaviors. Prey should use direct cues of predator presence (i.e., visual, olfactory, or acoustic cues) to evaluate the likelihood of a predator attack and modulate investment in antipredator behavior accordingly (Kats and Dill 1998, Brown 1999, Brown et al. 1999, Hettena et al. 2014, Weissburg et al. 2014). The ability for prey to detect and aptly respond to direct predator cues is particularly important in the context of global change (Guiden et al. 2019). For example, failing to respond to a direct cue of predator presence can lead to reduced survival and extinction, as has been repeatedly observed in naïve, insular prey populations when predators are introduced (Savidge 1987, Blackburn et al. 2004, Roehmer et al. 2009, Hanna and Cardillo 2014) as well as in the case of predator reintroductions (Olivier et al. 2001). In dynamic landscapes where predation risk varies across space and time, the utilization of antipredator behavior can be variable across different habitat contexts (Brown et al. 1999, Orrock et al. 2004, Hernández and Laundré 2005, Kohl et al. 2018, Gaynor et al. 2019). The primacy of habitat context in modifying prey responses to direct cues of risk is critical because global changes, such as habitat fragmentation, exotic plant species, and altered disturbance regimes, may lead to significant changes in the habitats where predator-prey interactions occur, potentially modifying how prey respond to direct cues (Guiden et al. 2019). For example, recent work demonstrates that past and present disturbances modify prey antipredator behavior (Bartel and Orrock 2021); however, it is unclear if prey responses to predator cues depend upon past and present disturbance regimes of the habitat in which the cue is detected.

In addition to direct cues of predator presence, prey also use indirect cues of risk (e.g., habitat structure) informing the probability of predator encounter, detection, or escape from attack (Orrock et al. 2004, Parsons and Blumstein 2010, Gaynor et al. 2019). Since prey use many different types of information to assess risk, our understanding of the context-specificity of antipredator behavior requires embracing how context affects different types of cues. Importantly, the use of different cues is itself context specific, as prey should employ the cues that provide the most reliable information about imminent risk, which may differ depending upon characteristics of the habitat (Stankowich and Blumstein 2005, Griesser and Nystrand 2009, Parsons and Blumstein 2010, Morrison 2011, Nersesian et al. 2012, McCormick and Löonnstedt 2013) or characteristics of the cue (Kats and Dill 1998, Orrock et al. 2004, Hettena et al. 2014, Weissburg et al. 2014, Scherer and Smee 2016, Parsons et al. 2017). Although recent studies demonstrate how disturbance may affect indirect cues (McCormick and Löonnstedt 2013, Cherry et al. 2017, Spitz et al. 2018, Bartel and Orrock 2021), it is not clear whether the same disturbances affect how prey use direct cues. This is an important gap in our knowledge of animal behavior because the overall response to risk is a function of both cue types. For example, antipredator responses may be exacerbated when indirect and direct cues work in synergy, or they may be abated when indirect and direct cues work in opposition (Grostal and Dicke 1999, Parsons and Blumstein 2010, Morrison 2011, Nersesian et al. 2012, Farnworth et al. 2020). It is therefore critical to understand how disturbance affects antipredator responses to both indirect and direct cues of risk.

Past agricultural land use and contemporary fire are two common forms of disturbance that modify terrestrial habitat structure relevant to indirect cues of risk for large-mammal prey species. Fire can cause significant and rapid changes in large-mammal habitat structure by removing woody, midstory cover (Eisenberg et al. 2015, Cherry et al. 2017, Jorge et al. 2020, Bartel and Orrock 2021). Frequent fires can thereby increase perceived predation risk for large mammals that are prey to visual, cursorial predators (Cherry et al. 2017, Bartel and Orrock 2021). Moreover, fire often occurs in terrestrial habitats containing legacies of past disturbances, such as agricultural land use, which could alter the effects of fire on animal behavior. Legacies of past agricultural land use are pervasive: since 1700, agriculture has impacted 42-68% of terrestrial land, and degraded lands previously used for agriculture increased by 10-44x10^6 km^2 (Hurtt et al. 2006). Agricultural legacies can have lasting effects on plant communities that persist for decades and sometimes centuries (Foster 1993, Flinn and Vellend 2005, Kopecký and Vojta 2009, Mattingly et al. 2015, Culbert et al. 2017), and agricultural legacies can influence animal responses to contemporary disturbances (Hahn and Orrock 2015a, 2015b, Stuhler and Orrock 2016, Bartel and Orrock 2020).

Given the potential for agricultural legacies and contemporary fire regime to drastically alter the context in which large-mammal predator-prey interactions occur, it is likely that prey will exhibit predictably different responses to direct cues of predation risk across habitats with different land-use histories and fire regimes. For example, recent work in longleaf pine woodlands has found that white-tailed deer utilize different forms of antipredator behavior in post-agricultural woodlands than in woodlands without agricultural histories when responding to changes in perceived predation risk caused by fire (Bartel and Orrock 2021). Despite the consistent suppressive effects of frequent fires on vegetation cover, an indirect cue of risk, deer mitigated the increased risk from frequent fires through heightened vigilance in post-agricultural woodlands and shifts in activity timing (i.e., temporal predator avoidance) in nonagricultural woodlands (Bartel and Orrock 2021). Since temporal avoidance is a proactive antipredator behavior (i.e., one that may be used to avoid an encounter altogether) and vigilance is a reactive behavior to detect a predator once an encounter has occurred (Broekhuis et al. 2013, Creel et al. 2014), these findings indicate that deer perceive post-agricultural woodlands as generally less riskier spaces for encountering a predator. Despite evidence that agricultural legacies and contemporary fire regime have significant effects on deer perceptions of risk, no research has investigated if the interface of these two disturbances affects how deer respond to direct cues of predator activity. While this lacuna exists because of the difficulty in replicating large-scale experiments in habitats with known land-use histories and fire regimes and no other environmental differences (Flinn and Vellend 2005), it impedes our ability to predict how global shifts in disturbance frequency might alter predator-prey dynamics that determine species coexistence or extinction (Guiden et al. 2019).

In order to experimentally test if agricultural legacies and contemporary fire regime affect deer perceptions of risk, we evaluated deer antipredator responses to predator vocalizations (*Canis latrans*) across longleaf pine woodlands varying in both land-use history and fire regime (Fig. 1). In longleaf pine woodlands, coyote activity and predation affect deer behavior and population dynamics (Kilgo et al. 2012, Cherry et al. 2015, 2016, 2017, Chitwood et al. 2015, Gulsby et al. 2017). We deployed motion-activated cameras to measure how deer activity, vigilance, and foraging bout duration responded to acoustic cues of coyote presence under different disturbance contexts, evaluating two hypotheses: 1) deer only exhibit heightened vigilance in response to coyote vocalizations in frequently burned, nonagricultural woodlands, and 2) deer foraging bout duration will also decrease in response to coyote vocalization in frequently burned, nonagricultural woodlands in order to reduce the likelihood of a coyote encounter.

Methods

Study area

We conducted this experiment at the Savannah River Site (SRS; Aiken, SC), an ~80,000-ha National Environmental Research Park. SRS is located in the historic range of the longleaf pine ecosystem, much of which was converted to tillage agriculture between 1856 and 1950 (Frost 2006). Agricultural lands in SRS were small and dispersed, which created heterogeneous landscapes containing a mixture of patches of tilled farmland and intact forests (Kilgo and Blake 2005). When SRS was established in 1951, agricultural fields were abandoned and were planted in longleaf and loblolly pine by the US Forest Service, which has managed them since (Kilgo and Blake 2005). We selected 20 longleaf-pine woodland sites, spanning an 807-km^2 area, that differed in land-use history and fire frequency. We classified site land-use history based on aerial photography captured before land abandonment in 1951. We classified sites that were forested at the time as "nonagricultural woodlands" and sites that were farmland as "post-agricultural woodlands." We used annual fire records to determine the number of fires at each site since 1991. Sites were classified as high (5 or more burns) or low (less than 5 burns) fire frequency. This classification scheme was used to characterize these sites based on plant-community characteristics (Brudvig et al. 2014) and has been used in past studies investigating the effects of fire frequency on deer behavior (Bartel and Orrock *in review*). This site classification by land-use history and fire frequency resulted in four distinct habitat types (5 site replicates of each) equally distributed across the study area (Fig. 1).

Playback experiment

At each of our 20 sites, we deployed an infrared motion-activated camera trap for the same 12-day period in July 2019. This is within the range of typical study durations for field-based, playback experiments at single site (1-14 days; Pusenius and Ostfeld 2000, A. Schmidt 2006, Smith et al. 2017, Suraci et al. 2017, 2019). During this 12-day period, each site was exposed to three playback treatments, which were each deployed for 4 days: coyote calls (predator cue), pied butcherbird song (control sound), and silence. The pied butcherbird has been used as a control sound in past work examining ungulate responses to coyote cues because its low frequency is similar to that of a coyote call (Hettena et al. 2014). Since the pied butcherbird is native to Australia, it also represents a novel stimulus, allowing for us to disentangle deer responses to predator cues from deer responses to novel stimuli. We created separate mp3 files for each treatment by obtaining 16-bit, 44 kHz vocalizations from commercial websites. The coyote vocalization was a lone howl lasting 6 seconds, and the pied butcherbird song lasted 7 seconds. Each mp3 file played the vocalization once every 5 minutes. A single mp3 file was uploaded to a battery-powered mp3 player (AGPTEK, Brooklyn, NY, USA) and set on continuous repeat while connected to an Eco Extreme waterproof portable speaker (ECOXGEAR, Poway, CA, USA).

Each vocalization treatment was deployed at a site for 4, 24-hour periods. The order of treatment deployment was partially random and stratified across the 12 days such that every treatment was deployed once within a randomized 3-day period. For the coyote and control vocalization treatments, one portable speaker was attached to a tree 20 m away from the camera at the site. The speakers were calibrated to play a vocalization at 47 dB SPL using a digital sound level meter (BAFX, Muskego, WI, USA). Batteries in the mp3 players were replaced daily to preclude unexpected treatment cessation during deployment. To standardize forage quality and quantity at camera traps, we baited each trap with 18 L of whole corn that was checked daily and replenished as needed. Camera traps were set to take photos at 1-second intervals whenever motion was detected, enabling us to capture fine-scale individual behavior. To estimate deer visibility at each site, we measured vertical vegetation cover near each camera-trap station. Measurements were taken by a single observer using a density board that estimated percent visibility across 1 x 1 foot quadrats (Griffith and Youtie 1988, Nudds 2018). The density board was positioned 15-m from the observer standing at the camera-trap station, and the observer took one measurement in each cardinal direction from the station.

All photos were subsequently sorted and analyzed by a single observer who was blind to the playback treatment and disturbance classification associated with each photo or site. For every photo capturing deer activity, the observer recorded the sex of the individual, whether or not it was in a group, group size, the date and time, and if the individual was foraging or vigilant as a binomial variable. If the individual's head was down in a feeding posture, then the photo was classified as foraging (1), and if the individual's head was up in a non-feeding posture, then the photo was classified as vigilant (0; Lashley et al. 2014, Cherry et al. 2017). Following standard procedure for characterizing independent detections of large mammals (Kelly 2003, Kelly and Holub 2008, Wang et al. 2015, O'Connor and Rittenhouse 2017), independent foraging bouts were characterized as a sequence of same-sex deer photos captured within 30 minutes at a site. For each foraging bout, we calculated the total number of vigilant and foraging photos of an individual deer as well as the bout duration based on the timestamp of the first and last photo.

Data analysis

To test how land-use history and fire frequency affects deer visibility, we employed a linear model with land-use history, fire frequency, and the interaction of land-use history and fire as fixed effects and the proportion of density-board visibility as a response variable. To test how land-use history, fire frequency, and predator vocalizations affect the frequency of deer activity, we used a linear mixed effects model (LMM) with land-use history, fire frequency, playback treatment, and the interaction of land-use, fire, and playback treatment as fixed effects; site as a random intercept; and the log-transformed total number of foraging bouts each site for each playback treatment as a response variable. To test how land-use history, fire frequency, and predator vocalizations affect deer vigilance during foraging bouts, we used a binomial generalized linear mixed effects model with land-use history, fire frequency, playback treatment, and the interaction of land-use history, fire frequency, and playback treatment as fixed effects; site as a random intercept; and proportion of vigilant photos for each individual bout (i.e., individual allocation to vigilance within a bout) as a response variable. To test how land-use history, fire frequency, and predator vocalizations affect bout duration, we used an LMM with land-use history, fire frequency, playback treatment, the interaction of land-use history and fire, the interaction of land-use history and playback treatment, the interaction of fire and playback treatment, and the interaction of land-use history, fire frequency, and playback treatment as fixed effects; site as a random intercept; and bout duration (log-transformed minutes) as a response variable.

Results

We collected 4,471 photos of white-tailed deer activity across 17 of the 20 sites in our study. Out of the 155 total foraging boats captured, 88 were from individuals foraging alone (46 individual females, 41 individual males, and 1 individual juvenile) and 67 were from individuals foraging with one or two individuals (38 individual females, 23 individual males, and 6 individual juveniles). We captured 84 individual females, 64 individual males, and 7 juveniles of indistinguishable sex.

There was a significant effect of fire frequency on deer visibility ($F_{1,14} = 4.87$, $p = 0.045$) such that deer were more visible in frequently burned sites regardless of land-use history (Fig. 2). There was not a significant effect of land-use history ($F_{1,14} = 1.31$, $p = 0.271$) or the interaction between land-use history and fire frequency on deer visibility ($F_{1,14} = 0.60$, $p = 0.453$). The frequency of deer activity was not significantly affected by land-use history, fire frequency, or playback treatment (Table 1). Deer vigilance was significantly affected by playback treatment, the interaction of land-use history and fire frequency, and the interaction of fire frequency and playback treatment (Table 1). The coyote vocalization treatment led to significantly greater levels of deer vigilance in frequently burned, nonagricultural woodlands (Fig. 3A) but did not affect vigilance in post-agricultural woodlands or infrequently burned woodlands. The probability of deer vigilance was 1.6 times greater under the coyote vocalization treatment than under the control or silent treatment. Bout duration was significantly affected by land-use history, the interaction of land-use history and playback treatment, and the interactions of land-use history, fire frequency, and playback treatment (Table 1). The coyote vocalization treatment led to significantly longer bout durations in frequently burned, nonagricultural woodlands (Fig. 3B) but did not affect bout durations in post-agricultural woodlands or infrequently burned woodlands.

Discussion

Understanding how habitat context affects the anti-predator behavior of ungulates is important in contemporary landscapes where animals experience multiple disturbances that modify the risk of predation. Our large-scale study reveals that habitat context is an essential component of how ungulates use cues of predation risk to modify their anti-predator behavior. Moreover, we find that this context results from the interplay of contemporary disturbance (prescribed fire regime) and disturbances that occurred 60 years ago (past agricultural land use). Deer responded to direct cues of predator presence (playbacks of coyote calls) by increasing vigilance and bout duration in frequently burned woodlands without a history of agricultural land use (Fig. 3). In forests with a history of agricultural use, or infrequently burned woodlands without an agricultural history, there was no change in anti-predator behavior in response to direct predator cues (Fig. 3). These findings have several implications for understanding how multiple forms of disturbance affect both individuals and communities. First, individual responses to direct cues of predation risk may be contingent upon indirect cues of risk produced by past and present disturbance regimes. Second, the overlay of both past and present disturbances across a landscape may generate spatial variation in non-consumptive effects of predators on prey and the occurrence of trophic cascades.

Past and present disturbances affect how individuals respond to cues of risk

Predators can have non-consumptive effects on prey fitness when predator presence elicits behavioral or physiological responses in prey (Peckarsky et al. 2008, Zanette et al. 2011, Sheriff et al. 2020b). By reducing vegetation cover, frequent fires increase deer visibility to cursorial predators (Fig. 2), and our results confirm emerging evidence that fire regime has substantial effects on deer perceptions of risk (Cherry et al. 2017, Bartel and Orrock 2021) and, more broadly, ungulate antipredator behavior (Spitz et al. 2018). Importantly, despite the consistent effects of fire on deer visibility across woodlands with different land-use histories (Fig. 2), deer only responded to direct cues of risk (coyote vocalizations) when a specific indirect cue was available (reduced vegetation cover) through increased vigilance and bout duration in woodlands without agricultural legacies (Fig. 3). These findings reveal that legacies of disturbances which occurred over 60 years ago can have significant impacts on contemporary prey perceptions of immediate risk.

Interestingly, our results both reflect and inform past work finding that deer antipredator behavior varies with fire regime and past land use. In an observational study, Bartel and Orrock (2021) found that deer utilized a proactive antipredator strategy (temporal avoidance) in nonagricultural woodlands and a reactive strategy (vigilance) in post-agricultural woodlands when responding to indirect cues of predation risk caused by high fire frequency; hence, it was suggested that deer may perceive nonagricultural woodlands as riskier habitats where the likelihood of encountering a coyote is greater than in post-agricultural woodlands. This hypothesis is supported by past studies of coyote habitat use (see Bartel and Orrock 2021 for a discussion). In our study site, nonagricultural woodlands have a mixture of hardwood and pine while post-agricultural woodlands are dominated by pine (Brudvig et al. 2013). In the southeastern US, habitats characterized by hardwoods are preferred denning sites for coyotes (Hickman et al. 2015) and exhibit greater coyote densities (Jorge et al. 2020). Our results demonstrate that deer may be most fearful of encountering a coyote in nonagricultural woodlands, illustrating the importance of considering past land use in studies of predator-prey dynamics in highly degraded landscapes. Differences in habitat structure between post-agricultural and nonagricultural woodlands may also explain why deer did not respond to predator cues in frequently burned post-agricultural woodlands. While our measures of vertical vegetation cover at a 15-m distance from an observer did not detect a difference in deer visibility between frequently burned post-agricultural woodlands and frequently burned nonagricultural woodlands, it is possible that differences in habitat structure due to past land use manifest at longer distances from the observer. Importantly, mature trees in post-agricultural woodlands were initially planted in distinct rows typical of pine plantations at the time of restoration (Kilgo and Blake 2005), whereas nonagricultural woodlands are composed of mature trees that are more randomly dispersed. It is possible that the distinct rows of mature trees in post-agricultural woodlands improves the ability for deer to escape an attack once initiated by increasing movement efficiency. It is appreciated that linear habitat features can improve movement efficiency for large mammals (DeMars and Boutin 2018, Dickie et al. 2020); however, these linear features are roads, pipelines, and seismic lines (DeMars and Boutin 2018, Dickie et al. 2020). It is unclear if the linear alignment of mature trees in post-agricultural pine stands have similar effects on large-mammal movement efficiency. Our results indicate that deer perceive lower predation risk in frequently burned post-agricultural woodlands than nonagricultural woodlands, but future research is needed to understand if the underlying mechanism is due to differences in coyote habitat use or movement efficiency among the two habitat contexts.

Importantly, our results revealed that direct cues of predation risk modify how prey budget their time on fine temporal scales only under certain disturbance contexts. The past work by Bartel and Orrock (2021) examining deer responses to an indirect cue of risk (reduced vegetation cover) created by fire found that this indirect cue modified how deer budgeted time over broader temporal scales in nonagricultural woodlands: deer exhibited nocturnal activity in frequently burned woodlands and crepuscular activity in infrequently burned woodlands. By evaluating how deer budget their time on a finer temporal scale (i.e., duration of foraging bout as opposed to diel timing of bout) in response to a cue of immediate predation risk, our results show that deer increase the time spent foraging in a location when there are cues of immediate risk in habitats that are generally perceived as risky (i.e., nonagricultural woodlands with frequent fires).

Increased bout duration may be a cost of vigilance or an antipredator strategy in response to cues of predator presence. Since many prey species face a behavioral trade-off of allocating time to vigilance versus foraging, heightened vigilance can lead to reduced food intake if this is not mitigated by increased bout duration (Underwood 1982, Lima and Dill 1990, Illius and Fitzgibbon 1994, Fortin et al. 2004). When deer increase vigilance in response to cues of risk, they might attempt to mitigate lost foraging opportunities through increased bout duration. Since increased bout duration may also incur costs to the prey (e.g., missed opportunity costs), prey behavioral responses to direct cues of risk can carry costs both in foraging opportunities and time. Increased bout duration may also be an adaptive antipredator strategy when prey are in risky habitats and detect cues of predator presence. When prey detect the cue of a predator that uses vision to locate prey, the prey may benefit from remaining stationary to reduce visual detectability, as opposed to fleeing. Remaining stationary with increased vigilance may allow prey to collect more information, such as the predator’s location, movement direction, and behavioral state, which is particularly relevant for launching an effective defense against a cursorial predator (Sheriff et al. 2020a). Moreover, features of the habitat in which the cue is detected may affect the potential to escape an attack and should therefore affect the prey's decision on if and when to flee from a cursorial predator like the coyote (Lingle and Pellis 2002, Stankowich and Coss 2007). Our study indicates that both agricultural legacies and contemporary fire regimes can affect this decision. Since white-tailed deer were less likely to flee and more likely to remain stationary (i.e., increased bout duration) in response to the cue of coyote presence in frequently burned nonagricultural woodlands, our results indicate that in this disturbance context, immediate flight may not be an effective antipredator strategy or that deer require more information before launching an effective flight response.

Since we detected neither an increase nor decrease in deer bout duration in response to cues of coyote activity in woodlands with agricultural legacies or nonagricultural woodlands with infrequent fire regimes, we found no evidence that deer were employing either a flight or stationary antipredator strategy in these disturbance contexts, providing further evidence that deer perceive these habitats as relatively safe. However, an alternative hypothesis is that post-agricultural woodlands are also areas where deer are at high risk of coyote attack, but deer fail to optimally launch an antipredator response (i.e., deer experience an evolutionary trap; (Schlaepfer et al. 2002, Sih et al. 2011, Guiden et al. 2019). Agricultural legacies in woodlands are a relatively new disturbance from an evolutionary perspective and may create a novel habitat context for predator-prey interactions. Moreover, coyotes are novel predators in the southeastern US (Parker 1995, Chitwood et al. 2015). Since novel habitat contexts and novel predators may preclude prey from making accurate risk assessments or using effective antipredator strategies (Guiden et al. 2019), it is possible that the probability of encountering and escaping a coyote in post-agricultural woodlands is much greater than what the behavior of white-tailed deer suggests. This possible alternative hypothesis underscores the critical need for future research that evaluates how agricultural legacies affect every stage of the predator-prey encounter sequence in order to predict if this globally pervasive disturbance may generate evolutionary traps (Schlaepfer et al. 2002, Sih et al. 2011) and determine predator-prey coexistence (Guiden et al. 2019).

