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Human-mediated trophic mismatch between fire, plants and herbivores

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Trophic mismatches are commonly reported across a wide array of taxa and can have important implications for species participating in the interaction. However, to date, examples of trophic mismatch have centrally focused on those induced by shifts in climate. Here we report on the potential for humans to induce trophic mismatch by shifting the phenology of fire. Globally, anthropogenic fire ignitions are phenologically mismatched to that of historic lightning ignitions but the effects of this phenological mismatch on trophic interactions are poorly understood. Using fire records from 1980 to 2016 from the southeastern USA, a hotspot of anthropogenic fire, we demonstrate that there is a temporal mismatch between anthropogenic and lightning lit fires in this region. The peak of anthropogenic ignitions (i.e. 45% during March and April) occurred 3 months earlier than the peak in lightning-ignited fires (i.e. 44% occurred during June and July), a pattern consistent with reports from several other regions and continents. We demonstrate with a field experiment conducted at a nutrient-poor site in the southeastern U.S., that anthropogenic fire phenology shifts nutrient pulses in resprouting plants so that they mismatch herbivore reproductive demands. Consequently, plant nutrient quality in four commonly consumed forages was below the threshold to meet lactation requirements. Neonates subsequently were more likely to starve when born far from areas burned during the peak month of lightning fire phenology. Our data indicate that human activities may be an additional causative agent of trophic mismatch.

Keywords: climate change, deer, fire phenology, nutrient pulse, plant nutrients, trophic mismatch

Introduction

Trophic mismatches have long been recognized as a regulating force of population dynamics (match-mismatch hypothesis (Cushing 1974)) and are now

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commonly reported across a wide-range of taxa and ecosystems (Kerby et al. 2012). These mismatches can have severe fitness consequences because many consumers have distinct, short periods of heightened nutritional demands that remain phenologically similar from year to year. For example, lactation is the most nutritionally demanding physiological condition in mammals (Bronson 1989), and in birds, demands are greatest during migration or reproduction (Bairlein 1990). Nearly universal to all consumers is that increased nutritional demands usually co-occur with natural pulses in the resources they exploit. For example, ungulate reproductive synchrony and phenology are driven by vegetation phenology (Sinclair et al. 2000), frugivore demands co-occur with fruit availability (Bairlein 1990), insectivore needs co-occur with insect availability (Bronson 1989), and even migrations are often timed with resource pulses at stopover or destination areas (Buler et al. 2007). Thus, matching phenology of nutritional demands with seasonal pulses in available nutrition is a nearly universally important natural history trait among consumers.

To date, virtually all examples of trophic mismatches have been linked to climate change (Kharouba et al. 2018). In fact, we were unable to find mention of other potential causes in the recent empirical literature. The most severe consequences of phenological shifts to food webs come when the response of the resource and its consumers are asynchronous to the shared change (Visser and Both 2005, Parmesan 2006, Both et al. 2009, Thackeray et al. 2010, Kerby et al. 2012). Climate-driven mismatches have been reported in a variety of ecosystems with varying species and community-level consequences (e.g. birds (Visser et al. 1998, Both et al. 2009, Grémillet and Boulinier 2009), herbivores (Visser and Holleman 2001, Post and Forchhammer 2008), pollinators (Hegland et al. 2009) and fish (Edwards and Richardson 2004, Winder and Schindler 2004)). Global climate change is predicted to affect most food webs in this way (Walther et al. 2002, Post et al. 2009) and may have dramatic consequences on the structure and function of those communities (Costello et al. 2006, Parmesan 2006, Borcherding et al. 2010). While reports of trophic mismatches resulting from climate change have advanced our understanding of the mechanisms at play and their consequences, it is unlikely that climate change is the only proximate mechanism inducing trophic mismatches. Given the vast impact of humans on the earth system, and the widespread importance of fire, human use of fire may provide an example of human-induced trophic mismatch.

Fire has affected the spatial distribution of terrestrial ecosystems for billions of years (Scott 2000, Bond et al. 2005, Archibald et al. 2013). Hence, many terrestrial plant communities evolved adaptations to fire (Pausas and Keeley 2009, Keeley et al. 2011). Similarly, primary and secondary consumers in those communities evolved to exploit resources whose availability is regulated by fire (Brennan et al. 1998, Harper et al. 2016). Entire food webs are influenced by fire, and changes to fire regimes could affect interactions in those food webs. Harnessing fire as a tool has been essential to humans (Glikson 2013), and anthropogenic fire has been used for tens of thousands of years to manipulate the environment (Bar-Yosef 2002, Archibald et al. 2012). However, even contemporary anthropogenic fire regimes, despite a shift in focus to ecological restoration, phenologically mismatch that of lightning season fires across the world (Saamak 2001, Bartlein et al. 2008, Bird et al. 2008, Knapp et al. 2009, Balch et al. 2017). Around 4 million km^2 of the terrestrial landscape burns annually (Giglio et al. 2006), and humans are the dominant ignition source in all ecosystems. Moreover, humans have tripled the length of the fire season, and human-ignited fires affect a much larger portion of the terrestrial landscape than do lightning-ignited fires (Archibald et al. 2012, Balch et al. 2017).