Prey behavior in disturbed habitats may impact communities

By altering the foraging behavior of herbivores, predator non-consumptive effects can sometimes have stronger cascading effects on primary producers than those generated by consumption of prey (Schmitz et al. 1997, Creel et al. 2017). However, non-consumptive effects and resulting trophic cascades are not consistently detected across all systems, spaces, and times, likely because prey perceptions of predation risk can vary across space and time within a single system (Orrock et al. 2004, LaManna and Martin 2016, Kohl et al. 2018, Gaynor et al. 2019). In finding that white-tailed deer behavior only responded to a direct cue of coyote presence in frequently burned woodlands without agricultural legacies, our results suggest that past and present disturbances affect prey perceptions of risk and may mediate the strength of predator non-consumptive effects. Since the non-consumptive effects of coyotes on white-tailed deer can elicit behaviorally-mediated trophic cascades in longleaf pine woodlands (Cherry et al. 2016), variation in deer behavioral responses to cues of coyote presence due to land-use history and fire regime may lead to predictable spatial variation in the strength of trophic cascades across highly disturbed landscapes. Since coyote presence may release understory plants from deer herbivory in longleaf-pine woodlands (Cherry et al. 2016, 2017), the impacts of agricultural legacies and contemporary fire regimes on deer antipredator behavior may have unappreciated consequences for the conservation of plant diversity in longleaf pine woodlands.

Interestingly, our past work using experimental manipulations of herbivore access in this system found that the effects of deer herbivory on deer-preferred plant species richness were dependent on fire regime: deer herbivory only reduced species richness in woodlands with low fire frequencies, particularly in post-agricultural woodlands (Chapter 3). It is hypothesized that this variation in the effects of deer herbivory on plant communities may be explained by variation in deer foraging behavior due to perceptions of risk across these different habitat contexts. Our past work shows that deer spend more time being vigilant and less time foraging in frequently burned, post-agricultural woodlands (Bartel and Orrock 2021) in the absence of direct cues of immediate predation risk, indicating that deer perceptions of risk related to habitat structure in this habitat context may reduce the magnitude of deer herbivory. However, this past work did not find a difference in deer vigilance in nonagricultural woodlands with different fire regimes (Bartel and Orrock 2021), providing little explanation for why we did not detect on effect of deer herbivory on plant species richness in frequently burned, nonagricultural woodlands (Chapter 3). This study provides a critical missing link for this past work in suggesting a mechanism for why deer herbivory did not affect focal plant species richness in nonagricultural woodlands. While deer may not use vigilance as a preemptive antipredator behavior (i.e., regardless of presence of predator cues) in frequently burned nonagricultural woodlands, our results show that deer react to cues of predator activity with increased vigilance in frequently burned nonagricultural woodlands. This heightened perception of risk of encountering a predator in frequently burned nonagricultural woodlands may lead to long-term reductions in the magnitude of deer herbivory in these woodlands, which may explain why we did not detect an effect of deer herbivory on focal plant communities in these woodlands after 6 years of herbivore-access manipulation (Chapter 3).

Conclusions and future directions

In this study, we found that prey respond to information about the risk of an imminent predator encounter differently under different disturbance contexts, illustrating how disturbances that alter indirect cues of risk mediate how prey respond to direct cues of risk. When prey detect cues of escalating risk in high-risk habitats, they may balance the urgency with the uncertainty of the situation through vigilance by remaining in place to acquire more information about the encounter to launch an appropriate defense, if necessary. Despite a growing body of knowledge of how agricultural legacies affect animal behavior and species interactions in longleaf pine woodlands (Hahn and Orrock 2015a, 2016, Stuhler and Orrock 2016, Bartel and Orrock 2020), there is still limited research in other ecosystems where agricultural land-use history is pervasive. Future research evaluating past land use and contemporary disturbance regime may resolve unexplained spatial variation in large-mammal behavior, predator-prey dynamics, and trophic cascades in human-modified landscapes.

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References

A. Schmidt, K. 2006. Non-additivity among multiple cues of predation risk: a behaviorally-driven trophic cascade between owls and songbirds. Oikos 113:82–90.

Bartel, S. L., and J. L. Orrock. 2020. Past and present disturbances generate spatial variation in seed predation. Ecosphere 11:e03116.

Bartel, S. L., and J. L. Orrock. 2021. Past agricultural land use affects multiple facets of ungulate antipredator behavior. Behavioral Ecology 32:961–969.

Blackburn, T. M., P. Cassey, R. P. Duncan, K. L. Evans, and K. J. Gaston. 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305:1955–1958.

Broekhuis, F., G. Cozzi, M. Valeix, J. W. Mcnutt, and D. W. Macdonald. 2013. Risk avoidance in sympatric large carnivores: Reactive or predictive? Journal of Animal Ecology 82:1098–1105.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. Evolutionary Ecology Research 1:49–71.

Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385–399.

Brudvig, L. A., E. Grman, C. W. Habeck, J. L. Orrock, and J. A. Ledvina. 2013. Strong legacy of agricultural land use on soils and understory plant communities in longleaf pine woodlands. Forest Ecology and Management 310:944–955.

Brudvig, L. A., J. L. Orrock, E. I. Damschen, C. D. Collins, P. G. Hahn, W. B. Mattingly, J. W. Veldman, and J. L. Walker. 2014. Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities. PLoS ONE 9:e86604.

Caro, T. 2005. Antipredator Defenses in Mammals and Birds. University of Chicago Press, Chicago, IL.

Cherry, M. J., L. M. Conner, and R. J. Warren. 2015. Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. Behavioral Ecology 26:1091–1099.

Cherry, M. J., R. J. Warren, and L. M. Conner. 2016. Fear, fire, and behaviorally mediated trophic cascades in a frequently burned savanna. Forest Ecology and Management 368:133–139.

Cherry, M. J., R. J. Warren, and L. M. Conner. 2017. Fire-mediated foraging tradeoffs in white-tailed deer. Ecosphere 8:e01784.

Chitwood, M. C., M. A. Lashley, J. C. Kilgo, C. E. Moorman, and C. S. Deperno. 2015. White-tailed deer population dynamics and adult female survival in the presence of a novel predator. The Journal of Wildlife Management 79:211–219.

Creel, S., E. Dröge, J. M'soka, D. Smit, M. Becker, D. Christianson, and P. Schuette. 2017. The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey. Ecology 98:2081–2092.

Creel, S., P. Schuette, and D. Christianson. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behavioral Ecology 25:773–784.

Culbert, P. D., I. Dorresteijn, J. Loos, M. K. Clayton, J. Fischer, and T. Kuemmerle. 2017. Legacy effects of past land use on current biodiversity in a low-intensity farming landscape in Transylvania (Romania). Landscape Ecology 32:429–444.

DeMars, C. A., and S. Boutin. 2018. Nowhere to hide: Effects of linear features on predator–prey dynamics in a large mammal system. Journal of Animal Ecology 87:274–284.

Dickie, M., S. R. McNay, G. D. Sutherland, M. Cody, and T. Avgar. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. Journal of Animal Ecology 89:623–634.

Eisenberg, C., D. E. Hibbs, and W. J. Ripple. 2015. Effects of predation risk on elk (*Cervus elaphus*) landscape use in a wolf (*Canis lupus*) dominated system. Canadian Journal of Zoology 93:99–111.

Farnworth, B., J. Innes, M. Davy, L. Little, V. Cave, and J. R. Waas. 2020. Antipredator responses of ship rats to visual stimuli: Combining unimodal predation cues generates risk avoidance. Animal Behaviour 168:149–157.

Flinn, K. M., and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3:243–250.

Fortin, D., M. S. Boyce, E. H. Merrill, and J. M. Fryxell. 2004. Foraging costs of vigilance in large mammalian herbivores. Oikos 107:172–180.

Foster, D. R. 1993. Land-use History and Forest Transformations in Central New England. Pages 91–110 Humans as Components of Ecosystems. Springer New York, New York, NY.

Frost, C. 2006. History and Future of the Longleaf Pine Ecosystem. Pages 9–48 *in* S. Jose, E. J. Jokela, and D. L. Miller, editors. The Longleaf Pine Ecosystem. Springer-Verlag New York, New York, NY.

Gaynor, K. M., J. S. Brown, A. D. Middleton, M. E. Power, and J. S. Brashares. 2019. Landscapes of fear: Spatial patterns of risk perception and response. Trends in Ecology and

Evolution 34.

Griesser, M., and M. Nystrand. 2009. Vigilance and predation of a forest-living bird species depend on large-scale habitat structure. Behavioral Ecology 20:709–715.

Griffith, B., and B. A. Youtie. 1988. Two devices for estimating foliage density and deer hiding cover. Wildlife Society Bulletin 16:206–210.

Grostal, P., and M. Dicke. 1999. Direct and indirect cues of predation risk influence behavior andreproduction of prey: a case for acarine interactions. Behavioral Ecology 10:422–427.

Guiden, P. W., S. L. Bartel, N. W. Byer, A. A. Shipley, and J. L. Orrock. 2019. Predator-prey interactions in the Anthropocene: Reconciling multiple aspects of novelty. Trends in Ecology and Evolution 34:616–627.

Gulsby, W. D., J. C. Kilgo, M. Vukovich, and J. A. Martin. 2017. Landscape heterogeneity reduces coyote predation on white-tailed deer fawns. Journal of Wildlife Management 81:601–609.

Hahn, P. G., and J. L. Orrock. 2015a. Land-use legacies and present fire regimes interact to mediate herbivory by altering the neighboring plant community. Oikos 124:497–506.

Hahn, P. G., and J. L. Orrock. 2015b. Spatial arrangement of canopy structure and land-use history alter the effect that herbivores have on plant growth. Ecosphere 6:Article 193.

Hahn, P. G., and J. L. Orrock. 2016. Neighbor palatability generates associational effects by altering herbivore foraging behavior. Ecology 97:2103–2111.

Hanna, E., and M. Cardillo. 2014. Island mammal extinctions are determined by interactive effects of life history, island biogeography and mesopredator suppression. Global Ecology and Biogeography 23:395–404.

Hernández, L., and J. W. Laundré. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. Wildlife Biology 11:215–220.

Hettena, A. M., N. Munoz, and D. T. Blumstein. 2014. Prey responses to predator's sounds: A review and empirical study. Ethology 120:427–452.

Hickman, J. E., W. D. Gulsby, C. H. Killmaster, J. W. Bowers, M. E. Byrne, M. J. Chamberlain, and K. V Miller. 2015. Home range, habitat use, and movement patterns of female coyotes in Georgia: implications for fawn predation. Journal of the Southeastern Association of Fish and Wildlife Agencies 2:144–150.

Hurtt, G. C., S. Frolking, M. G. Fearon, B. Moore, E. Shevliakovas, S. Malyshev, S. W. Pacala, and R. A. Houghton. 2006. The underpinnings of land-use history: Three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. Global Change Biology 12:1208–1229.

Illius, A. W., and C. Fitzgibbon. 1994. Costs of vigilance in foraging ungulates. Animal Behaviour 47:481–484.

Jorge, M. H., E. P. Garrison, L. M. Conner, and M. J. Cherry. 2020. Fire and land cover drive predator abundances in a pyric landscape. Forest Ecology and Management 461:117939.

Kats, L. B., and L. M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Écoscience 5:361–394.

Kelly, M. J. 2003. Jaguar monitoring in the Chiquibul Forest, Belize. Caribbean Geography 13:19–32.

Kelly, M. J., and E. L. Holub. 2008. Camera trapping of carnivores: Trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. Northeastern Naturalist 15:249–262.

Kilgo, J., and J. I. Blake, editors. 2005. Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site. Island Press, Washington, DC, USA.

Kilgo, J. C., H. S. Ray, M. Vukovich, M. J. Goode, and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. The Journal of Wildlife Management 76:1420–1430.

Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. Ecological Monographs 88:638–652.

Kopecký, M., and J. Vojta. 2009. Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. Applied Vegetation Science 12:251–260.

LaManna, J. A., and T. E. Martin. 2016. Costs of fear: Behavioural and life-history responses to risk and their demographic consequences vary across species. Ecology Letters 19:403–413.

Lashley, M. A., C. C. Chitwood, M. T. Biggerstaff, D. L. Morina, and C. E. Moorman. 2014. White-tailed deer vigilance: The influence of social and environmental factors. PLoS ONE 9:90652.

Lima, S. L. 1998. Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215–290.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68:619–640.

Lind, J., and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. Behavioral Ecology 16:945–956.

Lingle, S., and S. M. Pellis. 2002. Fight or flight? Antipredator behavior and the escalation of coyote encounters with deer. Oecologia 131.

Mattingly, W. B., J. L. Orrock, C. D. Collins, L. A. Brudvig, E. I. Damschen, J. W. Veldman, and J. L. Walker. 2015. Historical agriculture alters the effects of fire on understory plant beta diversity. Oecologia 177:507–518.

McCormick, M. I., and O. M. Löonnstedt. 2013. Degrading habitats and the effect of topographic complexity on risk assessment. Ecology and Evolution 3:4221–4229.

Morrison, E. B. 2011. Vigilance behavior of a tropical bird in response to indirect and direct cues of predation risk. Behaviour 148:1067–1085.

Nersesian, C. L., P. B. Banks, and C. Mcarthur. 2012. Behavioural responses to indirect and direct predator cues by a mammalian herbivore, the common brushtail possum. Behavioral Ecology and Sociobiology 66:47–55.

Nudds, T. D. 2018. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113–117.

O'Connor, K. M., and T. A. G. Rittenhouse. 2017. Temporal activity levels of mammals in patches of early successional and mature forest habitat in eastern Connecticut. The American Midland Naturalist 177:15–28.

Olivier, J. G. J., E. Version, J. Berger, J. E. Swenson, and I. Persson. 2001. Recolonizing carnivores and naıve prey: Conservation lessons from pleistocene extinctions. Science 291:1036–1040.

Orrock, J. L., B. J. Danielson, and R. J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behavioral Ecology 15:433–437.

Parker, G. 1995. Eastern Coyote: The Story of Its Success. 1st edition. Nimbus Publishing, Halifax, Nova Scotia.

Parsons, M. H., R. Apfelbach, P. B. Banks, E. Z. Cameron, C. R. Dickman, A. S. K. Frank, M. E. Jones, I. S. Mcgregor, S. Mclean, D. Müller-Schwarze, E. E. Sparrow, and D. T. Blumstein. 2017. Biologically meaningful scents: A framework for understanding predator-prey research across disciplines.

Parsons, M. H., and D. T. Blumstein. 2010. Feeling vulnerable? Indirect risk cues differently influence how two marsupials respond to novel dingo urine. Ethology 116:972–980.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, O. J. Schmitz, and G. C. Trussell. 2008. Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology 89:2416–2425.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86:501–509.

Pusenius, J., and R. S. Ostfeld. 2000. Effects of stoat's presence and auditory cues indicating its presence on tree seedling predation by meadow voles. Oikos 91:123–130.

Roehmer, G. W., M. E. Gompper, and B. Van Valkenburgh. 2009. The ecological role of the mammalian mesocarnivore. Bioscience 59:165–173.

Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. Ecology 68:660–668.

Scherer, A. E., and D. L. Smee. 2016. A review of predator diet effects on prey defensive responses. Chemoecology 26:83–100.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17:474–480.

Schmitz, O. J., A. P. Beckerman, and K. M. O'brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78:1388–1399.

Sheriff, M. J., J. L. Orrock, M. C. O. O. Ferrari, R. Karban, E. L. Preisser, A. Sih, and J. S. Thaler. 2020a. Proportional fitness loss and the timing of defensive investment: A cohesive framework across animals and plants. Oecologia 193:273–283.

Sheriff, M. J., S. Peacor, D. Hawlena, and M. Thaker. 2020b. Non-consumptive predator effects on prey population size: a dearth of evidence. Journal of Animal Ecology.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4:367–387.

Smith, J. A., J. P. Suraci, M. Clinchy, A. Crawford, D. Roberts, L. Y. Zanette, and C. C. Wilmers. 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. Proceedings of the Royal Society B: Biological Sciences 284.

Spitz, D. B., D. A. Clark, M. J. Wisdom, M. M. Rowland, B. K. Johnson, R. A. Long, and T. Levi. 2018. Fire history influences large-herbivore behavior at circadian, seasonal, and successional scales. Ecological Applications 28:2082–2091.

Stankowich, T., and D. T. Blumstein. 2005. Fear in animals: A meta-analysis and review of risk assessment. Proceedings of the Royal Society B: Biological Sciences 272:2627–2634.

Stankowich, T., and R. G. Coss. 2007. Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. Behavioral Ecology 18:358–367.

Stuhler, J. D., and J. L. Orrock. 2016. Past agricultural land use and present-day fire regimes can interact to determine the nature of seed predation. Oecologia 181:463–473.

Suraci, J. P., D. J. Roberts, M. Clinchy, and L. Y. Zanette. 2017. Fearlessness towards extirpated large carnivores may exacerbate the impacts of naïve mesocarnivores. Behavioral Ecology 28:439–447.

Suraci, J. P., J. A. Smith, M. Clinchy, L. Y. Zanette, and C. C. Wilmers. 2019. Humans, but not their dogs, displace pumas from their kills: An experimental approach. Scientific Reports 9:1–8.

Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. Behaviour 79:81–107.

Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

Wang, Y., M. L. Allen, and C. C. Wilmers. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation 190:23–33.

Weissburg, M., D. L. Smee, and M. C. Ferner. 2014. The sensory ecology of nonconsumptive predator effects. The American Naturalist 184:141–157.

Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. Science 334:1398–1401.

Figures and tables

Table 1. Test statistics and p-values for the fixed effects in the LMM and binomial GLM. Significant fixed effects ($p < 0.05$) are marked with asterisks.

	LMM						Binomial GLMM		
	Deer activity			Bout duration			Vigilance		
Effect	F	*P*		F	*P*		χ^2	*P*	
Intercept	9.28	0.007	*	95.05	<0.001	*	61.60	<0.001	
Land-use history	1.55	0.229		4.92	0.037	*	2.28	0.131	
Fire frequency	0.32	0.579		0.44	0.518		0.01	0.925	
Playback treatment	1.16	0.328		0.84	0.433		18.50	<0.001	*
Land-use x fire	0.28	0.604		1.15	0.296		6.46	0.011	*
Land-use x playback	3.27	0.054		4.50	0.013	*	5.98	0.050	*
Fire x playback	1.12	0.342		2.39	0.095		9.59	0.008	*
Land-use x fire x playback	0.96	0.397		4.64	0.011	*	4.12	0.127	

Figure 1. We conducted our experiment at 20 longleaf pine woodlands within the Savannah River Site near Aiken, SC, USA. Woodlands were classified by past land use and contemporary fire frequency, yielding 5 replicate woodlands for each disturbance category. The images above were captured within our sites during the experimental period and are representative of the variation in habitat structure captured in this study. The two photos on the bottom row from low-fire woodlands depict vigilant white-tailed deer in the foreground. Further in the background of the low-fire, nonagricultural woodland photo, a second white-tailed deer is foraging.

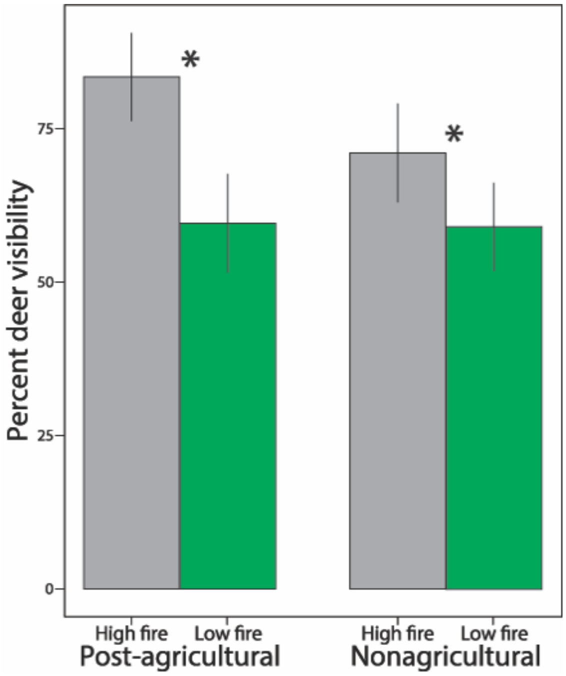

Figure 2. Contemporary fire regime significantly affected deer visibility as a result of vertical vegetation cover consistently across different land-use histories. Deer were more visible in sites with high fire frequencies than in those with low fire frequencies. Bars represented estimated marginal means for each disturbance group, and asterisks denote significant differences between fire frequencies at an alpha level of 0.05.

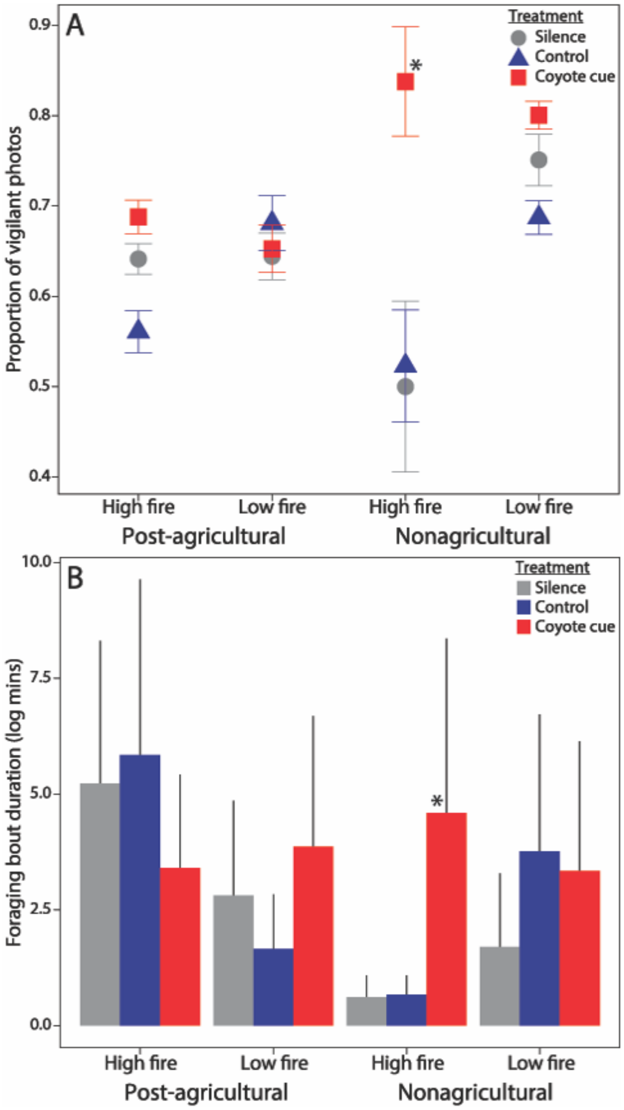

Figure 3. Past land use and contemporary fire significantly affected deer behavioral responses to a direct cue of predation risk, coyote vocalization. **A)** In nonagricultural woodlands with high fire frequencies, deer vigilance (i.e., proportion of vigilant photos per bout) was significantly greater when deer were exposed to the coyote cue than when exposed to a control vocalization (pied butcherbird) or silence. Deer vigilance in response to the coyote cues was not significantly different from the control cue or silence in all other disturbance contexts. **B)** In nonagricultural woodlands with high fire frequencies, deer bout duration was significantly greater when deer were exposed to the coyote cue than when expose to a control vocalization (pied butcherbird) or silence. Deer bout duration in response to the coyote cues was not significantly different from the control cue or silence in all other disturbance contexts. Bars represent estimated marginal means for each disturbance and cue treatment group. Asterisks denote significant differences between the coyote cue and the other cue treatments within a disturbance group at an alpha level of 0.05.

CHAPTER 5

An omnivorous mesopredator modifies predation of omnivore-dispersed seeds

Savannah L. Bartel and John L. Orrock

Bartel, S. L., J. L. Orrock. An omnivorous mesopredator modifies predation of omnivore-dispersed seeds. Ecosphere 11:e03116.

Abstract: Post-dispersal seed predation is an important determinant of plant recruitment. Although many plant species are dispersed following consumption by omnivorous vertebrates, the potential for these dispersal agents to indirectly affect seed fate by modifying seed-predator behavior is poorly understood. We evaluated the hypothesis that the scat of an omnivorous vertebrate (coyote, *Canis latrans*), which is also a rodent predator, would reduce seed predation by rodent granivores. We also hypothesized that scat would lead to increased removal by arthropod seed predators by providing a resource that attracts ants and other arthropods. We examined the role of omnivore deposition on seed predation of two animal-dispersed species that differed in size: larger *Prunus serotina* seeds are attacked only by rodents, whereas smaller *Rubus allegheniensis* seeds are attacked by arthropods and rodents. Using an experiment that manipulated the presence of coyote scat as well as access by different granivore guilds, we found that scat reduced the total number of seeds removed from full-access depots by 12%, but it increased the total number of seeds removed from arthropod-only depots by 43%. Rodent

removal of *P. serotina* seeds was 21% lower in the presence of scat. Scat composition was also important in affecting rodent seed predation, with seed predation 50% lower in the presence of meat-rich scat compared to mixed or fruit-rich scat. Arthropod removal of *R. allegheniensis* seeds was 43% higher in the presence of scat. *Prunus serotina* seeds were generally removed at great rates than *R. allegheniensis* seeds in full-access trays; however, scat reduced this difference in removal rates from 37% more *P. serotina* seeds removed to 18% more *P. serotina* seeds removed. These findings illuminate a new pathway through which omnivores may influence plant populations by modifying post-dispersal seed predation by arthropods and rodents. Moreover, our results indicate that the ultimate effect of vertebrate omnivores on seed survival in a given region may depend upon omnivore diet, dominant seed predator guilds, and differences in granivore seed preference.

Introduction

Seed survival can strongly affect the potential for plant recruitment (Harper 1977, Clark et al. 1998, 2007, Crawley 2000, Turnbull et al. 2000, Auffret et al. 2017); consequently, seed predation can substantially shape patterns of plant establishment and community composition (Howe et al. 2006, Chen and Valone 2017, Dylewski et al. 2020). Understanding patterns of seed predation is therefore important for understanding plant demography (Hobbs 1985, Hulme 1998, Crawley 2000, Orrock et al. 2006), patterns in plant communities (Inouye et al. 1980, Ostfeld et al. 1997, Howe and Brown 2000, Paine and Beck 2007, Larios et al. 2017), plant responses to climate change (Brown and Vellend 2014), and outcomes of biological invasions (Wolfe et al. 2004, Nuñez et al. 2008, Pearson et al. 2011, Orrock et al. 2015). Understanding the factors that affect granivore foraging provides an important means to understand seed survival because variation in granivore activity and behavior can generate spatiotemporal variation in seed predation (Orrock et al. 2003, Bricker et al. 2010, Lichti et al. 2014, Chandler et al. 2016, Brehm et al. 2019). For example, seeds consumed by granivores may depend critically on the presence of other nearby resources in the environment that serve to attract or distract foraging granivores (Veech 2001, Ostoja et al. 2013, Lichti et al. 2014). Granivore foraging may also be modified by the presence of natural enemies in the environment: arthropod and rodent granivores are both highly sensitive to risk of attack by predators and modify their activities accordingly (Brown and Kotler 2004, Orrock and Fletcher 2014, Blubaugh et al. 2017). As a result of the importance of the environment in modifying granivore decisions, it is essential to understand if common, yet unexplored, features of the environment give rise to significant variation in granivore activity and seed survival.

Granivores may often encounter seeds after they have been dispersed by vertebrates: 64% of gymnosperm and 27% of angiosperm plant species are dispersed by vertebrates (Herrera 1989), and thus their seeds are often found deposited in vertebrate feces (scat). Given that this fate is common for a large number of plant species, the scat of vertebrates may represent a widespread component of the environment in which a seed either dies or survives. Scat might modify granivory by causing changes in the foraging behavior or local abundance of granivores. For example, omnivorous vertebrates (e.g., bears, coyotes, foxes) that are agents of seed dispersal can also be predators of vertebrate granivores. As a cue of predation risk, mesopredator scat can repel rodent granivores (Kats and Dill 1998, Orrock 2010), thereby reducing predation of seeds within scat. In Alaska, where seed-rich bear scat can be a resource subsidy for rodent populations (Shakeri et al. 2018), seeds dispersed in bear scat exhibited decreased removal rates by rodents (Bermejo et al. 1998). Since rodents are known to show greater antipredator behavioral responses to urine of highly carnivorous than omnivorous predators (Nolte et al. 1994, Osburn and Cramer 2013, Scherer and Smee 2016), it is possible that differences in scat composition related to intraspecific diet variation may modify scat's effect on rodent behavior. Conversely, removal of seeds from animal scat by arthropod granivores, particularly ants, is well documented (Levey and Byrne 1993, Passos and Oliveira 2003, Pizo et al. 2005, Manzano et al. 2010, Fricke et al. 2016), and mammalian scat may increase seed predation when its odor attracts arthropods that utilize additional resources found in scat (Sainz-Borgo 2015). Alternatively, mammalian scat deposition may impede arthropod granivory by reducing seed apparency (Pizo et al. 2005) or by acting as a physical barrier to arthropod handling, much like seed mucilage (LoPresti et al. 2019). To our knowledge, no research has compared the roles of different granivore guilds (e.g., rodents vs. arthropods) in post-dispersal predation of seeds deposited in mesopredator scat. Since rodents and arthropods are known to prefer seeds of different sizes (i.e., arthropods prefer smaller seeds than those preferred by rodents; Orrock et al. 2003, 2006, Orrock and Damschen 2005, Chandler et al. 2016), the effects of mesopredator scat on seed survival may vary with seed size. These potentially important effects of mesopredator scat and its composition for post-dispersal seed fate are largely unexplored because they require intensive experiments that measure seed predation in the presence and absence of mesopredator scat across a gradient of dietary composition.

In this study, we use experimental manipulation of mesopredator scat and granivore guild to test whether the presence of mesopredator scat leads to different patterns of seed predation by arthropod and rodent granivores. Specifically, we determine if mesopredator scat generates different patterns of seed predation of two animal-dispersed seeds that differ in size (*Prunus serotina* and *Rubus allegheniensis*) from depots that manipulated rodent access in the presence or absence of mesopredator (*Canis latrans*) scat with varying composition (meat-rich, fruit-rich, mix). Further, we compared *P. serotina* removal by rodents in the presence of mesopredator scat and a non-predator omnivore's (*Sus scrofa*) scat to evaluate whether rodent antipredator behavior explained the effect of mesopredator scat and its composition on rodent granivory. Finally, we compared initial arthropod recruitment to seed piles in the presence and absence of mesopredator scat to test if scat attracts arthropod granivores. We hypothesized that mesopredator scat would reduce *P. serotina* removal by rodents due to rodent aversion to predator cues (Fig. 1a) and increase *R. allegheniensis* removal by arthropods due to arthropod attraction to scat (Fig. 1b).

Methods

Study area

We conducted our experiment in a 4-ha early-successional field at the Savannah River Site (SRS), a National Environmental Research Park near Aiken, SC, USA. The field was clear of mature trees and was surrounded on all sides by pine (*Pinus taeda*) plantation. The study area was selected because early successional habitats are common areas of establishment for the two plant species we examined, *P. serotina* and *R. allegheniensis*. Other plant species commonly found in the study area included *Chaemacrista fasciculata*, *Lespedeza* spp., *Desmodium* spp., *Vitis* spp., *Diospyros virginiana*, *Rubus cuneifolius*, and *Toxicodendron pubescens*. The study area is habitat for vertebrate species (e.g., oldfield mouse, *Peromyscus polionotus*) and numerous arthropod species (e.g., *Solenopsis* spp., *Pogonomyrmex badius*, and coleopterans) that are important post-dispersal seed predators (Orrock and Damschen 2005, Orrock et al. 2006, Craig et al. 2011, Chandler et al. 2016). Coyotes are widespread, omnivorous mesopredators that were first documented at SRS in 1989 (Cothran et al. 1991, Gulsby et al. 2017). Coyotes in the southeast are highly omnivorous and have significant variation in their diets (Thornton et al. 2004, Schrecengost et al. 2008, Mastro 2011, Cherry et al. 2016). At SRS, soft mast, chiefly

Prunus spp. and *Rubus* spp., is the most common food item from spring to late fall while small mammals are consistently present throughout the year (Schrecengost et al. 2008).

Scat composition and granivore identity experiment

Our experiment was conducted from 10 July-11 August 2018, with three sampling sessions lasting 10 days each (Session 1: 7/10/18-7/20/18; Session 2: 7/22/18-8/1/18; Session 3: 8/1/18-8/11/18). The timing of this experiment is within the realistic window of when the focal seed species are naturally available at SRS (Schrecengost et al. 2008). The duration of our sampling sessions was longer than typical seed-removal studies (Moles and Westoby 2003), and research shows that the majority of seed removal occurs within the first 24 hours of deployment (Boman and Casper 1995, Holl and Lulow 1997, Kollmann et al. 1998, Moles and Westoby 2003, Hammond 2020). During each session, we established 10 foraging stations, each containing 4 seed depots, on a 5 x 2 grid that separated neighboring stations by 20 m. For each session, a new 5 x 2 grid was established 20-m adjacent to the previous session's grid such that a 5 x 6 grid spanning the 3 sessions was built (Appendix S1). Each station contained 4 seed depots to generate a fully factorial cross of scat presence and rodent access. For the two depots that had scat present, we split a single piece of coyote scat in half and put one half in each depot. By splitting the scat in half, we assumed that each half would be equal in its composition (e.g., amounts of animal and plant material), allowing us to control for such factors at the station level. Within a station, depots were randomly placed in a 2 x 2 grid 0.5 m from each other and >1 m from any possible rodent refuge (i.e., woody debris and vegetation cover) or ant nest. Seed depots were 27 x 27 x 11 cm in size with 2.5-cm openings, and they were covered with tight-fitting lids. Lids excluded avian granivores and prevented scat and seed loss from wind and rain. Each depot was filled with 1.5 L of sand, similar to the sandy soils of our study area. One depot was open only to arthropods (hardware cloth at the depot entrance prohibited access by organisms wider than 1.5-cm^2) and did not contain scat; a second depot was open only to arthropods and contained scat; a third depot was open to arthropods and rodents (openings were not barred) and did not contain scat; and a fourth depot was open to arthropods and rodents and contained scat. This general seed depot design has been successfully used to measure seed removal by both arthropod and rodent granivores in numerous ecological settings (Bartowitz and Orrock 2016, Linabury et al. 2019), including our study area (Orrock and Damschen 2005, Craig et al. 2011, Chandler et al. 2016). Because it was not possible to create a treatment where only rodents (and not also arthropods) had access to trays, we assume that the effect of rodents on seed removal is additive to the effect of arthropods. This assumption is also made in other studies with similar experimental designs in our study system (Orrock et al. 2003, Orrock and Damschen 2005). Because *P. serotina* is not removed by arthropods (Orrock and Damschen 2005, Chandler et al. 2016), this assumption is most important for our interpretation of rodent removal of *R. allegheniensis* seeds (since *R. allegheniensis* is removed by both arthropods and rodents).The 0.5-m distance between depots within a station is a standard design utilized in studies evaluating rodent foraging at SRS (Orrock and Danielson 2005, Craig et al. 2011) as well as studies evaluating the effect of fecal predator cues on rodent foraging in other systems (Orrock 2010). This distance ensures that the paired depots share the same microhabitat, allowing us to assume that other explanations for differences in seed removal rates between paired depots unrelated to our treatments are unlikely.

Within each depot, we scattered 20 seeds of each species (*P. serotina* and *R. allegheniensis*) across the sandy surface. Seeds were procured from a commercial supplier and were free of pulp (Sheffield’s Seed Supply, Locke, New York, USA). This amount is representative of natural seed deposition for these species (Smith 1975) and replicates the densities of similar seed removal studies in this system (Orrock and Damschen 2005, Chandler et al. 2016). We chose *P. serotina* because it is the most common *Prunus* species in coyote diets at SRS (Schrecengost et al. 2008). *Rubus allegheniensis* is among the three possible species of *Rubus* found in our study area that are detected in coyote diets (Schrecengost et al. 2008). *Prunus serotina* (6.29-6.71 mm diameter, 0.068–0.084 g; Orrock and Damschen 2005) is significantly larger than *R. allegheniensis* (2.29-2.62 mm, 0.002–0.003 g). We confirmed the presence of common rodent species through camera and live trapping (Appendix S2). We confirmed the presence of common arthropod granivores (e.g., *Solenopsis invicta*) using visual mound survey and a bait-recruitment assay (Appendix S3). In order to investigate if scat affected arthropod granivore recruitment to dispersed seeds, we conducted a follow-up experiment comparing arthropod granivore recruitment to *R. allegheniensis* seeds in the presence and absence of coyote scat (see Appendix S3).

We assume that removed seeds were consumed and not secondarily dispersed for several reasons. Explicit tracking of 28,000 *Quercus nigra* seeds in nearby old-field habitats like the one used in this study during the same season as this study found no evidence of directed dispersal by rodents in this ecosystem (Bartel and Orrock *in press*). Excavation of *P. polionotus* burrows found large quantities of seed fragments but no intact seeds (Gentry and Smith 1968). *Solenopsis invicta* was the primary arthropod granivore in our experiment (Appendix S3) and is known to be a highly effective seed predator (Ready and Vinson 1995, Zettler et al. 2001, Seaman and Marino 2003, Ness and Bronstein 2004). Past work conducted in our study area shows that the number of seed-coat fragments in full-access foraging trays correlates with seed removal (Craig et al. 2011), and other studies in our system have also found destroyed seeds (Chandler et al. 2016), supporting past evidence that seed removal by arthropods and rodents is indicative of seed death (Bartel and Orrock 2020, Orrock and Damschen 2005, Orrock et al. 2006).

Coyote scat was collected by surveying roads across an ~80,000 ha area at SRS. We collected only fresh coyote scat for each sampling session 0-3 days prior to deployment. Field-collected scat was inspected prior to the experiment and the composition of the scat was categorized by a single observer (SLB). Scat was classified as meat-rich scat (>75% animal material), fruit-rich scat (>75% fleshy fruit material), or a fruit-meat mix (>50% plant material with visible animal material). A total of 30 pieces of coyote scat were used for this experiment: 9 meat-rich scat, 8 fruit-rich scat, and 13 mixed-composition scat. Scat compositions were stratified across the 3 sessions.

Rodent responses to predator and non-predator scat experiment

In order to examine whether the effect of coyote scat on rodent seed removal was driven by rodents avoiding the scat of a predator rather than simply an aversion to scat itself, we conducted an experiment comparing rodent foraging responses to coyote scat (omnivorous predator) and feral hog scat (*S. scrofa*; omnivorous non-predator). This experiment was conducted in 15 July-20 July 2019 at the same field as the past experiment. We established 20 foraging stations, each containing 3 seed depots, on a 10 x 2 grid that separated neighboring stations by 20 m. Each of the 3 seed depots allowed rodent access and contained 20 *P. serotina* seeds. One depot contained coyote scat, one depot contained hog scat, and one control depot did not contain scat. To replicate the methods of the first experiment, all scat was locally collected within 0-3 days prior to deployment, and depots within a station were randomly placed in a triangular grid 0.5 m from each other and >1 m from any habitat structure that might affect rodent foraging by serving as a predation refuge (Orrock et al. 2004). At the end of the deployment period, we counted the number of seeds remaining in the depots.

Statistical Analyses

We used generalized linear mixed effects models (GLMMs) with a binomial response distribution to examine the proportion of seeds removed. All analyses were conducted in R ver. 3.5.1, and GLMMs were constructed using the "lme4" package (Bates et al. 2015). To evaluate how forager identity and scat affected *R. allegheniensis* seed removal, we examined depot access, scat presence, and scat composition as fixed effects with intercepts varying among stations and rodent access treatments within a station. To evaluate how scat composition affected *R. allegheniensis* arthropod responses to scat in arthropod-only depots, we examined scat presence and scat composition as fixed effects with station as a random intercept. To evaluate how scat and scat composition affected *P. serotina* seed removal by rodents in full-access depots, we examined scat presence and scat composition as fixed effects and station as a random intercept. To estimate the difference between *R. allegheniensis* and *P. serotina* in seeds remaining in a full-access depot, we subtracted the proportion of *P. serotina* seeds remaining from the proportion of *R. allegheniensis* seeds remaining in each depot. To evaluate if scat changed the difference in removal rates between the two species, we used the difference in seeds remaining as the dependent variable, scat and scat composition as fixed effects, and station as a random intercept. To evaluate if rodent seed predation was more strongly affected by the scat of an omnivorous predator than that of an omnivorous non-predator, we examined the scat treatment (coyote, hog, or control) as a fixed effect with station as a random intercept.

Results

Scat composition and forager identity

Arthropods did not remove *P. serotina* seeds, and allowing rodents access always increased the number of *P. serotina* seeds removed (Fig. 2a). In full-access depots, the removal of *P. serotina* seeds was significantly affected by scat ($\chi^2 = 16.95$, $p < 0.001$; Table 1). Scat decreased *P. serotina* removal by 21% in full-access depots (Fig. 2a). Seed removal of *P. serotina* in full-access depots was significantly affected by the interaction of scat and composition (Table 1; Fig. 3c). *Rubus allegheniensis* seed removal was significantly affected by rodent access ($\chi^2 = 16.85$, $p < 0.001$) and the interaction of rodent access and scat ($\chi^2 = 8.420$, $p = 0.004$; Fig. 2b). Scat did not change the removal of *R. allegheniensis* is full-access depots, but it increased removal by 43% in arthropod-only depots (Fig. 2b). Seed removal of *R. allegheniensis* in arthropod-only depots was not significantly affected by the interaction of scat and composition (Table 1; Fig. 3a,b). The effect size of meat-rich scat was over 50% greater than that of fruit-rich and mixed scat (Fig. 3d). The difference in *R. allegheniensis* and *P. serotina* seeds remaining in the depots was not significantly affected by the interaction of rodent access and scat ($F = 0.24$, $p = 0.625$), but there was a significant effect of scat ($F = 9.10$, $p = 0.004$) and access ($F = 80.81$, $p < 0.001$). In full-access depots, *P. serotina* was always removed at a greater rate than *R. allegheniensis* (Fig. 4), but scat significantly reduced this difference in removal ($t = 3.02$, $p = 0.004$). In arthropod-only depots, *R. allegheniensis* always experienced greater removal than *P. serotina,* especially in the presence of scat ($t = 3.71$, $p = 0.001$).

Rodent responses to predator and non-predator scat

In the additional experiment testing rodent foraging on *P. serotina* in the presence of coyote or hog scat, there was a significant effect of the scat treatment ($\chi^2 = 14.65$, $p < 0.001$) on *P. serotina* seed removal. Rodents removed significantly less *P. serotina* seeds in the presence of coyote scat than in the presence of hog scat or no scat (Fig. 5). There was not a significant difference in *P. serotina* seed removal between depots with hog scat and depots without scat (Fig. 5).

Discussion

Seed predation can play an important role in plant population establishment and persistence. Our study illustrates that coyotes can play multiple roles in plant recruitment: in addition to their roles in dispersing seeds and limiting rodent granivore populations (Howe and Smallwood 1982, Willson 1993, Herrera and Pellmyr 2002, Mastro 2011), we show that coyotes may also affect seed predation by modifying the behavior of multiple granivore guilds. In finding that a reduction or enhancement in post-dispersal seed predation is an unappreciated consequence of endozoochory by coyotes, our work adds an important facet to our increasing appreciation of the myriad roles that omnivorous vertebrates play in food webs (Fagan 1997, McCann et al. 1998, Williams and Martinez 2000, Levey et al. 2002, Emmerson and Yearsley 2004, Duffy et al. 2007, Rudolf 2007, Thompson et al. 2007). Our findings have several implications. First, our study shows that post-dispersal seed survival of coyote-dispersed seeds is contingent upon seed traits (Fig. 4). Additionally, coyote diets are known to be highly variable (Andelt et al. 1987, Mastro 2011), and our results show that variation in coyote scat composition modifies seed predation, which may contribute to large-scale variation in post-dispersal seed fate (Fig. 3). Finally, our findings suggest that changes in coyote abundances and diets could have unappreciated effects on seed fate.

The effect of coyote omnivory on post-dispersal seed predation is contingent upon seed traits

If rates of seed predation can be linked to seed traits (e.g., size), this may provide a powerful way to make general predictions about rates of predation among different plant species (Moles and Westoby 2003, Orrock and Damschen 2005, Larios et al. 2017). Seed size may be particularly important for predicting predation by specific granivore guilds, as evidenced by a recent meta-analysis finding that seed size predicted global patterns of seed predation by small mammals (Dylewski et al. 2020). We found that coyote scat reduced post-dispersal removal of the larger *P. serotina* seeds by rodents in full-access depots. In contrast, scat increased seed removal of the smaller *R. allegheniensis* seeds by arthropods in arthropod-only depots and had no effect on overall *R. allegheniensis* removal in full-access depots (Fig. 2). One explanation for the absence of an effect of coyote scat on overall *R. allegheniensis* removal is because arthropod attraction to scat compensated for rodent aversion to coyote scat. Significant increases in *R. allegheniensis* seed removal when rodents had access to control depots suggests that rodents visiting control depots did contribute to *R. allegheniensis* seed removal, just as *P. serotina* removal was greater in control depots (Fig. 2). Results from our ant-recruitment assay found that ants were more likely to recruit to scat-associated *R. allegheniensis* seeds first (Appendix S3), indicating that ant attraction to scat may explain increased *R. allegheniensis* removal in arthropod-only depots. Those findings, coupled with further results showing that rodent removal of *P. serotina* seeds was reduced in the presence of coyote scat but not feral hog scat (Fig. 5) provide additional evidence that coyote scat promotes *P. serotina* seed survival through rodent repulsion but has no effect on *R. allegheniensis* survival due to the contrasting responses to scat by its two predator guilds. Interpretation of these results hinges on the assumption that rodent and arthropod granivory is additive (see Methods). Although past work has found evidence of antagonistic interactions between rodents and arthropods in which rodent access led to a decrease in overall *Rubus cuneifolius* seed removal by arthropods, this interaction was strongly dependent on the distance to the mound of an invasive ant species, *Solenopsis invicta* (Chandler et al. 2016), a factor that was not evaluated in our study. Moreover, Chandler et al. (2016) reported substantially lower rates of *P. serotina* seed removal rates (22% on average) in full-access depots than what our study detected (86% on average). This difference in *P. serotina* removal suggests that rodents were less abundant or less active in the previous study site than in our study site. Our results finding an increase in seed removal with rodent access show no evidence of antagonistic interactions possibly due to these differences in study design and rodent activity.

Since our study only measured seed removal by two species of different sizes, we are limited in our understanding of the role of seed size in generating these patterns of differential removal. Future experiments measuring removal across a greater breadth of seed species and sizes will be necessary to fully elucidate the importance seed traits in this system. The patterns of differential seed removal by rodents and arthropods in our study match the results of past experiments using *P. serotina* and *Rubus* spp. seeds in our study area (Orrock and Damschen 2005, Chandler et al. 2016), indicating that environmental factors with contrasting effects on rodent and arthropod behavior may have consequences for plant communities. Although their study did not evaluate guild-specific seed removal, reduced *P. serotina* seed removal in full-access depots containing scat is consistent with the results found in a study by Bermejo et al. (1998) examining seed removal of bear-dispersed seeds in Alaska. Our findings that arthropod seed removal increased in the presence of scat contrast with the findings of Pizo et al. (2005) that arthropod seed removal in Brazilian tropical forests was reduced by mammalian scat. Viewed in light of the strong effects of scat we observed, these studies provide additional evidence that scat-mediated changes in seed fate may be important in different ecosystems. Importantly, the study-specific variation in the effect of scat on seeds suggests that scat effects may be context specific and that future studies are needed to evaluate how the strength of scat effects may be modified by local variation in abiotic and biotic conditions. For example, *Solenopsis invicta* was the only ant species that we visually detected foraging in our study (Appendix S3); however, research in habitats containing more diverse ant communities found that competitive displacement of other ant species by *S. invicta* generates spatial variation in *Rubus* seed removal, contingent on distance to *S. invicta* mounds (Chandler et al. 2016). Spatial patterns in scat deposition relative to *S. invicta* mounds may be important in the nature of seed removal from scat when multiple ant species are present. Further, our follow-up experiment found *S. invicta* recruitment to scat-associated seeds occurred within 0-20 minutes whereas seeds that were not associated with scat experienced no recruitment within the 60-minute observation window (Appendix S3), indicating that scat may improve the ability of *S. invicta* to detect seeds. Our results indicate that the effect of scat on post-dispersal seed removal is contingent upon granivore guild, and the fate of scat-dispersed seeds may diverge among systems containing different granivore communities.

Changes in seed predation rates among plant species can elicit changes in plant communities (Inouye et al. 1980, Howe and Brown 2000, Howe et al. 2006, Paine and Beck 2007). In finding that scat has contrasting effects on seed predation of *P. serotina* and *R. allegheniensis*, our results suggest that scat presence and composition may promote differential survival of one plant species over another. Past experiments conducted on anther animal-dispersed plant species, *Phytolacca americana*, in our study system found that seed predation by rodents and arthropods is a limiting factor on plant recruitment (Orrock et al. 2003, 2006). We therefore expect that scat-mediated changes in granivore behavior documented in our study have the potential to generate consequences for plant recruitment in our system. However, since plant dynamics are also the result of many processes, including seed dispersal, seed predation, and herbivory (Vander Wall 1994, Auffret et al. 2017), future studies that explicitly incorporate scat and the role of mesopredators as seed dispersers into multi-stage experiments will be needed to understand the effect of scat-mediated changes in predation on local plant communities. Importantly, we were not able to track potential secondary seed dispersal events in our experiment, though significant evidence suggests that these events are extremely rare in our system (see Methods). Future studies that track secondary seed dispersal may be important for understanding how coyote scat determines seed fate in ecosystems where it is more common.

Coyote diet variability affects rodent granivory

Coyote scat reduced *P. serotina* seed removal by rodents, and meat-rich scat had a significantly stronger effect on rodent granivory than fruit-rich or mix scat. It is possible that rodents reduced *P. serotina* seed removal in the presence of coyote scat because rodents detected it as a cue of predation risk (Kats and Dill 1998) or a cue of disease risk (Buck et al. 2018). Since rodent removal of *P. serotina* seeds was not affected by feral hog scat, an omnivore that is not a predator (Fig. 5), we expect that the negative effect of coyote scat on rodent foraging was driven by rodent antipredator responses. Past research in our study system found that rodents did not respond differently to the urine of a suite of native and non-native predators (fox, bobcat, coyote, and ocelot) than to native deer urine or water (Orrock et al. 2004). Our findings that rodent seed removal was reduced by predator scat and not by non-predator scat indicate that the ability of prey to discriminate between the cues of predators and non-predators may be contingent upon the type of cue that is deposited (e.g., urine, scat, or mucus; Kats and Dill 1998). The significantly stronger effect of meat-rich coyote scat than that of fruit-rich or mix coyote scat on *P. serotina* seed removal by rodents also suggests that rodents may equate an individual's degree of carnivory to an indicator of predation risk (Nolte et al. 1994).

Coyote ranges and abundances have increased rapidly across the globe due to a combination of anthropogenic disturbances (Parker 1995, Crooks and Soulé 1999, Prugh et al. 2009). These changes in coyote populations have been shown to modify prey populations and behavior, generating cascading effects on primary producers and disease transmission (Prugh et al. 2009, Brashares et al. 2010, Levi et al. 2012). Our results illuminate an unappreciated consequence of such changes for seed predation through coyote endozoochory (Fig. 1), indicating that fluctuations in coyote densities may cause fluctuations in seed predation of animal-dispersed seeds. Further, coyote diets are highly variable, and our results show that factors driving changes in diets could affect seed fate. For example, the proportions of fruit and animal matter in coyote diets can vary not only seasonally (Andelt et al. 1987, Quinn 1997, Schrecengost et al. 2008) but also spatially in relation to human disturbance (Morey et al. 2007, Grigione et al. 2011, Wallace and Gipson 2014). As the ways in which human activities modify predator-prey interactions become more appreciated (Guiden et al. 2019), it is important to consider how human-induced changes in coyote diets may modify rodent responses to predator cues and generate cascading effects on seed fate.

Conclusions and future directions

Coyotes have the potential to indirectly affect post-dispersal seed predation through the direct effects of coyote scat on granivore behavior. Since granivore guilds that vary in their seed preferences also show differing responses to coyote scat (i.e., attraction vs. aversion), coyote scat may cause differential seed predation, making the benefits of this mode of dispersal contingent upon seed traits related to granivore preferences. In this study we show that the nature and magnitude of the effects of coyote scat on seed predation were contingent upon granivore identity, seed species, and scat composition. In order to understand if these patterns in seed fate modify plant recruitment, long-term studies comparing recruitment of animal-dispersed species in the presence and absence of coyotes is necessary. Since variation in scat composition can yield variation in nutrient availability and consequently determine seedling establishment (Traveset et al. 2001), future studies that explicitly track the effects of individual-level diet choice on both seed predation and subsequent recruitment are needed to understand the ultimate consequences of coyote omnivory for plant populations.

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References

Andelt, W. F., J. G. Kie, F. F. Knowlton, and K. Cardwell. 1987. Variation in coyote diets associated with season and successional changes in vegetation. Journal of Wildlife Management 51:273–277.

Auffret, A. G., Y. Rico, J. M. Bullock, D. A. P. Hooftman, R. J. Pakeman, M. B. Soons, A. Suárez-Esteban, A. Traveset, H. H. Wagner, and S. A. O. Cousins. 2017. Plant functional connectivity - integrating landscape structure and effective dispersal. Journal of Ecology 105:1648–1656.

Bartel, S. L., and J. L. Orrock. 2020. Past and present disturbances generate spatial variation in seed predation. Ecosphere 11:e03116.

Bartowitz, K. J., and J. L. Orrock. 2016. Invasive exotic shrub (*Rhamnus cathartica*) alters the timing and magnitude of post-dispersal seed predation of native and exotic species. Journal of Vegetation Science 27:789–799.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bermejo, T., A. Traveset, and M. Willson. 1998. Post-dispersal seed predation in the temperate rainforest of Southeast Alaska. The Canadian Field-Naturalist 112:510–512.

Blubaugh, C. K., I. V. Widick, and I. Kaplan. 2017. Does fear beget fear? Risk-mediated habitat selection triggers predator avoidance at lower trophic levels. Oecologia 185:1–11.

Boman, J. S., and B. B. Casper. 1995. Differential postdispersal seed predation in disturbed and intact temperate forest. American Midland Naturalist 134:107–116.

Brashares, J. S., L. R. Prugh, C. J. Stoner, and C. W. Epps. 2010. Ecological and conservation implications of mesopredator release. Page *in* J. W. Terborgh and J. A. Estes, editors. Trophic Cascades. Island Press.

Brehm, A. M., A. Mortelliti, G. A. Maynard, and J. Zydlewski. 2019. Land-use change and the ecological consequences of personality in small mammals. Ecology Letters 22:1387–1395.

Bricker, M., D. Pearson, and J. Maron. 2010. Small-mammal seed predation limits the recruitment and abundance of two perennial grassland forbs. Ecology 91:85–92.

Brown, C. D., and M. Vellend. 2014. Non-climatic constraints on upper elevational plant range expansion under climate change. Proceedings of the Royal Society B 281:20141779.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

Buck, J. C., S. B. Weinstein, and H. S. Young. 2018. Ecological and evolutionary consequences of parasite avoidance. Trends in Ecology and Evolution 33:619–632.

Chandler, J. L., J. L. Orrock, and J. Resasco. 2016. Invasive ants generate heterogeneity in patterns of seed survival. American Midland Naturalist 176:289–297.

Chen, T. C., and T. J. Valone. 2017. Rodent granivory strengthens relationships between seed size and plant abundance in a desert annual community. Journal of Vegetation Science 28:808–814.

Cherry, M. J., K. L. Turner, M. Brent Howze, B. S. Cohen, L. Mike Conner, and R. J. Warren. 2016. Coyote diets in a longleaf pine ecosystem. Wildlife Biology 22:64–70.

Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. The American Naturalist 170:128–142.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in Southern Appalachian forests. Ecological Monographs 68:213–235.

Cothran, E. G., M. H. Smith, J. O. Wolff, and J. B. Gentry. 1991. Mammals of the Savannah River Site. SRO-NERP-21, Aiken, SC: Savannah River Site.

Craig, M. T., J. L. Orrock, and L. A. Brudvig. 2011. Edge-mediated patterns of seed removal in experimentally connected and fragmented landscapes. Landscape Ecology 26:1373–1381.

Crawley, M. J. 2000. Seed predators and plant population dynamics. Pages 167–182 *in* M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. Second edition. CABI, Wallingford, UK.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Duffy, J. E., B. J. Cardinale, K. E. France, P. B. Mcintyre, E. T. Bault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecology

Letters 10:522–538.

Dylewski, Ł., Y. K. Ortega, M. Bogdziewicz, and D. E. Pearson. 2020. Seed size predicts global effects of small mammal seed predation on plant recruitment. Ecology Letters 23:1024–1033.

Emmerson, M., and J. M. Yearsley. 2004. Weak interactions, omnivory and emergent food-web properties. Proceedings of the Royal Society B 271:397–405.

Fagan, W. F. 1997. Omnivory as a stabilizing feature of natural communities. The American Naturalist 150:554–567.

Fricke, E. C., C. David, Haak, J. Douglas, Levey, and J. J. Tewksbury. 2016. Gut passage and secondary metabolites alter the source of post-dispersal predation for bird-dispersed chili seeds. Oecologia 1:905–910.

Gentry, J. B., and M. H. Smith. 1968. Food habits and burrow associates of *Peromyscus polionotus*. Journal of Mammalogy 49:562–565.

Grigione, M. M., P. Burman, S. Clavio, S. J. Harper, D. Manning, R. J. Sarno, M. M. Grigione, P. Burman, S. Clavio, : D Manning, S. J. Harper, and R. J. Sarno. 2011. Diet of Florida coyotes in a protected wildland and suburban habitat. Urban Ecosystems 14:655–663.

Guiden, P. W., S. L. Bartel, N. W. Byer, A. A. Shipley, and J. L. Orrock. 2019. Predator-prey interactions in the Anthropocene: Reconciling multiple aspects of novelty. Trends in Ecology and Evolution 34:616–627.

Gulsby, W. D., J. C. Kilgo, M. Vukovich, and J. A. Martin. 2017. Landscape heterogeneity reduces coyote predation on white-tailed deer fawns. Journal of Wildlife Management 81:601–609.

Hammond, D. S. 2020. Post-dispersal seed and seedling mortality of tropical dry forest trees after shifting agriculture, Chiapas, Mexico. Journal of Tropical Ecology 11:295–313.

Harper, J. L. 1977. Population Biology of Plants. Page Population biology of plants. Academic Press., London, UK.

Herrera, C. M. 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos 55:250–252.

Herrera, C. M., and O. Pellmyr. 2002. Plant–Animal Interactions: An Evolutionary Approach. Wiley-Blackwell, Hoboken, NJ.

Hobbs, R. J. 1985. Harvester ant foraging and plant species distribution in annual grassland. Oecologia 67:519–523.

Holl, K. D., and M. E. Lulow. 1997. Effects of species, habitat, and distance from edge on post-dispersal seed predation in a tropical rainforest. Biotropica 29:459–468.

Howe, H. F., and J. S. Brown. 2000. Early effects of rodent granivory on experimental forb communities. Ecological Applications 10:917–924.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201–228.

Howe, H. F., B. Zorn-Arnold, A. Sullivan, and J. S. Brown. 2006. Massive and distinctive effects of meadow voles on grassland vegetation. Ecology 87:3007–3013.

Hulme, P. E. 1998. Post-dispersal seed predation: consequences for plant demography and evolution. Perspectives in Plant Ecology, Evolution and Systematics 1:32–46.

Inouye, R. S., G. S. Byers, and J. H. Brown. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. Ecology 61:1344–1351.

Kats, L. B., and L. M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Écoscience 5:361–394.

Kollmann, J., D. A. Coomest, and S. M. Whitet. 1998. Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. Functional Ecology 12:683–690.

Larios, L., D. E. Pearson, and J. L. Maron. 2017. Incorporating the effects of generalist seed predators into plant community theory. Functional Ecology 31:1856–1867.

Levey, D. J., and M. M. Byrne. 1993. Complex ant-plant interactions: rain-forest ants as secondary dispersers and post-dispersal seed predators. Ecology 74:1802–1812.

Levey, D. J., W. R. Silva, and M. Galetti. 2002. Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation. CABI, New York, NY.

Levi, T., A. M. Kilpatrick, M. Mangel, and C. C. Wilmers. 2012. Deer, predators, and the emergence of Lyme disease. Proceedings of the National Academy of Sciences 109:10942–10947.

Lichti, N. I., M. A. Steele, H. Zhang, and R. K. Swihart. 2014. Mast species composition alters seed fate in North American rodent-dispersed hardwoods. Ecology 95:1746–1758.

Linabury, M. C., N. E. Turley, and L. A. Brudvig. 2019. Insects remove more seeds than mammals in first-year prairie restorations. Restoration Ecology 27:1300–1306.

LoPresti, E. F., V. Pan, J. Goidell, M. G. Weber, and R. Karban. 2019. Mucilage-bound sand reduces seed predation by ants but not by reducing apparency: A field test of 53 plant species. Ecology 100:e02809.

Manzano, P., F. M. Azcárate, B. Peco, and J. E. Malo. 2010. Are ecologists blind to small things? The missed stories on non-tropical seed predation on feces. Oikos 119:1537–1545.

Mastro, L. L. 2011. Life history and ecology of coyotes in the Mid-Atlantic states: a summary of the scientific literature. Southeastern Naturalist 10:721–730.

McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794–798.

Moles, A. T., and M. Westoby. 2003. Latitude, seed predation and seed mass. Journal of Biogeography 30:105–128.

Morey, P. S., E. M. Gese, and S. Gehrt. 2007. Spatial and temporal variation in the diet of coyotes in the Chicago Metropolitan area. American Midland Naturalist 158:147–161.

Ness, J. H., and J. L. Bronstein. 2004. The effects of invasive ants on prospective ant mutualists. Biological Invasions 6:445–461.

Nolte, D. L., J. R. Mason, G. Epple, E. Aronov, and D. L. Campbell. 1994. Why are predator urines aversive to prey? Journal of Chemical Ecology 20:1505–1516.

Nuñez, M. A., D. Simberloff, and M. A. Relva. 2008. Seed predation as a barrier to alien conifer invasions. Biological Invasions 10:1389–1398.

Orrock, J. L. 2010. When the ghost of predation has passed: do rodents from islands with and without fox predators exhibit aversion to fox cues? Ethology 116:338–345.

Orrock, J. L., and E. I. Damschen. 2005. Corridors cause differential seed predation. Ecological Applications 15:793–798.

Orrock, J. L., and B. J. Danielson. 2005. Patch shape, connectivity, and foraging by oldfield mice (Peromyscus polionotus). Journal of Mammalogy 86:569–575.

Orrock, J. L., B. J. Danielson, and R. J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behavioral Ecology 15:433–437.

Orrock, J. L., B. J. Danielson, M. J. Burns, and D. J. Levey. 2003. Spatial ecology of predator-prey interactions: corridors and patch shape influence seed predation. Ecology 84:2589–2599.

Orrock, J. L., H. P. Dutra, R. J. Marquis, and N. Barber. 2015. Apparent competition and native consumers exacerbate the strong competitive effect of an exotic plant species. Ecology 96:1052–1061.

Orrock, J. L., and R. J. Fletcher. 2014. An island-wide predator manipulation reveals immediate and long-lasting matching of risk by prey. Proceedings of the Royal Society of London B: Biological Sciences 281.

Orrock, J. L., D. J. Levey, B. J. Danielson, and E. I. Damschen. 2006. Seed predation, not seed dispersal, explains the landscape-level abundance of an early successional plant. Journal of Ecology 94:838–845.

Osburn, D. J., and M. J. Cramer. 2013. Foraging response of *Erethizon dorsatum* and *Lepus americanus* to specialized and generalized predator scents. American Midland Naturalist 169:66–73.

Ostfeld, R. S., R. H. Manson, and C. D. Canham. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. Ecology 78:1531–1542.

Ostoja, S. M., E. W. Schupp, S. Durham, and R. Klinger. 2013. Seed harvesting is influenced by associational effects in mixed seed neighbourhoods, not just by seed density. Functional Ecology 27:775–785.

Paine, C. E. T., and H. Beck. 2007. Seed predation by neotropical rain forest mammals increase diversity in seedling recruitment. Ecology 88:3076–3087.

Parker, G. 1995. Eastern Coyote: The Story of Its Success. 1st edition. Nimbus Publishing, Halifax, Nova Scotia.

Passos, L., and P. S. Oliveira. 2003. Interactions between ants, fruits and seeds in a restinga forest in south-eastern Brazil. Journal of Tropical Ecology 19:261–270.

Pearson, D. E., R. M. Callaway, and J. L. Maron. 2011. Biotic resistance via granivory: establishment by invasive, naturalized, and native asters reflects generalist preference. Ecology 92:1748–1757.

Pizo, M. A., P. R. Guimarães, and P. S. Oliveira. 2005. Seed removal by ants from faeces produced by different vertebrate species. Écoscience 12:136–140.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

Quinn, T. 1997. Coyote (*Canis latrans*) food habits in three urban habitat types of western Washington. Northwest Science 71:1–5.

Ready, C. C., and S. B. Vinson. 1995. Seed selection by the red imported fire ant (Hymenoptera: Formicidae) in the laboratory. Environmental Entomology 24:1422–1431.

Rudolf, V. H. W. 2007. The interaction of cannibalism and omnivory: consequences for community dynamics. Ecology 88:2697–2705.

Sainz-Borgo, C. 2015. Bird feces consumption by fire ant Solenopsis geminata (Hymenoptera: *Formicidae*). Entomological News 124:295–299.

Scherer, A. E., and D. L. Smee. 2016. A review of predator diet effects on prey defensive responses. Chemoecology 26:83–100.

Schrecengost, J. D., J. C. Kilgo, D. Mallard, H. S. Ray, and K. V Miller. 2008. Seasonal food habits of the coyote in the South Carolina Coastal Plain. Southeastern Naturalist 7:135–144.

Seaman, R. E., and P. C. Marino. 2003. Influence of mound building and selective seed predation by the red imported fire ant (*Solenopsis invicta*) on an old-field plant assemblage. Journal of the Torrey Botanical Society 130:193–201.

Shakeri, Y. N., K. S. White, and T. Levi. 2018. Salmon-supported bears, seed dispersal, and extensive resource subsidies to granivores. Ecosphere 9:e02297.

Smith, A. J. 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. Ecology 56:19–34.

Thompson, R. M., M. Hemberg, B. M. Starzomski, and J. B. Shurin. 2007. Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. Ecology 88:612–617.

Thornton, D. H., M. E. Sunquist, and M. B. Main. 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in south-central Florida. Journal of Mammalogy 85:973–982.

Traveset, A., T. Bermejo, and M. Willson. 2001. Effect of manure composition on seedling emergence and growth of two common shrub species of Southeast Alaska. Ecology 155:29–34.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225–238.

Veech, J. A. 2001. The foraging behavior of granivorous rodents and short-term apparent competition among seeds. Behavioral Ecology 12:467–474.

Vander Wall, S. B. 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. Ecology 75:1911–1926.

Wallace, M. C., and P. S. Gipson. 2014. Comparison of coyote (*Canis latrans*) diets in continuous and fragmented short-grass prairie in the Texas Panhandle. Texas Journal of Science 66:25–41.

Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. Nature 404:180–183.

Willson, M. F. 1993. Mammals as seed-dispersal mutualists in North America. Oikos 67:159–

176.

Wolfe, L. M., J. A. Elzinga, and A. Biere. 2004. Increased susceptibility to enemies following introduction in the invasive plant Silene latifolia. Ecology Letters 7:813–820.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25:443–466.

Zettler, J. A., T. P. Spira, and C. R. Allen. 2001. Ant-seed mutualisms: can red imported fire ants sour the relationship? Biological Conservation 101:249–253.

Tables and figures

Table 1. Coefficients, test statistics, and P-values for our binomial GLMMs evaluating the effects of scat and scat composition on seed removal.

	P. serotina (full-access)			*R. allegheniensis* (arthropod-only)		
Effect	β	χ^2	P	β	χ^2	P
Scat	-2.91	16.95	<0.001***	-1.30	17.27	<0.001***
Composition	3.36	3.77	0.152	-0.46	0.91	0.339
Scat x composition	-3.69	8.65	0.013*	0.26	2.49	0.288

Notes: GLMMs, generalized linear mixed-effects models. Since arthropods do not remove *P. serotina*, only data from full-access depots were analyzed to understand how scat and scat composition modify rodent behavior. In order to understand how scat and scat composition specifically modify arthropod behavior, only *R. allegheniensis* removal data from arthropod-only depots were analyzed. *P < 0.05, **P < 0.01, ***P < 0.001.

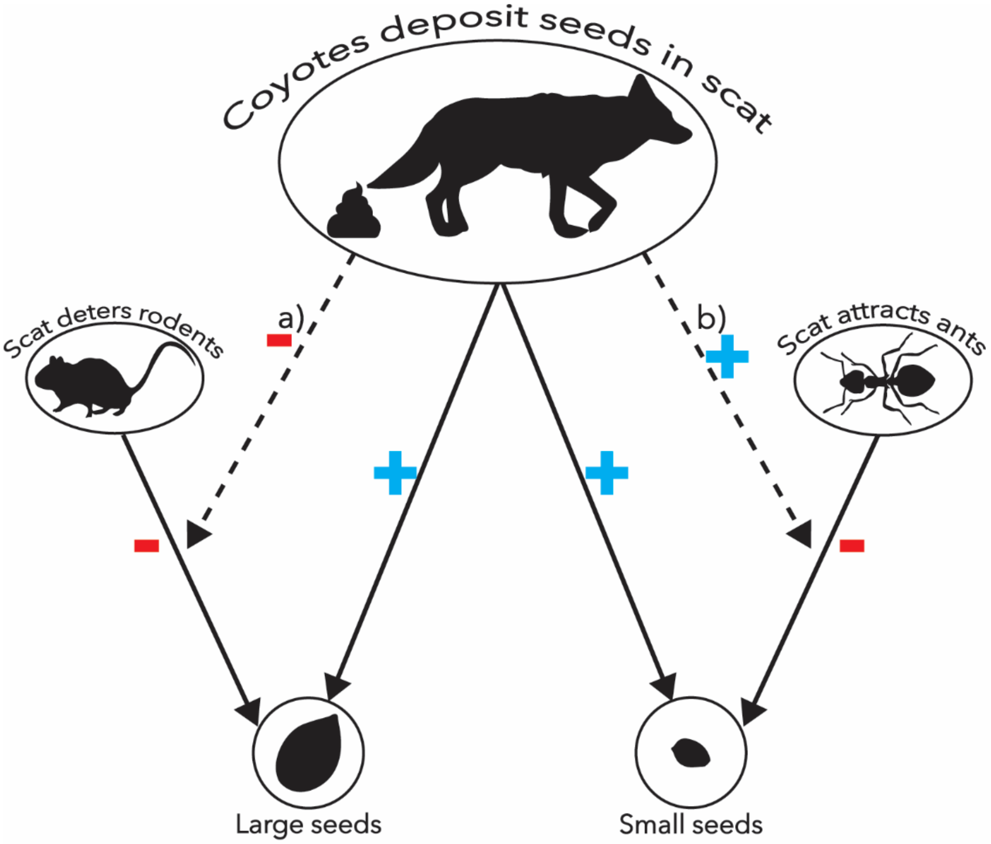

Figure 1. Coyotes can directly affect seed fate by consuming fleshy fruits and dispersing seeds in scat. We hypothesize that coyotes can indirectly affect seed fate through the effects of scat on granivore foraging behavior. Solid lines represent direct effects of organisms on seeds, and dashed lines represent indirect effects of coyotes on seeds through interaction modifications (Wootton 1994). Positive and negative signs with each line represent whether the organism has a positive or negative effect on seeds (solid lines) or seed–granivore interaction strength (dashed lines). (a) Coyote scat is a cue of predation risk for rodent granivores, so it may decrease rodent foraging activity, reducing the strength of the rodent–seed interaction and increasing survival of seeds favored by rodents (i.e., larger seeds). (b) Coyote scat may attract arthropod granivores, so it may increase the strength of the arthropod–seed interaction, reducing survival of seeds favored by arthropods (i.e., smaller seeds)

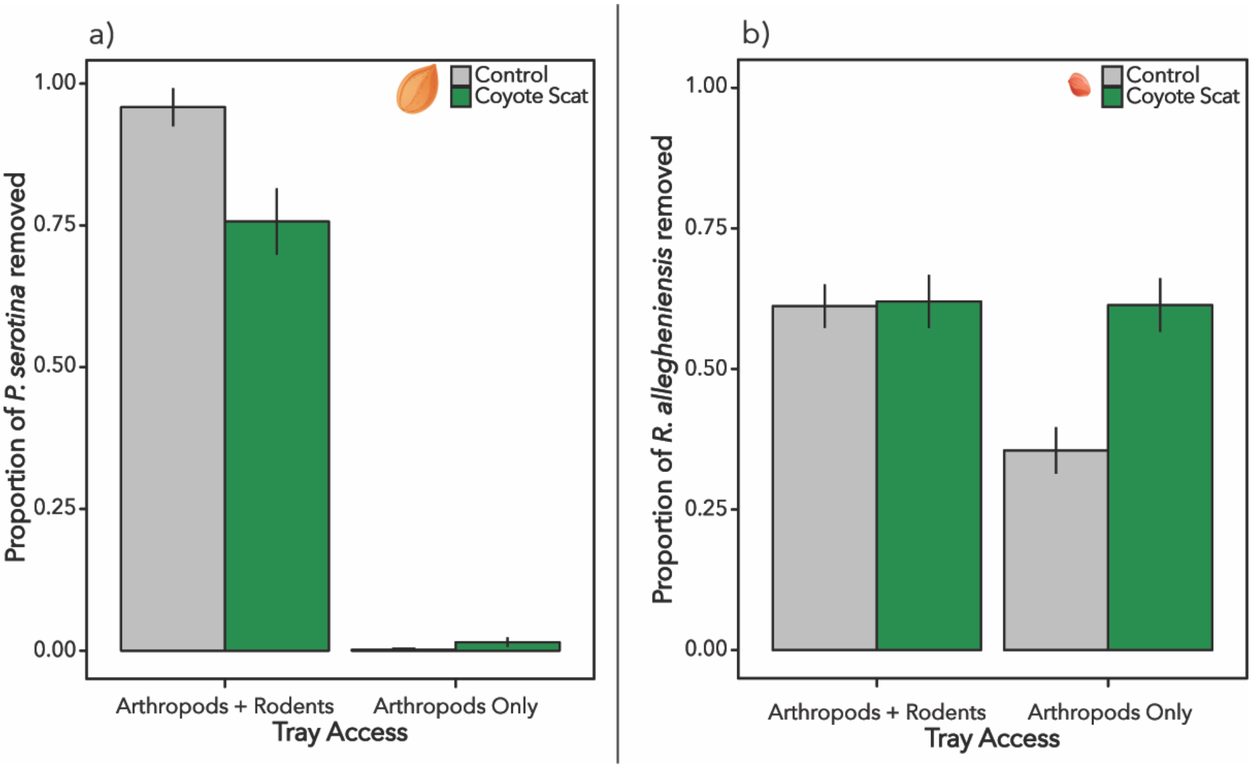

Figure 2. Bar graphs depict the average seed removal rates of each seed species based on granivore access and scat treatment combination. Error bars represent one standard error. (a) *Prunus serotina* seeds were only removed from full-access depots. In full-access depots, scat significantly decreased the proportion of *P. serotina* seeds removed. (b) *Rubus allegheniensis* seed removal was significantly affected by the interaction of rodent access and scat presence. In full-access depots, there was no effect of scat on *R. allegheniensis* seed removal. In arthropod-only depots, *R. allegheniensis* seed removal was significantly greater in the presence of scat. Significant increases *in R. allegheniensis* seed removal when rodents had access to scat-free control trays suggest that rodents visiting control trays did contribute to *R. allegheniensis* seed removal, just *as P. serotina* removal was greater in control trays. In the absence of rodents, scat led to an increase in *R. allegheniensis* seed removal.

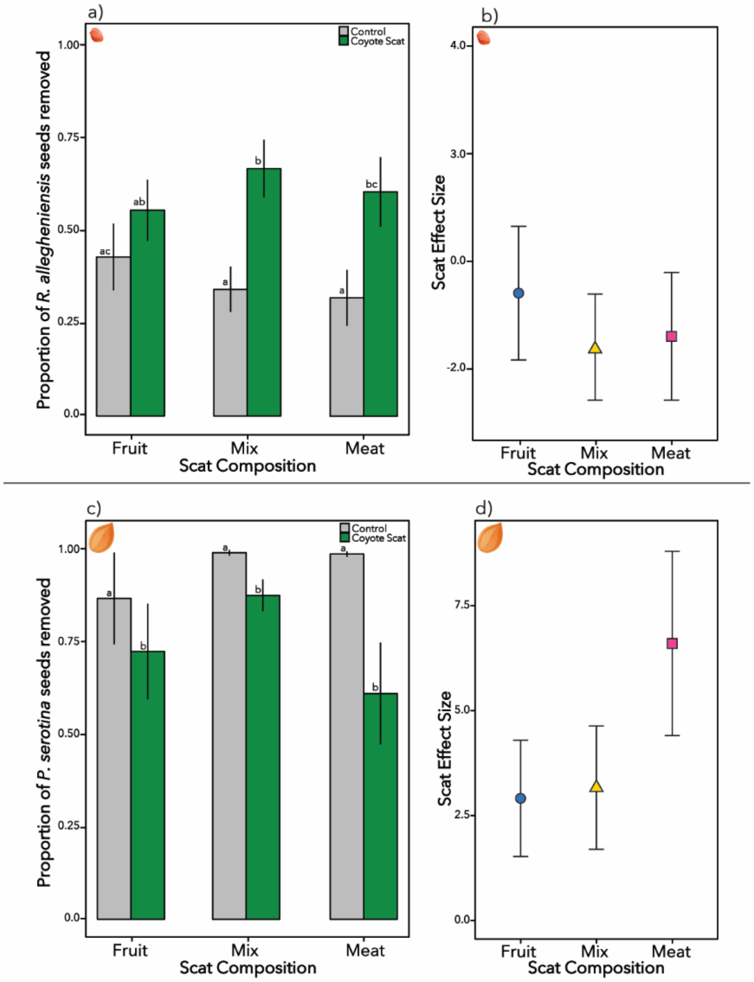

Figure 3. Bar graphs on the left depict the average seed removal rates of each seed species for each scat treatment and scat composition. Graphs on the right plot the effect size of the scat treatment on seed removal for each scat composition category. Error bars represent one standard error; bars that share a letter represent means that are not significantly different (i.e., P>0.05). (a) In arthropod-only depots, scat significantly increased *Rubus allegheniensis* seed removal in mix and meat-rich scat, but there was no significant interaction of scat and scat composition on seed removal by arthropods. (b) There was no difference in the strength of scat's effect on *R. allegheniensis* seed removal by arthropods between the different types of scat composition. (c) In full-access depots, scat and the interaction of scat and scat composition significantly affected *Prunus serotina* seed removal by rodents. (d) Meat-rich scat had a greater negative effect on *P. serotina* removal by rodents than mix or fruit-rich scat.

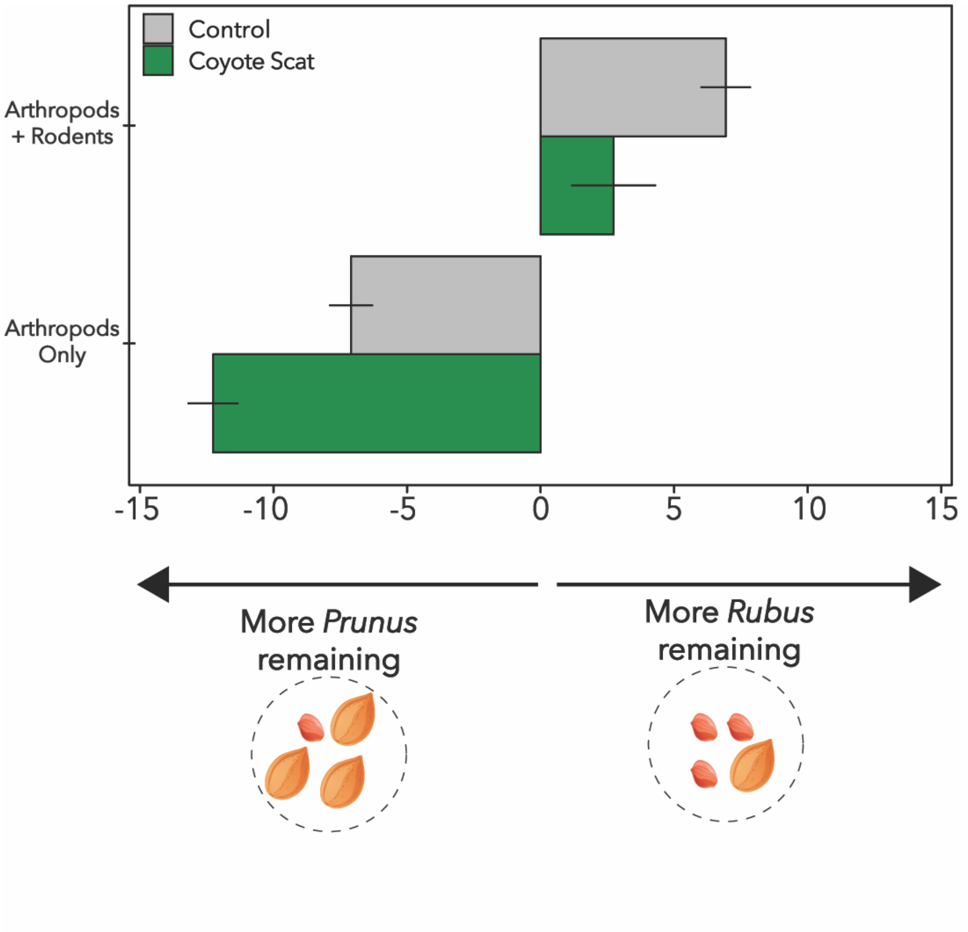

Figure 4. For each seed depot, we subtracted the number of *Prunus serotina* seeds remaining from the number of *Rubus allegheniensis* seeds after the deployment period to estimate how scat and granivore access modified the difference in removal rates between the two species. Bar graphs depict the average for each granivore access and scat treatment combination. Error bars represent one standard error. In full-access depots, *P. serotina* always had greater removal rates than *R. allegheniensis*, but scat significantly reduced this difference. In arthropod-only depots, *R. allegheniensis* always had greater removal rates than *P. serotina*, and this difference was greatest in the presence of scat.

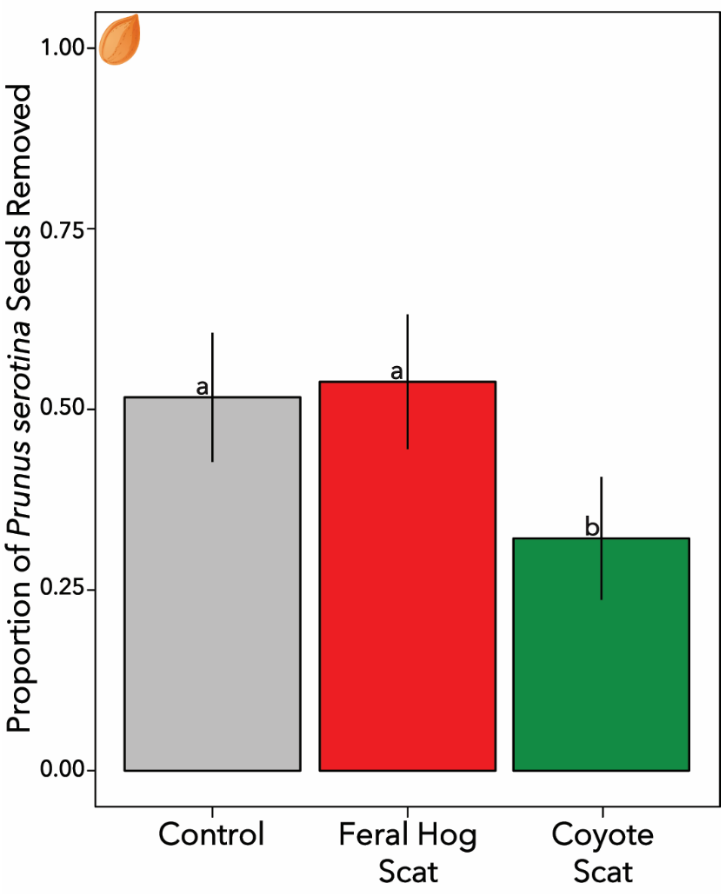

Figure 5. Bar graphs depict the average seed removal rates of *Prunus serotina* for each scat treatment. Error bars represent one standard error; bars that share a letter represent means that are not significantly different (i.e., P>0.05). Seed removal of *P. serotina* was significantly lower in depots containing coyote scat than in depots containing feral hog scat or no scat. There was no difference in the proportion of *P. serotina* seeds removed in depots containing feral hog scat and depots containing no scat.

CHAPTER 6

Social environment and time of day affect individual foraging decisions of a solitary forager, *Canis latrans*

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Bartel, S. L. Social environment and time of day affect individual foraging decisions of a solitary forager, *Canis latrans*. In preparation for submission to Ethology.

Abstract: Animal foraging decisions that shape individual fitness can determine species persistence and modify the strength of species interactions, like predation and seed dispersal. Many social animals, like coyotes (*Canis latrans*), may forage solitarily but have overlapping home ranges or territories with conspecifics. As a result, foraging individuals must navigate complex social environments to maximize energy intake while minimizing the costs of encounters with conspecific competitors, and the probability of encountering conspecific while foraging may predictably vary across both space and time. I examined how individual coyote foraging decisions at experimental resource patches were affected by time of day and conspecific visitation to patches. I found that solitary coyotes were more likely to investigate a resource patch towards the end of the diel activity period (β = -0.20, SE = 0.16) and were less likely to consume resources at patches that were visited by other individuals (β = 2.69, SE = 1.14). Juvenile coyotes were also more likely to consume resources at a patch than were adult coyotes. These results suggest that solitary foragers are responsive to the social environments in which

they forage and may make dynamic foraging decisions to reduce the likelihood of encountering a conspecific competitor while foraging. Moreover, these results highlight that animal foraging decisions may change over the course of the diel activity period, indicating that studies evaluating variation in behavior across the activity period may provide new insights into how animals respond to temporal changes in the environment.

Introduction

Animal foraging decisions can affect individual fitness (Stephens and Krebs 1986, Lima and Dill 1990, Brown et al. 1999, Lind and Cresswell 2005, Stephens et al. 2007, Kelt et al. 2019) as well as the nature and strength of species interactions (e.g., Orrock et al. 2003, Fortin et al. 2005, Ford et al. 2014, Smith et al. 2017, 2019a, Deacy et al. 2018, Gil et al. 2019, Tsuji et al. 2020). Hence, understanding how an individual's environment shapes individual foraging behavior may inform predictions of how rapid environmental changes may affect both species populations and ecological communities (Sih et al. 2011, 2012, Guiden et al. 2019, Manlick and Newsome 2021, Bartel and Orrock 2022). Significant advances have been made in the understanding of broad-scale foraging behavior of large animals, such as movement, habitat use, and activity time (i.e., where and when to forage), in part due to the proliferation of remote-sensing technologies (e.g., Wilson et al. 2012, Kohl et al. 2018, Guiden and Orrock 2019, Wittemyer et al. 2019, Owen-Smith et al. 2020, Smith et al. 2020, Gilbert et al. 2022); however, the fine-scale foraging decisions that animals make while active and within resource patches are less understood, particularly for elusive large mammals (Moll et al. 2007, Thompson et al. 2012, Northrup et al. 2019). For example, when an individual animal encounters a resource patch, it must make fine-scale foraging decisions to either bypass (ignore) the patch or to spend time investigating the patch and/or consuming resources in the patch. Such foraging decisions are mediated by aspects of the environment that affect the risk of attack by predators, competition with conspecifics or other species, and resource availability (i.e., patch quality; Stephens and Krebs 1986; Brown 1988; Brown and Kotler 2004). For example, an individual might choose to bypass a resource patch if the individual detects a cue in the environment of recent predator activity, or an individual may choose to investigate a resource patch to gather more information about the profitability of foraging in the patch.

An individual's social environment can affect individual foraging decisions by providing social information of resource patch quality and by determining the frequency and outcome of intraspecific interactions. Individuals may gain social information about the location of resources by observing the foraging behavior and foraging success of conspecifics (Thorpe 1963, Krebs et al. 1972, Giraldeau 1997, Giraldeau et al. 2002, Valone and Templeton 2002). Moreover, the presence of conspecifics in a patch can serve as a cue of patch quality, leading to a phenomenon known as conspecific attraction whereby individuals are more likely to select resource patches that are already utilized by conspecifics (Stamps 1988, Muller et al. 1997, Pérez-Cembranos and Pérez-Mellado 2015, Buxton et al. 2020). While this type of social information may allow individuals to reduce time and energy spent searching for resource patches and investigating the profitability of patches, foraging in patches that are utilized by other conspecifics can also reduce foraging efficiency by increasing intraspecific competition. "Cryptic interference competition" – whereby individuals experience reduced energy intake rates when foraging in the presence of conspecifics because they must spend time avoiding antagonistic encounters with conspecifics – has been found to occur in a variety systems in which animals forage in social groups (Henderson and Hart 1991, Gompper 1995, Gyimesi et al. 2010, Bijleveld et al. 2012, Zhao et al.

2020). However, it is unclear if cryptic interference competition affects individual foraging decisions in systems where social animals forage solitarily.

Many carnivores forage solitarily but share the same breeding territory with conspecifics, resulting in the formation of social groups that may contain mated pairs, offspring of mated pairs, and, in some cases, “helpers” of mated pairs that assist in rearing offspring (Moehlman and Hofer 1997, de Waal and Tyack 2003, Ward and Webster 2016a). Within such cooperative social groups, intra-group competition for resources can result in the formation of dominance hierarchies wherein dominant individuals sequester defensible resources and subordinate individuals often forego foraging efficiency to avoid aggressive encounters with dominants (Tilson and Hamilton 1984, Creel et al. 1991, Gese et al. 1996b, Gilbert-Norton et al. 2013, Ward and Webster 2016b). Moreover, the home ranges of individuals can overlap with the home ranges of individuals outside of these cooperative social groups, resulting in complex social environments that individuals must navigate while foraging to maximize energy intake while minimizing the costs of encounters with conspecific competitors. The costs of encountering conspecifics can be variable: subordinate individuals encountering dominant individuals in their group may simply cede a resource to dominant individuals without contest, whereas individuals that are not in the same group may engage in costly physical contests to establish or defend territory boundaries (Ward and Webster 2016b). These social environments are known to generate broad-scale patterns in foraging behavior such that individuals that are competitively subordinate to other individuals within their home range move farther distances during foraging forays to avoid encounters with more dominant conspecifics (Gese 2001a, Henry et al. 2005, Dorning and Harris 2017, Kamler et al. 2019, Dorning and Harris 2019). However, it is less appreciated how social environments may shape fine-scale individual foraging decisions, specifically decisions made once an individual encounters a resource patch (i.e., bypass, investigate, or consume resources). For example, individuals may be more likely to bypass an encountered resource patch and less likely to spend time consuming resources within the patch if the patch is frequently visited by conspecifics. Since these fine-scale foraging decisions can shape individual diet composition (Charnov 1976, Stephens and Krebs 1986), this current lacuna inhibits our ability to predict how changes in animal social environments may lead to drastic changes in the magnitude and nature of trophic interactions that shape ecological communities (e.g., frugivory and seed dispersal by animals; Bartel & Orrock 2022).

Another aspect of the environment that may be an important factor influencing individual foraging decisions is the time of day at which the resource patch is encountered. Time of day may provide information to a forager on the likelihood of encountering a predator or competitor (Alanara et al. 2001, Kronfeld-Schor and Dayan 2003, Kohl et al. 2018, Smith et al. 2019b, Cunningham et al. 2019, Bonnot et al. 2020). As a result, solitary foragers in social environments may be more likely to investigate a patch or consume resources at a patch towards the end of the population’s diel activity period (the window of time during which individuals are active each day) when conspecific activity is waning. Alternatively, an individual’s energetic condition may also change across its diel activity period (Houston and Mcnamara 2014), which may be another mechanism by which individual foraging decisions may depend upon the time of day at which the patch is encountered (Beauchamp and McNeil 2003, Ferguson et al. 2019). Since an individual’s energetic reserves tend to increase over the course of its diel activity period (Houston and Mcnamara 2014), individuals may be less likely to spend time investigating a resource patch early in the activity period when energetic reserves are low. While there is a growing body of literature showing that competition, predation risk, and human activities can modify the times of day at which individuals are active (e.g., Kronfeld-Schor and Dayan 2003, Tambling et al. 2015, Gaynor et al. 2018, Connolly and Orrock 2018, Kohl et al. 2018, Smith et al. 2019, 2020, Guiden and Orrock 2020, Bartel and Orrock 2021, Gilbert et al. 2022), it is unclear if individuals make different foraging decisions across the diel activity period.

Coyotes (*Canis latrans*) are social carnivores that often forage solitarily and exhibit a high degree of plasticity in both social and foraging behavior (Bekoff 1977, Bekoff and Wells 1986, Terry Bowyer 1987, Parker 1995, Gese et al. 1996a, Gese and Ruff 1997, Poessel et al. 2014). While coyote densities and the degree of home range overlap among individuals can be highly variable among landscapes (Parker 1995, Mastro 2011), resident coyotes often defend breeding territories, and individual space use is often a product of its social environment (Knowlton and Stoddart 1984, Andelt 1985, Gese et al. 1988, 1996a, Chamberlain et al. 2000, 2021, Kamler and Gipson 2000, Gese 2001b, Kamler et al. 2005, Schrecengost et al. 2009, Hickman et al. 2015, Hinton et al. 2015, Gifford et al. 2017). Research using pairs of captive coyotes has illuminated that an individual's social environment can mediate fine-scale individual foraging decisions (Gilbert-Norton et al. 2013). Interestingly, subordinate individuals learned to quickly relocate a resource patch when foraging alone in experimental foraging arenas; however, when the more dominant member of the pair was also foraging in the arena, subordinate individuals were less efficient at relocating the patch and were displaced from the patch by the dominant individual (Gilbert-Norton et al. 2013). These results provide strong evidence that fine-scale foraging decisions of coyotes are affected by the social environment, but there is still limited understanding of how the social environment shapes foraging decisions in wild populations where numerous individuals may utilize the same resource patches. The time of day at which a coyote encounters a patch may also affect these foraging decisions. Individuals may be more likely to investigate a patch or consume resources in a patch towards the end of the diel activity period when the likelihood of encountering a conspecific is waning. In order to evaluate how the social environment and time of day affects individual foraging decisions of wild coyotes, I established experimental resource patches in forested habitat in South Carolina and monitored individual coyote behavior at the resource patches using remote cameras. I used individual coyote foraging data from remote-camera video recordings to evaluate our 2 hypotheses: 1) individuals are more likely to investigate a resource patch late in the diel activity period and when the resource patch is not visited by other conspecific competitors, and 2) individuals are more likely to consume resources in a patch later in the diel activity period and when the resource patch is not visited by other conspecific competitors.

Methods

Study area and experimental resource patch design

This study was conducted at the Department of Energy (DOE) Savannah River Site (SRS; Aiken, SC), and 80,125-ha National Environmental Research Park (NERP). SRS was established by the DOE in 1951, and the USDA Forest Service manages the site on behalf of DOE. The majority of landcover (97%) at SRS is forest, and the canopy is predominantly composed of longleaf (*Pinus palustris*) and loblolly pines (*P. taeda*) (Kilgo and Blake 2005). The geographic range of coyotes has only recently expanded into the southeastern US over the past 60 years (Hill et al. 1987, Parker 1995), and the presence of coyotes in SRS was first documented in 1986 (Kilgo and Blake 2005). A 2005 survey of the coyote population at SRS estimated a density of 1.5 coyotes/km^2 (Schrecengost 2005). This survey also found that the average coyote home range at SRS was 30.5-31.85 km^2 (Schrecengost et al. 2009). Coyote home range overlap averaged 24% when excluding mated pair interactions, and 87.5% of coyotes had overlapping home ranges with one or more individuals (Schrecengost et al. 2009).

In July 2021, I created 19 experimental resource patches in forested habitat at SRS. Experimental patches were haphazardly selected to be in mature pine stands and 5-m from a secondary USFS road. In order to capture foraging behavior of the same individual at different stations, stations were concentrated in a 117-km^2 area and were separated by > 1 km. At each experimental patch, I added a food resource of 10 lbs of frozen, raw chicken breast at midday. Patches were checked daily and replenished with this resource as needed. Chicken breast was intentionally added in a frozen state in order to prevent depletion of the patch by diurnal scavengers before nocturnal coyotes would encounter the patch. A motion-activated camera trap with infrared flash (Bushnell 16MP Trophy Cam HD; Bushnell Corporation, Overland Park, KS) was positioned at each experimental patch for the duration of the experiment to capture individual coyote foraging decisions at the patch. Cameras were set to capture 15-second videos upon activation with a 10-second lag time between motion-activated recordings. Experimental patches were deployed for a total of 16 nights: starting midday 16 July 2021 and ending midday 1 August 2021.

Individual coyote foraging decision data collection

All videos of animal detections at the experimental patches were subsequently sorted and analyzed by a single observer to control for possible variation in behavioral classification and individual identification. I distinguished individual coyotes from photographs based on variation in fur coloration (normal coloration vs. melanistic), general age classification (juvenile vs. adult), coloration of the tip of the tail, amount of black banding patterns on the back, amount of white around the mouth, and distinctive physical abnormalities due to injury or disease (Séquin 2001, Séquin et al. 2003, Larrucea et al. 2007). Individual identifications were reviewed multiple times following initial video processing. I characterized independent detections at a patch as any sequence of videos of the same individual captured within 30 min at a patch; a common threshold for characterizing independent detections of large mammals (Kelly 2003, Kelly and Holub 2008, Wang et al. 2015, O'Connor and Rittenhouse 2017). For each independent detection, I recorded the date and time at which the individual arrived at the patch, and the behavior of the individual. Individual behaviors at patches were classified as bypass, investigate, and consume, and each behavior was treated as a binary variable. If the individual was detected at the patch but continued to travel past the patch without investigating or consuming the resource, then the individual was scored 1 for bypass behavior. If the individual did not bypass the patch and either investigated or consumed the resource, then the individual was scored 0 for bypass behavior. If the individual was detected at the patch, investigated the patch (i.e., spent time inspecting the resource from a distance and/or slowly approaching the resource), and did not consume the resource, then the individual behavior was scored 1 for investigation behavior. If the individual bypassed the patch or consumed the resource, then the individual was scored 0 for investigation behavior. If the individual consumed any amount of the raw-chicken resource, then the individual was scored 1 for resource consumption behavior. If the individual did not consume the resource, then the individual was scored 0 for resource consumption behavior. I also measured the distance in time between each coyote detection at a patch to account for the potential that patch depletion may affect individual foraging decisions (i.e., exploitation competition; see Appendix S1 for methods and results).

Data analysis

For each experimental patch, I calculated the total number of coyote individuals detected. I constructed a categorical variable of intraspecific competition to evaluate the effect of conspecific activity at a patch on individual foraging decisions. Patches where only one individual was detected were classified as “no competition,” and patches where more than one individual was detected were classified as “competition.” Since most of the coyote detections occurred within the diel period spanning evening to morning of the next day (i.e., crepuscular and nocturnal timing), I created a continuous variable, “hours since noon,” to quantify the timing of the detection. For detections that occurred after 12:00:00 and before 23:59:59, I calculated the difference in time between the initiation of that detection and 12:00:00 of that day. For detections that occurred after midnight and before 12:00:00, I calculated the difference in time between the initiation of that detection and 12:00:00 of the previous day (i.e., detection captured 1:30:00 would be calculated as 13.50 hours since noon).

To test how conspecific competition and time of day affects coyote decisions to investigate a resource patch, I used a binomial generalized linear mixed effects model (GLMM) with conspecific competition at the patch and hours since noon as fixed effects; individual ID as a random intercept; and investigation behavior as a binary response variable. To test how conspecific competition, time of day, and individual age affects coyote decisions to consume resources at a patch, I used a GLMM with conspecific competition at the patch, hours since noon, and age classification as fixed effects; individual ID as a random intercept; and resource consumption as a binary response variable. GLMMs were constructed using the *lme4* package (Bates et al. 2015) in R (R Core Development Team 2019).

Results

I detected coyotes at 16 of our 19 experimental resource patches. Across those 16 experimental resource patches, 7 of the patches were only visited by one unique individual (classified as patches with no intraspecific competition), and 9 of the patches were visited by multiple unique individuals (classified as patches with intraspecific competition). I captured 80 independent detections of coyote individuals, and 11 of the 80 detections were of juvenile coyotes. I identified 12 individual coyotes: 8 adults and 4 juveniles. Juvenile coyotes were only detected in patches with intraspecific competition. Coyotes chose to investigate experimental patches in 54% of the detections and chose to consume the resource in the patches in 21% of detections. The average distance in time between sequential coyote detections at a resource patch was 29.0 hours, indicating that coyote detections at a given resource patch rarely occurred on the same night (Appendix S1). Coyote activity was consistently distributed throughout the crepuscular and nocturnal diel period, starting in the evening and continuing until the morning (Fig. 1).

Time of day had a significant effect on the probability of an individual choosing to investigate a resource patch ($\beta = 0.23$, SE = 0.11, $X^2 = 4.58$, $P = 0.032$) such that individuals were more likely to investigate a patch towards the end of the diel activity period (Fig. 2). Conspecific competition at a patch ($\beta = -1.00$, SE = 0.74, $X^2 = 1.80$, $P = 0.179$) did not affect the probability of an individual choosing to investigate a resource patch. Conspecific competition had a significant effect on the probability of an individual choosing to consume the resource in a patch ($\beta = 2.69$, SE = 1.14, $X^2 = 5.54$, $P = 0.019$) such that individuals were more less likely to consume resources in patches that were visited by other individuals (Fig. 3). Time of day ($\beta = -0.20$, SE = 0.16, $X^2 = 1.52$, $P = 0.218$) did not affect the probability of an individual choosing to consume the resource in a patch. Individual age had a moderately significant effect on the probability of an individual consuming the resource (β = 2.43, SE = 1.37, X^2 = 3.16, P = 0.076) such that juveniles were more likely to consume resources than adults (Fig. 4).

Discussion

In this study, I found that individual coyote foraging decisions are affected by an individual's social environment as well as the time of day at which a resource patch is encountered. While the diel period of coyote activity started in the late evening, persisted throughout the night, and declined in the morning, coyotes were more likely to investigate resource patches when those patches were encountered later in the night, towards the end of the diel activity period. Individual coyotes were also less likely to consume resources at patches that were visited by other individuals. These results have two broad implications for our understanding of how aspects of an individual's environment may shape individual foraging decisions. First, an individual's social environment can affect resource consumption by solitary foragers. In finding a marginally significant effect of individual age on the individual's choice to consume resources, these results indicate that individual experience may also play an important role in mediating the foraging decisions of solitary foragers. Second, individual foraging decisions are likely to change across the diel activity period, which highlights the value of study designs that are able to capture fine-scale temporal variation in animal foraging.

The social environment of solitary foragers affects foraging decisions

In finding that individuals were less likely to consume resources at patches that were visited by other individuals, these results suggest that solitary foragers are responsive to the social environments in which they forage. While it is generally appreciated that individuals foraging in social groups may consume less energy due to exploitation or interference competition with conspecifics (Henderson and Hart 1991, Gompper 1995, Goubault et al. 2005, Aragón 2009, Gyimesi et al. 2010, Bijleveld et al. 2012, Fayet et al. 2015, Zhao et al. 2020), there is a limited understanding of how intraspecific competition may affect energy intake of solitary foragers (but see López-Bao et al. 2011). I expect that cryptic interference competition, whereby individuals forego foraging efficiency to avoid encounters with conspecifics, is a likely mechanism by which patch visitation by conspecifics may reduce the likelihood of resource consumption by solitary individuals. Past research on movement and space use of social carnivores that forage solitarily provides strong evidence that individuals are keenly aware of the space use of conspecifics (Gese 2001a, Henry et al. 2005, Dorning and Harris 2017, 2019, Kamler et al. 2019, Facka and Powell 2021). Individuals may acquire information about the likelihood of encountering a conspecific at a given patch either by experience (e.g., previously observing a conspecific at or near a patch) or by detecting cues of recent conspecific activity (e.g., conspecific odors). While it is unclear how individual coyotes acquire knowledge of conspecific visitation to resource patches, these results provide evidence that individuals may be aware of the probability of encountering a conspecific at a patch and may choose to forego consuming resources to avoid an encounter. These results suggest that coyotes may perceive encounters with conspecifics at resource patches as potentially costly events, and the costs of those encounters might outweigh the benefits of consuming an easily accessible resource, like the piles of raw chicken used in this study. While it is appreciated that defense of preferred resources by dominant individuals may cause subordinate individuals to consume secondary resources to avoid antagonistic encounters with dominants (Bartel and Orrock 2022), these results illustrate that the active defense of a resource by conspecifics is not necessary for some individuals to choose to avoid consuming resources in patches visited by conspecifics. Since intraspecific competition for resources can drive variation in resource use among individuals, leading to individual-level niche variation (Bolnick et al. 2003, Svanbäck and Bolnick 2007, Sheppard et al. 2018), it is possible that the effects of the social environment at a resource patch on coyote foraging decisions may be an important mechanism by which individual-level variation in diet arises in coyote populations (Fedriani and Kohn 2001, Ward et al. 2018). At the population level, coyotes typically have relatively wide niches with diets composed of a variety of animals and fruits (Schrecengost et al. 2008, Mastro 2011), and individual-level specialization and interindividual variation in diet can lead to populations having wide niche breadths (Bolnick et al. 2003). These behavioral results indicate that cryptic interference competition may be an important mechanism by which individual-level niche specialization and population-level niche generalization may arise in coyote populations. Since intraspecific variation in resource use by social animals can explain intraspecific variation in important trophic interactions like frugivory and seed dispersal (Zwolak and Sih 2020, Bartel and Orrock 2022), future research that examines how coyote social environments shape individual diet composition may reveal the importance of coyote sociality in mediating trophic interactions.

Individual experience may also play an important role in the decision to consume resources in new resource patches. These results found that juveniles were more likely to consume resources when encountering an experimental patch (Fig. 4), but the effect of individual age on this decision was only marginally significant. My ability to evaluate the importance of individual age in mediating foraging decisions was limited by sample size since only 11 of the 80 coyote detections were of juveniles (4 total individuals). These limited data do, however, show a clear trend (Fig. 4) that individuals of different age classes make different foraging decisions. It is possible that this difference in decision-making is either due to differences in individual experience or differences in the propensity to engage in riskier behaviors due to social status.

Many coyote populations are persecuted or exploited by human trappers and hunters, but exploitation is typically ineffective in reducing coyote populations because populations are able to rebound quickly via compensatory reproduction and immigration (Crabtree and Sheldon 1999, Knowlton et al. 1999, Kierepka et al. 2017, Kilgo et al. 2017). The long history of coyote exploitation in North America may explain why coyotes in this study spent time investigating the experimental patch 54% of time and only consumed the resource 21% of the time. A 2005 survey of the SRS coyote population estimated that 60% of coyote mortalities were caused by human hunting or trapping outside the boundary of SRS (Schrecengost et al. 2009); hence, wariness towards novel items, like camera traps, in the environment is likely to improve individual fitness in this context (Séquin et al. 2003, Mettler and Shivik 2007). Since past work in California has found that younger coyotes are more vulnerable to trapping (Sacks et al. 1999), it is suggested that coyotes in exploited populations either learn to avoid baited traps (i.e., become more neophobic) or that trapping creates artificial selection for more neophobic adults (Sacks et al. 1999, Mettler and Shivik 2007). These results provide further evidence that juveniles may be less wary of bait and therefore more susceptible to trapping in their expanded geographic range of the southeastern US. Alternatively, it is possible that juvenile individuals are generally less likely than adults to approach an experimental resource patch with a camera trap, and only juveniles with particularly bold or exploratory personalities were detected in this study (though recent studies by Michelangeli et al. (2016) and Brehm and Mortelliti (2018) indicate that personality may not always be correlated with trappability). If this is the case, then these results showing that juveniles are more likely to consume resources at experimental patches may be an artifact of sampling bias towards more bold and exploratory juveniles. However, past research does not support this interpretation of the results and instead indicates that dominant adult coyotes (i.e., alphas) are more wary of camera trap stations than subordinate individuals, which would include juveniles (Séquin et al. 2003).

Fine-scale temporal variation in foraging decisions

With the proliferation of new technologies that allow scientists to measure the activity time of elusive animals (e.g., remote cameras and temperature-sensors in live traps; Orrock and Connolly 2016), there is a rapidly growing body of literature showing that the timing of activity is an important component of individual foraging decisions and behavioral responses to environmental change (for examples, see Kronfeld-Schor and Dayan 2003, Tambling et al. 2015, Gaynor et al. 2018, Connolly and Orrock 2018, Kohl et al. 2018, Smith et al. 2019, 2020, Guiden and Orrock 2020, Bartel and Orrock 2021, Gilbert et al. 2022). This study contributes to this growing body of knowledge by illuminating that the propensity for animals to investigate resource patches changes over the course of their diel activity period. I found that individual coyotes were more likely to choose to investigate a resource patch – as opposed to bypassing it or consuming its resources – when they encountered the patch later in the night, towards the end of the diel activity period (Fig. 2). Past work with other taxa has also found that individual foraging decisions depend on the time of day, but the mechanisms behind this temporal variation vary. For example, honeybees are more likely to make reconnaissance flights to resource patches (i.e., investigatory foraging behavior) in the mornings at the beginning of the diel activity period in order to recruit hive members to profitable patches in the afternoon (de Vries and Biesmeijer 1998). While I found that individual coyotes also frequently exhibit similar investigatory behaviors at resource patches, the time of day at which these behaviors were more common may reveal a strategy to avoid encountering conspecifics at a patch, or possibly alerting a conspecific to the existence of the patch (*sensu* social information; Thorpe 1963, Giraldeau et al. 2002).

Since coyote activity declines as it gets later in the night (Fig. 1), individuals that are seeking to reduce the risk of an encounter with a conspecific at a resource patch should be more likely to spend time investigating patches later in the night. My results on individual decisions to consume resources at patches support this hypothesis. Since I found that individuals were more likely to consume resources in spaces where conspecifics are absent (i.e., safe spaces), it is also likely that individuals may choose safe times of day, when conspecific activity is declining, to investigate patches.

Individuals may also make different foraging decisions at different times of day due to temporal variation in thermoregulatory costs or energetic condition. Some animals increase foraging intensity during times of day when thermoregulatory costs are lower (Du Toit and Yetman 2005, Abdulwahab et al. 2019, Guiden and Orrock 2020). Ferguson et al. (2019) found that honeyeaters were more reluctant to abandon a resource patch after detecting a predator in the morning than at midday, presumably because individual energy reserves are lowest in the morning and increase throughout the day (Houston and Mcnamara 2014). Since investigating a resource patch costs the individual time and energy, it is possible that coyotes are more likely to do this later in the night when energy reserves are higher. While it is unclear if this temporal variation in investigatory behavior is caused by social constraints, energetic constraints, or a combination of the two, these results clearly illustrate that fine-scale individual foraging decisions can be more clearly understood when fine-scale temporal variation is considered.

Future studies that do not group foraging bouts across the diel period but instead consider the potential for foraging behavior to change across the diel period may provide more clarity as to how fine-scale temporal changes in an individual’s social environment and energetic condition shape behavior. Remote cameras have been widely used to reveal exciting new insights on how animals use broad-scale shifts in diel activity periods to avoid predators and humans (Tambling et al. 2015, Gaynor et al. 2018, Connolly and Orrock 2018, Kohl et al. 2018, Smith et al. 2019, 2020, Bartel and Orrock 2021), and I highlight that remote cameras can similarly be used to capture fine-scale shifts in foraging behavior within diel activity periods. Future insights into how foraging decisions change across the diel activity period may help predict the consequences of broad-scale shifts in diel activity periods due to global change, such as increased nocturnality or the truncation or expansion of activity periods (e.g., Gaynor et al. 2018, Guiden and Orrock 2019). Moreover, this approach may provide new insights into the temporal dynamics of species interactions. For example, the increased propensity of coyotes to investigate resource patches later in the night (and in the early morning) may explain patterns in activity time of prey species, such as white-tailed deer. Past work at SRS has found that white-tailed deer in risky habitats (i.e., habitats with less vegetative concealment from predators due to frequent fires) are more active in the evenings (early night) and less active later in the night (early morning; (Bartel and Orrock 2021). These temporal patterns in white-tailed deer activity may be explained, in part, by the increased likelihood of encountering a coyote investigating a resource patch later in the night. Future research that not only evaluates when predators are active but also evaluates the temporal variation of predator foraging decisions may therefore explain spatiotemporal patterns in predator-prey interactions.

Conclusions and future directions

The foraging decisions of solitary foragers can be shaped by both the social environment of a resource patch and the time of at which an individual encounters a resource patch. Interestingly, this study on the foraging decisions of individual coyotes indicates that coyotes may choose to investigate resource patches at times of day where the likelihood of encountering a conspecific is low and to consume resources in locations where the likelihood of encountering a conspecific is low. These results indicate that, in the same way that prey may prefer to forage in places and times of day where the risk of attack by predators is low (Connolly and Orrock 2018, Kohl et al. 2018, Guiden and Orrock 2019, Smith et al. 2019b, Bartel and Orrock 2021), social predators may prefer to forage in places and times of day where the risk of encountering a conspecific is low. Future research that evaluates how a predator's social environment mediates spatiotemporal overlap of predators and prey may provide new insights into predatory-prey dynamics, particularly in systems where predator social environments can rapidly change.

References

Abdulwahab, U. A., S. T. Osinubi, and J. Abalaka. 2019. Risk of predation: a critical force driving habitat quality perception and foraging behavior of granivorous birds in a Nigerian forest reserve. Avian Research 10:33.

Alanara, A., M. D. Burns, and N. B. Metcalfe. 2001. Intraspecific resource partitioning in brown trout: The temporal distribution of foraging is determined by social rank. Journal of Animal Ecology 70:980–986.

Andelt, W. F. 1985. Behavioral ecology of coyotes in south Texas. Wildlife Monographs 94:10–27.

Aragón, P. 2009. Sex-dependent use of information on conspecific feeding activities in an amphibian urodelian. Functional Ecology 23:380–388.

Bartel, S. L., and J. L. Orrock. 2021. Past agricultural land use affects multiple facets of ungulate antipredator behavior. Behavioral Ecology 32:961–969.

Bartel, S. L., and J. L. Orrock. 2022. The important role of animal social status in vertebrate seed dispersal. Ecology Letters 00:1–16.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beauchamp, G., and R. McNeil. 2003. Vigilance in Greater Flamingos foraging at night. Ethology 109:511–520.

Bekoff, M. 1977. *Canis latrans*. Mammalian Species:1–9.

Bekoff, M., and M. C. Wells. 1986. Social ecology and behavior of coyotes. Advances in the Study of Behavior 16:251–338.

Bijleveld, A. I., E. O. Folmer, and T. Piersma. 2012. Experimental evidence for cryptic interference among socially foraging shorebirds. Behavioral Ecology 23:806–814.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: Incidence and implications of individual specialization. American Naturalist 161:1–28.

Bonnot, N. C., O. Couriot, A. Berger, F. Cagnacci, S. Ciuti, J. E. De Groeve, B. Gehr, M. Heurich, P. Kjellander, M. Kröschel, N. Morellet, L. Sönnichsen, and A. J. M. Hewison. 2020. Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe. Journal of Animal Ecology 89:132–145.

Brehm, A. M., and A. Mortelliti. 2018. Mind the trap: large-scale field experiment shows that trappability is not a proxy for personality. Animal Behaviour 142:101–112.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37–47.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385–399.

Buxton, V. L., J. K. Enos, J. H. Sperry, and M. P. Ward. 2020. A review of conspecific attraction for habitat selection across taxa. Ecology and Evolution 10:12690–12699.

Chamberlain, M. J., B. S. Cohen, P. H. Wightman, E. Rushton, and J. W. Hinton. 2021. Fine-scale movements and behaviors of coyotes (*Canis latrans*) during their reproductive period. Ecology and Evolution 11:9588.

Chamberlain, M. J., C. D. Lovell, and B. D. Leopold. 2000. Spatial-use patterns, movements, and interactions among adult coyotes in central Mississippi. Canadian Journal of Zoology 78:2087–2095.

Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. The American Naturalist 110:141–151.

Connolly, B. M., and J. L. Orrock. 2018. Habitat-specific capture timing of deer mice (*Peromyscus maniculatus*) suggests that predators structure temporal activity of prey. Ethology 124:105–112.

Crabtree, R. L., and J. Sheldon. 1999. Coyotes and canid coexistence in Yellowstone. Page *in* T. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in Ecosystems: The Yellowstone Experience. Yale University Press, New Haven, US.

Creel, S., N. Marusha Creel, M. G. L Mffls, and S. L. Monfort. 1991. Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. Behavioral Ecology 8:298–506.

Cunningham, C. X., V. Scoleri, C. N. Johnson, L. A. Barmuta, and M. E. Jones. 2019. Temporal partitioning of activity: rising and falling top-predator abundance triggers community-wide shifts in diel activity. Ecography 42:2157–2168.

Davies, N. B., J. R. Krebs, and S. A. West. 2012. Competing for Resources. Pages 116–146 An Introduction to Behavioural Ecology. 4th edition. John Wiley & Sons, West Sussex, UK.

Deacy, W. W., J. A. Erlenbach, W. B. Leacock, J. A. Stanford, C. T. Robbins, and J. B. Armstrong. 2018. Phenological tracking associated with increased salmon consumption by brown bears. Scientific Reports 8:1–9.

Dorning, J., and S. Harris. 2017. Dominance, gender, and season influence food patch use in a group-living, solitary foraging canid. Behavioral Ecology 28:1302–1313.

Dorning, J., and S. Harris. 2019. Individual and seasonal variation in contact rate, connectivity and centrality in red fox (*Vulpes vulpes*) social groups. Scientific Reports 9:1–11.

Facka, A. N., and R. A. Powell. 2021. Intraspecific competition, habitat quality, niche partitioning, and causes of intrasexual territoriality for a reintroduced carnivoran. Frontiers in Ecology and Evolution 9.

Fayet, A. L., R. Freeman, A. Shoji, O. Padget, C. M. Perrins, and T. Guilford. 2015. Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird. Animal Behaviour 110:79–89.

Fedriani, J. M., and M. H. Kohn. 2001. Genotyping faeces links individuals to their diet. Ecology Letters 4:477–483.

Ferguson, S. M., L. N. Gilson, and P. W. Bateman. 2019. Look at the time: diel variation in the flight initiation distance of a nectarivorous bird. Behavioral Ecology and Sociobiology 73:1–7.

Ford, A. T., J. R. Goheen, T. O. Otieno, L. Bidner, L. A. Isbell, T. M. Palmer, D. Ward, R. Woodroffe, and R. M. Pringle. 2014. Large carnivores make savanna tree communities less thorny. Science 346:346–9.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science 360:1232–1235.

Gese, E. M. 2001a. Territorial defense by coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: who, how, where, when, and why. Canadian Journal of Zoology 79:980–987.

Gese, E. M. 2001b. Territorial defense by coyotes (Canis latrans) in Yellowstone National Park, Wyoming: Who, how, where, when, and why.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1988. Home range and habitat use of coyotes in southeastern Colorado. The Journal of Wildlife Management 52:640.

Gese, E. M., and R. L. Ruff. 1997. Scent-marking by coyotes, *Canis latrans*: The influence of social and ecological factors. Animal Behavior 54:1155–1166.

Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996a. Social and nutritional factors influencing the dispersal of resident coyotes. Animal Behavior 52:1025–1043.

Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996b. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. Canadian Journal of Zoology 74:769–783.

Gifford, S. J., E. M. Gese, and R. R. Parmenter. 2017. Space use and social ecology of coyotes (Canis latrans) in a high-elevation ecosystem: relative stability in a changing environment. Journal of Ethology 35:37–49.

Gil, M. A., M. L. Baskett, and S. J. Schreiber. 2019. Social information drives ecological outcomes among competing species. Ecology 100:e02835.

Gilbert-Norton, L. B., R. R. Wilson, and J. A. Shivik. 2013. The effect of social hierarchy on captive coyote (*Canis latrans*) foraging behavior. Ethology 119:335–343.

Gilbert, N. A., J. L. Stenglein, T. R. Van Deelen, P. A. Townsend, and B. Zuckerberg. 2022. Behavioral flexibility facilitates the use of spatial and temporal refugia during variable winter weather. Behavioral Ecology 00:1–9.

Giraldeau, A., T. J. Valone, and J. J. Templeton. 2002. Potential disadvantages of using socially acquired information. Philosophical Transactions: Biological Sciences 357:1559–1566.

Giraldeau, L.-A. 1997. The ecology of information use. Pages 42–8 *in* J. R. Krebs and N. B. Davies, editors. Behavioural Ecology: an evolutionary approach. 4th edition. Wiley-Blackwell, Hoboken, US.

Gompper, M. E. 1995. Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. Behavioral Ecology 7:254–263.

Goubault, M., Y. Outreman, D. Poinsot, and A. M. Cortesero. 2005. Patch exploitation strategies of parasitic wasps under intraspecific competition. Behavioral Ecology 16:693–701.

Guiden, P. W., S. L. Bartel, N. W. Byer, A. A. Shipley, and J. L. Orrock. 2019. Predator-prey interactions in the Anthropocene: Reconciling multiple aspects of novelty. Trends in Ecology and Evolution 34:616–627.

Guiden, P. W., and J. L. Orrock. 2019. Invasive shrubs modify rodent activity timing, revealing a consistent behavioral rule governing diel activity. Behavioral Ecology 30:1069–1075.

Guiden, P. W., and J. L. Orrock. 2020. Seasonal shifts in activity timing reduce heat loss of small mammals during winter. Animal Behaviour 164:181–192.

Gyimesi, A., R. A. Stillman, and B. A. Nolet. 2010. Cryptic interference competition in swans foraging on cryptic prey. Animal Behaviour 80:791–797.

Henderson, I. G., and P. J. B. Hart. 1991. Age-specific differences in the winter foraging strategies of rooks *Corvus frugilegus*. Oecologia 85:492–497.

Henry, C., M.-L. Poulle, and J.-J. Roeder. 2005. Effect of sex and female reproductive status on seasonal home range size and stability in rural red foxes (*Vulpes vulpes*). Écoscience 12:202–209.

Hickman, J. E., W. D. Gulsby, C. H. Killmaster, J. W. Bowers, M. E. Byrne, M. J. Chamberlain, and K. V Miller. 2015. Home range, habitat use, and movement patterns of female coyotes in Georgia: implications for fawn predation. Journal of the Southeastern Association of Fish and Wildlife Agencies 2:144–150.

Hill, E. P., P. W. Sumner, and J. B. Wooding. 1987. Human influences on range expansion of coyotes in the Southeast. Wildlife Society Bulletin 15:521–524.

Hinton, J. W., F. T. van Manen, M. J. Chamberlain, M. Kelly, M. Vaughan, and L. Pedrotti. 2015. Space use and habitat selection by resident and transient coyotes (*Canis latrans*). PLOS ONE 10:e0132203.

Houston, A. I., and J. M. Mcnamara. 2014. Foraging currencies, metabolism and behavioural routines. Journal of Animal Ecology 83:30–40.

Kamler, J. F., W. B. Ballard, P. R. Lemons, R. L. Gilliland, and K. Mote. 2005. Home range and habitat use of coyotes in an area of native prairie, farmland and CRP fields. American Midland Naturalist 153:396–404.

Kamler, J. F., and P. S. Gipson. 2000. Space and habitat use by resident and transient coyotes. Canadian Journal of Zoology 78:2106–2111.

Kamler, J. F., U. Stenkewitz, T. Gharajehdaghipour, and D. W. Macdonald. 2019. Social organization, home ranges, and extraterritorial forays of black-backed jackals. Journal of

Wildlife Management 83:1800–1808.

Kelly, M. J. 2003. Jaguar monitoring in the Chiquibul Forest, Belize. Caribbean Geography 13:19–32.

Kelly, M. J., and E. L. Holub. 2008. Camera trapping of carnivores: Trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. Northeastern Naturalist 15:249–262.

Kelt, D. A., E. J. Heske, X. Lambin, M. K. Oli, J. L. Orrock, A. Ozgul, J. N. Pauli, L. R. Prugh, R. Sollmann, and S. Sommer. 2019. Advances in population ecology and species interactions in mammals. Journal of Mammalogy 100:965–1007.

Kierepka, E. M., J. C. Kilgo, and O. E. Rhodes. 2017. Effect of compensatory immigration on the genetic structure of coyotes. The Journal of Wildlife Management 81:1394–1407.

Kilgo, J., and J. I. Blake, editors. 2005. Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site. Island Press, Washington, DC, USA.

Kilgo, J. C., C. E. Shaw, M. Vukovich, M. J. Conroy, and C. Ruth. 2017. Reproductive characteristics of a coyote population before and during exploitation. The Journal of Wildlife Management 81:1386–1393.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52.

Knowlton, F. F., and L. C. Stoddart. 1984. Coyote population dynamics: another look. Pages 93–111 *in* F. L. Bunnell, D. S. Eastman, and J. M. Peek, editors. Symposium on Natural Regulation of Wildlife Populations. Forest, Wildlife, and Range Experiment Station University of Idaho, Moscow, US.

Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White,

D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. Ecological Monographs 88:638–652.

Krebs, J. R., M. H. MacRoberts, and J. M. Cullen. 1972. Flocking and feeding in the Great Tit *Parus major* - an experimental study. Ibis 114:507–530.

Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics 34:153–81.

Larrucea, E. S., P. F. Brussard, M. M. Jaeger, and R. H. Barrett. 2007. Cameras, coyotes, and the assumption of equal detectability. The Journal of Wildlife Management 71:1682–1689.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68:619–640.

Lind, J., and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. Behavioral Ecology 16:945–956.

López-Bao, J. V, F. Palomares, A. Rodríguez, and P. Ferreras. 2011. Intraspecific interference influences the use of prey hotspots. Oikos 120:1489–1496.

Manlick, P. J., and S. D. Newsome. 2021. Adaptive foraging in the Anthropocene: can individual diet specialization compensate for biotic homogenization? Frontiers in Ecology and the Environment 19:510–518.

Mastro, L. L. 2011. Life history and ecology of coyotes in the Mid-Atlantic states: a summary of the scientific literature. Southeastern Naturalist 10:721–730.

Mettler, A. E., and J. A. Shivik. 2007. Dominance and neophobia in coyote (Canis latrans) breeding pairs. Applied Animal Behaviour Science 102:85–94.

Michelangeli, M., B. B. M. Wong, and D. G. Chapple. 2016. It’s a trap: sampling bias due to animal personality is not always inevitable. Behavioral Ecology 27:62–67.

Moehlman, P. D., and H. Hofer. 1997. Cooperative breeding, reproductive suppression, and body mass in canids. Pages 76–128 *in* N. Solomon and J. French, editors. Cooperative Breeding in Mammals. Cambridge University Press, Cambridge, UK.

Moll, R. J., J. J. Millspaugh, J. Beringer, J. Sartwell, and Z. He. 2007. A new "view" of ecology and conservation through animal-borne video systems. TRENDS in Ecology and Evolution 22:660–668.

Muller, K. L., J. A. Stamps, V. V Krishnan, and N. H. Willits. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). The American Naturalist 150:650–661.

Northrup, J. M., A. Avrin, C. R. Anderson, E. Brown, and G. Wittemyer. 2019. On-animal acoustic monitoring provides insight to ungulate foraging behavior. Journal of Mammalogy 100:1479–1489.

O'Connor, K. M., and T. A. G. Rittenhouse. 2017. Temporal activity levels of mammals in patches of early successional and mature forest habitat in eastern Connecticut. The American Midland Naturalist 177:15–28.

Orrock, J. L., and B. M. Connolly. 2016. Changes in trap temperature as a method to determine timing of capture of small mammals. PLOS ONE 11:e0165710.

Orrock, J. L., B. J. Danielson, M. J. Burns, and D. J. Levey. 2003. Spatial ecology of predator-prey interactions: corridors and patch shape influence seed predation. Ecology 84:2589–2599.

Owen-Smith, N., T. Morrison, R. Hetem, E. Bennitt, and F. Van Langevelde. 2020. Movement ecology of large herbivores in African savannas: current knowledge and gaps. Mammal Review 50:252–266.

Parker, G. 1995. Eastern Coyote: The Story of Its Success. 1st edition. Nimbus Publishing, Halifax, Nova Scotia.

Pérez-Cembranos, A., and V. Pérez-Mellado. 2015. Local enhancement and social foraging in a non-social insular lizard. Animal Cognition 18:629–637.

Poessel, S. A., E. M. Gese, and J. K. Young. 2014. Influence of habitat structure and food on patch choice of captive coyotes. Applied Animal Behaviour Science 157:127–136.

R Core Development Team. 2019. R. R Foundation for Statistical Computing, Vienna, Austria.

Sacks, B. N., K. M. Blejwas, and M. M. Jaeger. 1999. Relative vulnerability of coyotes to removal methods on a northern California ranch. The Journal of Wildlife Management 63:939–949.

Schrecengost, J. D. 2005. Home range and food habits of the coyote (*Canis latrans*) at the Savannah River Site, South Carolina. University of Georgia, Athens, GA.

Schrecengost, J. D., J. C. Kilgo, D. Mallard, H. S. Ray, and K. V Miller. 2008. Seasonal food habits of the coyote in the South Carolina Coastal Plain. Southeastern Naturalist 7:135–144.

Schrecengost, J. D., J. C. Kilgo, H. S. Ray, and K. V Miller. 2009. Home range, habitat use and survival of coyotes in western South Carolina. The American Midland Naturalist 162:346–355.

Séquin, E. S. 2001. The influence of social status on coyote vulnerability to photo-capture. University of Nevada, Reno.

Séquin, E. S., M. M. Jaeger, P. F. Brussard, and R. H. Barrett. 2003. Wariness of coyotes to camera traps relative to social status and territory boundaries. Canadian Journal of Zoology 81:2015–2025.

Sheppard, C. E., R. Inger, R. A. Mcdonald, S. Barker, A. L. Jackson, F. J. Thompson, E. I. K.

Vitikainen, M. A. Cant, and H. H. Marshall. 2018. Intragroup competition predicts individual foraging specialisation in a group-living mammal. Ecology Letters 21:665–673.

Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. Ecology Letters 15:278–289.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4:367–387.

Smith, J. A., E. Donadio, O. R. Bidder, J. N. Pauli, M. J. Sheriff, P. L. Perrig, and A. D. Middleton. 2020. Where and when to hunt? Decomposing predation success of an ambush carnivore. Ecology 101:e03172.

Smith, J. A., E. Donadio, J. N. Pauli, M. J. Sheriff, O. R. Bidder, and A. D. Middleton. 2019a. Habitat complexity mediates the predator–prey space race. Ecology 100.

Smith, J. A., E. Donadio, J. N. Pauli, M. J. Sheriff, and A. D. Middleton. 2019b. Integrating temporal refugia into landscapes of fear: Prey exploit predator downtimes to forage in risky places. Oecologia 189:883–890.

Smith, J. A., J. P. Suraci, M. Clinchy, A. Crawford, D. Roberts, L. Y. Zanette, and C. C. Wilmers. 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. Proceedings of the Royal Society B: Biological Sciences 284.

Stamps, J. A. 1988. The effect of body size on habitat and territory choice in juvenile lizards. Herpetologica 44:369–376.

Stephens, D. W., J. S. Brown, and R. C. Ydenberg, editors. 2007. Foraging: Behavior and Ecology. Page Animals. University of Chicago Press, Chicago, USA.

Stephens, D. W., and J. R. Krebs. 1986. Foraging Theory. Princeton University Press, Princeton, New Jersey, USA.

Svanbäck, R., and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B 274:839–844.

Tambling, C. J., L. Minnie, J. Meyer, E. W. Freeman, R. M. Santymire, J. Adendorff, and G. I. H. Kerley. 2015. Temporal shifts in activity of prey following large predator reintroductions. Behavioral Ecology and Sociobiology 69:1153–1161.

Terry Bowyer, R. 1987. Coyote group size relative to predation on mule deer. Mammalia 51:515–526.

Thompson, I. D., M. Bakhtiari, A. R. Rodgers, J. A. Baker, J. M. Fryxell, and E. Iwachewski. 2012. Application of a high-resolution animal-borne remote video camera with global positioning for wildlife study: Observations on the secret lives of woodland caribou. Wildlife Society Bulletin 36:365–370.

Thorpe, W. H. 1963. Learning and Instinct in Animals. Methuen, London.

Tilson, R. L., and W. J. Hamilton. 1984. Social dominance and feeding patterns of spotted hyaenas. Animal Behaviour 32:715–724.

Du Toit, J. T., and C. A. Yetman. 2005. Effects of body size on the diurnal activity budgets of African browsing ruminants. Oecologia 143:317–325.

Tsuji, Y., A. Campos-Arceiz, S. Prasad, S. Kitamura, and K. R. Mcconkey. 2020. Intraspecific differences in seed dispersal caused by differences in social rank and mediated by food availability. Scientific Reports 10:1532.

Valone, T. J., and J. J. Templeton. 2002. Public information for the assessment of quality: a widespread social phenomenon. Philosophical Transactions of the Royal Society B-Biological Sciences 357:1549–1557.

de Vries, H., and J. C. Biesmeijer. 1998. Modelling collective foraging by means of individual behaviour rules in honey-bees. Behavioral Ecology and Sociobiology 44:109–124.

de Waal, F. B. M., and P. L. Tyack, editors. 2003. Animal Social Complexity. Cambridge University Press, Cambridge, US.

Wang, Y., M. L. Allen, and C. C. Wilmers. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation 190:23–33.

Ward, A., and M. Webster. 2016a. Sociality: The Behaviour of Group-Living Animals. Springer International Publishing AG Switzerland, Cham, Switzerland.

Ward, A., and M. Webster. 2016b. Distributions of the costs and benefits within groups. Pages 111–124 Sociality: The Behaviour of Group-Living Animals. Springer International Publishing AG Switzerland, Cham, Switzerland.

Ward, J. N., J. W. Hinton, K. L. Johannsen, M. L. Karlin, K. V. Miller, and M. J. Chamberlain. 2018. Home range size, vegetation density, and season influences prey use by coyotes (*Canis latrans*). PLoS ONE 13:1–22.

Wilson, R. P., F. Quintana, and V. J. Hobson. 2012. Construction of energy landscapes can clarify the movement and distribution of foraging animals. Proceedings of the Royal Society B: Biological Sciences 279:975–980.

Wittemyer, G., J. M. Northrup, and G. Bastille-Rousseau. 2019. Behavioural valuation of landscapes using movement data. Philosophical Transactions of the Royal Society B 374.

Zhao, J.-M., N. Lyu, W. Cheng, and L.-Z. Zhou. 2020. Cryptic competition from neighbours significantly reduces intake rate of foraging greater white-fronted geese. Animal Behaviour 167:119–126.

Zwolak, R., and A. Sih. 2020. Animal personalities and seed dispersal: A conceptual review.

Functional Ecology 34:1294–1310.

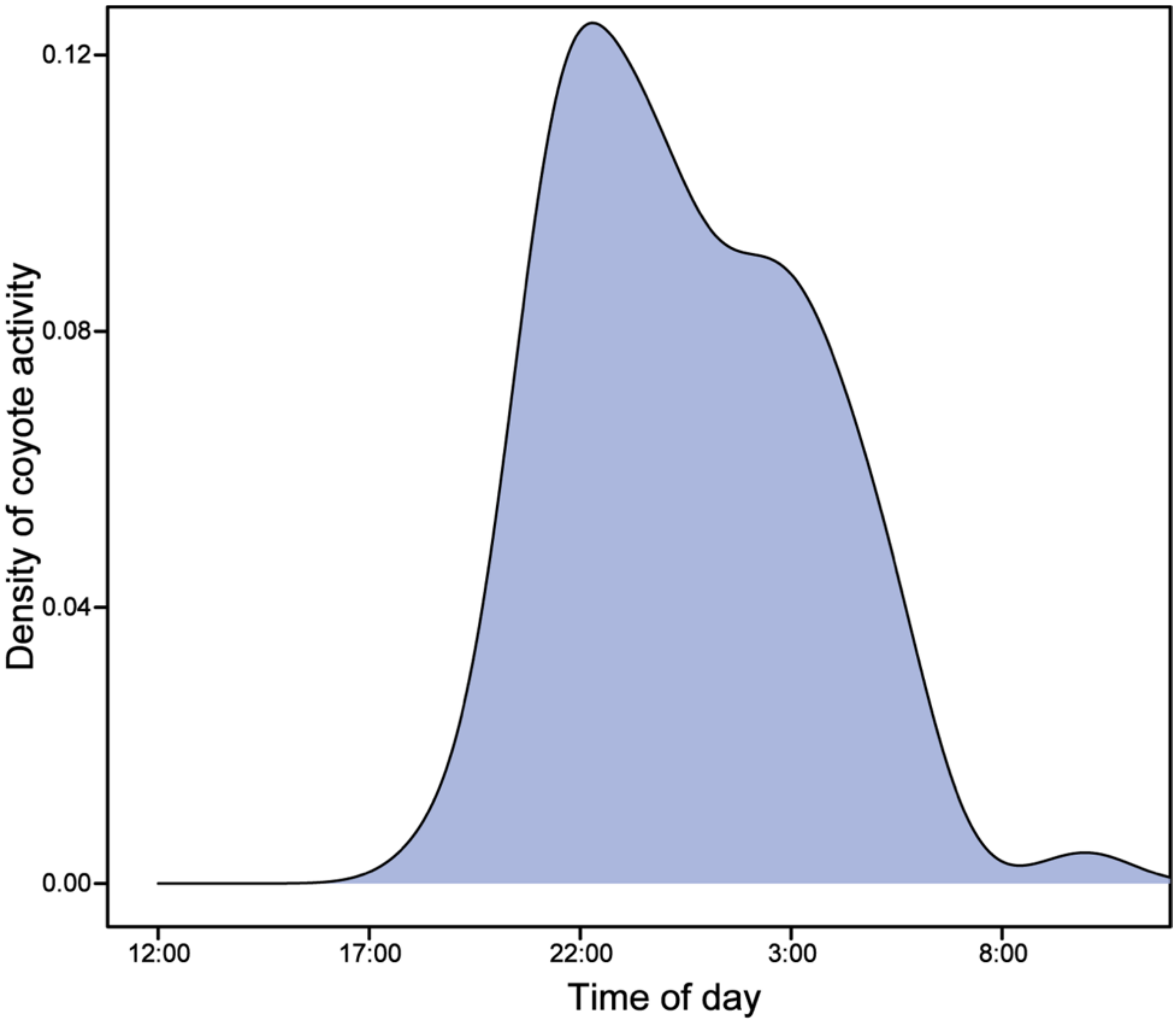

Figure 1. The distribution of coyote activity time peaked in the late evening and continued to decline later in the night.

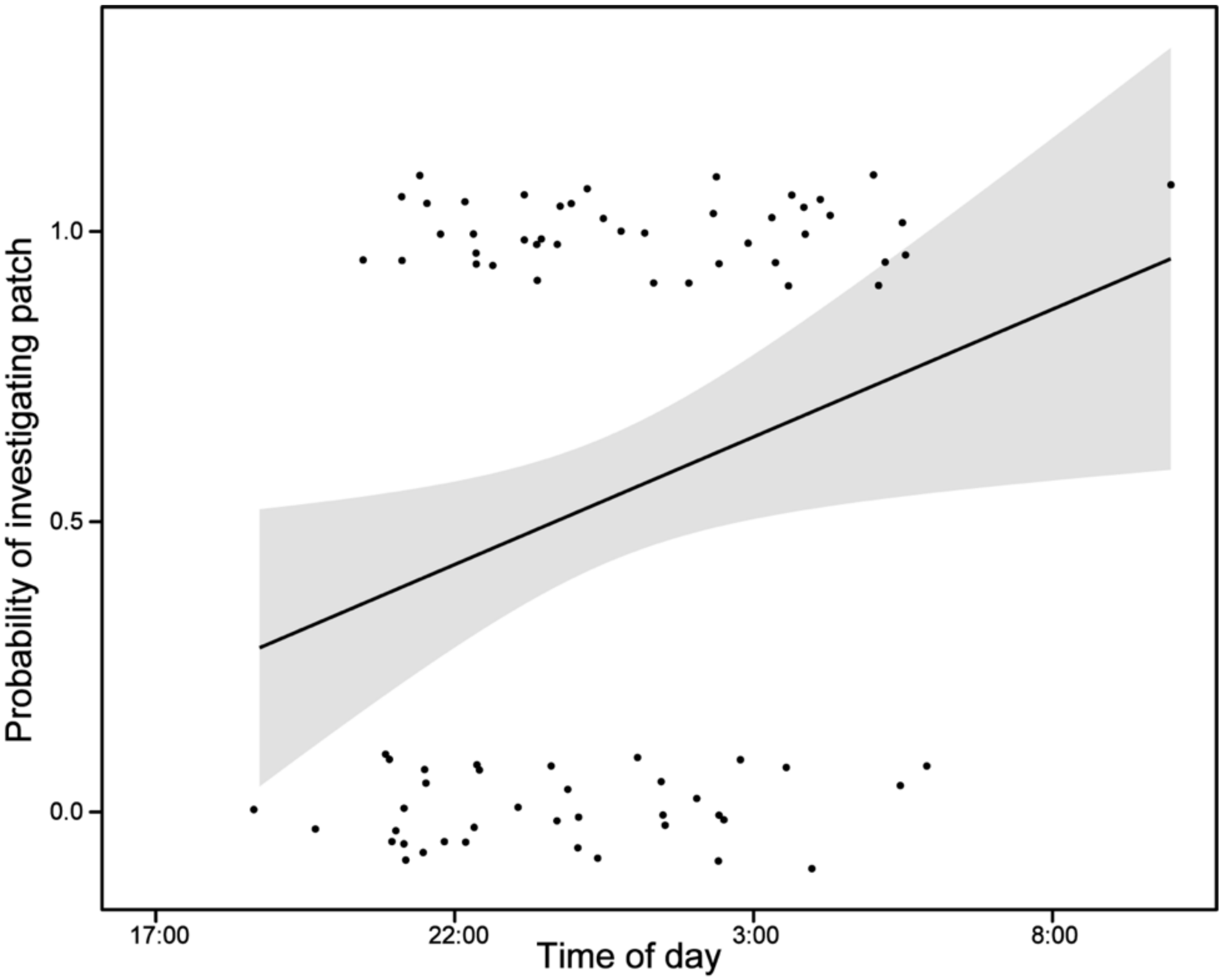

Figure 2. The probability that an individual coyote would investigate an experimental resource patch increased as it became later in the night, towards the end of the diel activity period. Points representing binary response data are scattered around 0 (did not investigate) and 1 (did investigate) to display otherwise overlapping points.

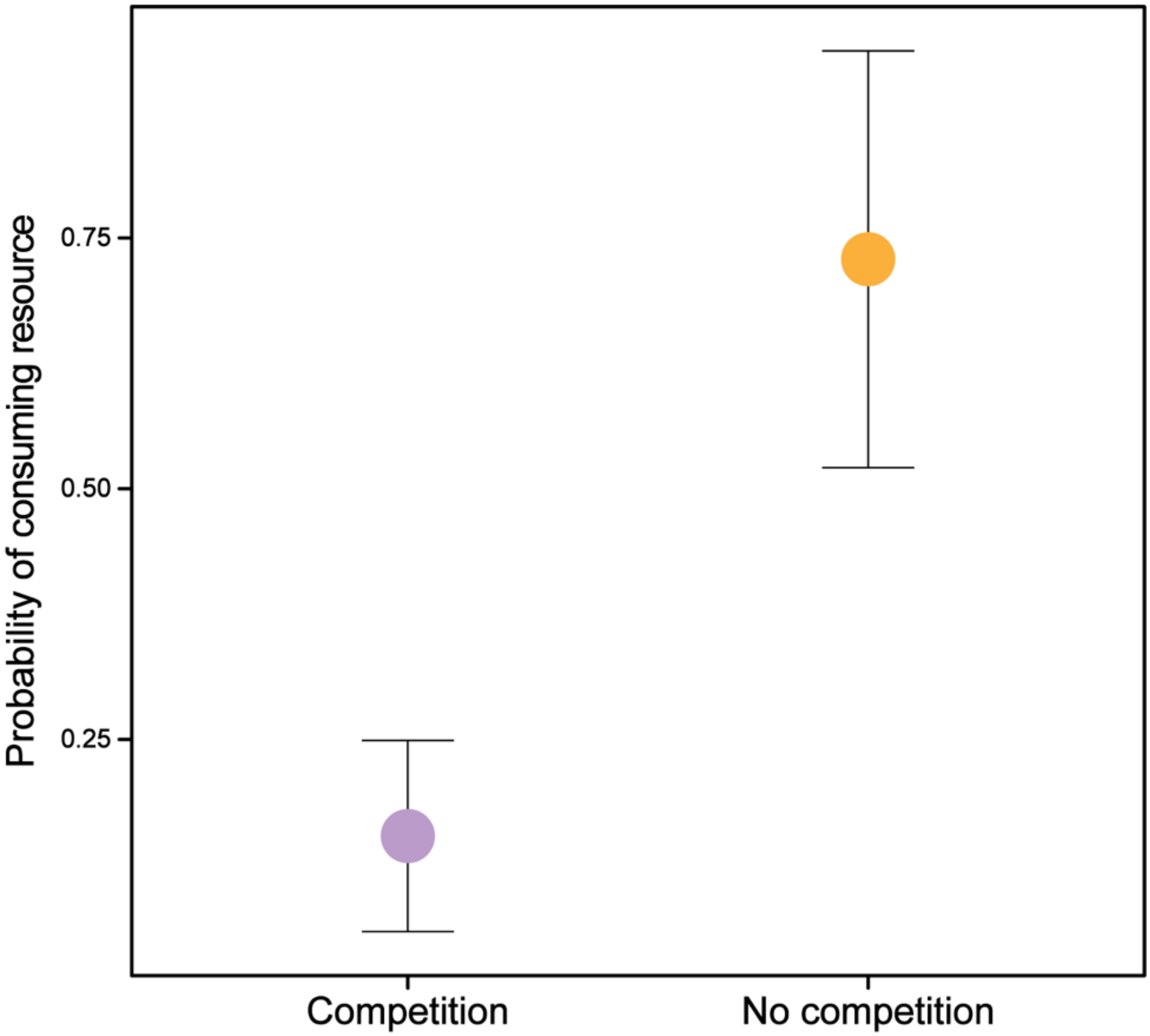

Figure 3. Individual coyotes were less likely to consume resources at experimental patches that were visited by other conspecific (i.e., patches with competition) than patches that were not visited by other conspecifics (i.e., patches with no competition). Circles show the estimated marginal means, and error bars show one standard error.

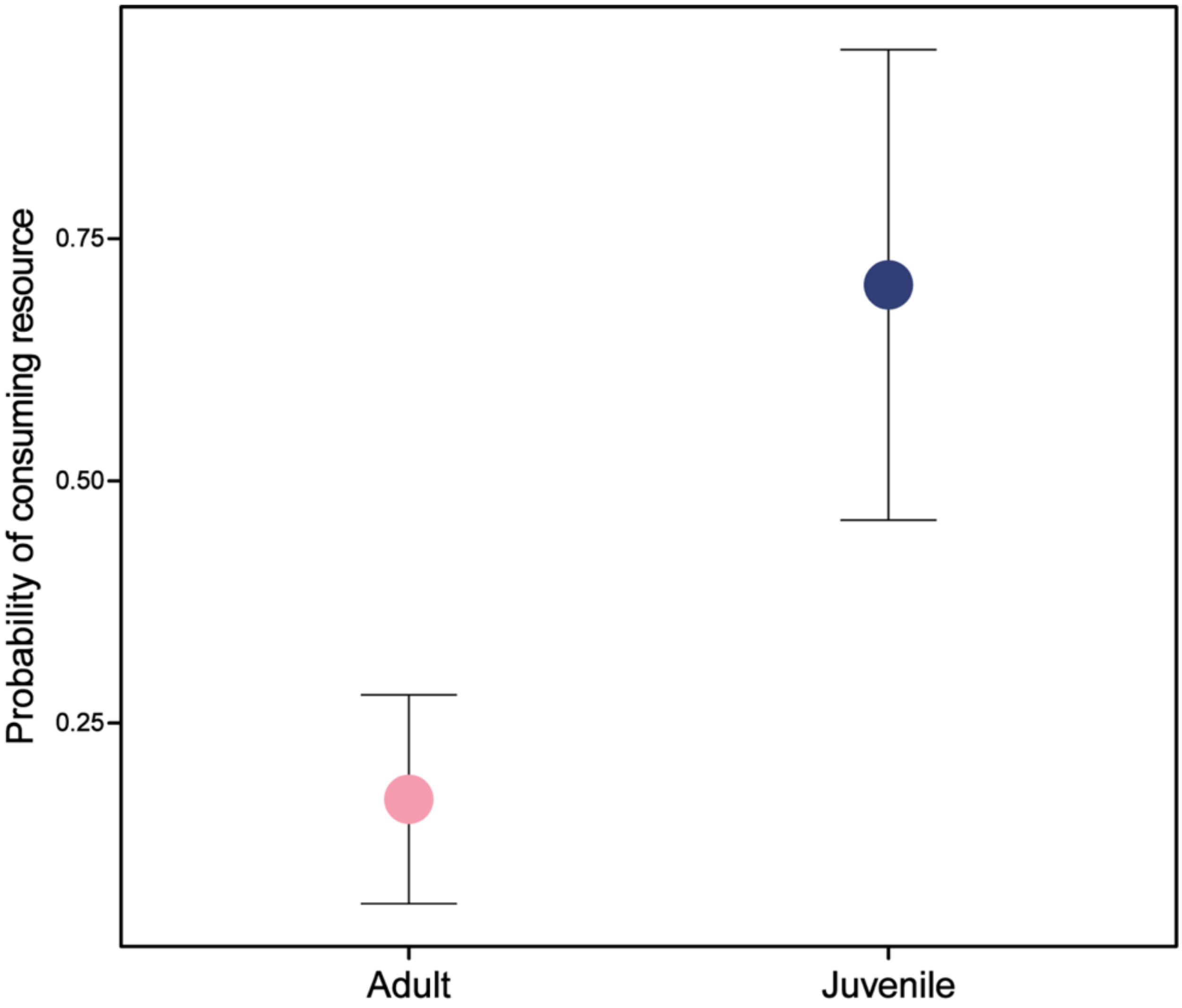

Figure 4. Adult coyotes were less likely to consume resources at experimental patches than were juveniles. Circles show the estimated marginal means, and error bars show one standard error.

Appendix S1. The distance in time between coyote detections at resource patches.

Methods: The presence of conspecifics at a resource patch may affect individual foraging decisions through exploitation competition (i.e., depletion of a resource by conspecifics; Davies et al. 2012). In order to reduce the likelihood that an experimental resource patch was depleted when individual coyote encountered the patch, patches were checked daily and replenished with this resource as needed. To further account for the potential effect of resource depletion by conspecifics on individual foraging decisions, I measured the distance in time between sequential coyote detections at a patch (i.e., time since previous coyote detection). I then constructed a generalized linear mixed effects model with a binomial distribution to measure how the time since the previous coyote detection affected an individual's decision to consume the resource at a patch. In this model, the consumption of the resource was the binary response variable, the hours since previous coyote dectection was a fixed effect, and individual identity was a random intercept.

Results: The average distance in time between sequential coyote detections at a resource patch was 29.0 hours, indicating that coyote detections at a given resource patch rarely occurred on the same night. I did not detect a significant effect of time since previous coyote detection on individual resource consumption ($\beta = 0.01$, SE = 0.01, $X^2 = 0.56$, $p = 0.455$).