One key adaptation of plants to fire is resprouting (Keeley et al. 2011, Clarke et al. 2013, Pausas and Keeley 2014, 2017), and one key adaptation of primary consumers to fire is to exploit resprouting plants (Archibald et al. 2005, Allred et al. 2011). The fire and herbivory interaction promotes a unique and dynamic outcome dissimilar to either force in isolation (Fuhlendorf et al. 2009, Westlake et al. 2020). Fire attracts herbivores, which decrease available fuel for subsequent fire by consuming plants (Archibald et al. 2005, Fuhlendorf et al. 2009). That interaction promotes spatiotemporal heterogeneity in community structure as herbivores follow fire to new areas (Edwards and Richardson 2004, Fuhlendorf et al. 2010, Bielski et al. 2018, Westlake et al. 2020). As a result, fire and herbivory interactions have a stabilizing effect on community structure when intact (Van Langevelde et al. 2003), but those interactions are likely sensitive to characteristics of the fire regime rather than fire itself (Keeley et al. 2011). While this point has been emphasized in the literature regarding frequency of fire in fire regimes (Keeley et al. 2011), far less attention has been paid to how the phenology of fire might affect biological interactions (Knapp et al. 2009, Lashley et al. 2015a).

Because fire causes a temporary nutrient pulse by increasing plant quality and biomass (Christensen 1977, Boerner 1982, Batmanian and Haridasan 1985, Singh 1993, Van de Vijver et al. 1999, Lashley et al. 2011, 2015a, Eby et al. 2014), fire phenology should affect nutrient availability for herbivores which may influence plant–herbivore interactions. For example, a mismatch between nutrient availability and herbivore demands is a near certainty if fires occur before the growing season because plant resprouting co-occurs with spring green-up when the fire occurs before the onset of growing season. Thus, fires that occur any time before green-up are unlikely to shift the timing of nutrient availability as compared to the normal plant green-up cycle. However, fires that top-kill plants after spring green-up necessitate that resprouting must be delayed relative to normal spring green-up. This relationship was observed recently when plant phenology, as measured by reaching full fruit maturity, was mediated by the timing of the previous fire (Lashley et al. 2015a). Delaying plant phenology could be an important attribute of fire timing to herbivores if their peak nutritional demand occurs later in the year than the peak resource availability of normal spring green-up.

We investigated anthropogenic use of fire as a cause of human-induced trophic mismatch. Using fire occurrence data, we evaluated seasonal timing of human-mediated fire versus lightning fire of the southeastern United States. We then designed a field experiment where we manipulated the seasonal timing of fire to test the hypothesis that fire phenology modulates the timing of resource availability relative to the nutritional demands of a local herbivore and measured the effect of proximity to that resource on survival probability of neonates.

Material and methods

Regional fire data

We downloaded wildland fire occurrence data for all fires that occurred in 11 states in the southeastern United States for the time period of 1980–2015 from the federal fire occurrence database (<https://wildfire.cr.usgs.gov/firehistory/data.html>). The states chosen included Alabama, Arkansas, Georgia, Florida, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, Virginia and West Virginia. We extracted all fires known to be caused by lightning and all fires that were known to be prescribed, along with their respective ignition dates. We used the start date listed for each fire to assign it to month of ignition. We then plotted the average percentage with standard error across years by month of anthropogenic and lightning ignited fires.

Field experiment study area

We sampled forage quality and neonate survival at Fort Bragg Military Installation (Fort Bragg), North Carolina, USA (35.1°N, −79.2°W). The 73 469 ha area was located in the Sandhills physiographic region of the longleaf pine *Pinus palustris* ecosystem. This ecosystem and the species within evolved over millennia with relatively frequent (3-year average), low-intensity surface fires occurring due to lightning, and native American activities over the past 10 000–20 000 years (Outcalt 2000). For the purposes of restoring ecosystem function and conserving endangered species, the United States Department of Defense has managed forested stands on a 3-yr fire regime (Lashley et al. 2014b). The parturition phenology of the local ungulate (i.e. white-tailed deer *Odocoileus virginianus*) peaks in early June (Chitwood et al. 2015a). Thus, because the peak nutritional demand occurs during lactation 3–6 weeks after parturition in white-tailed deer (Hewitt 2011), the peak nutritional demand based on reproductive phenology of this herbivore in this area is during July.

In this study area, soil productivity is particularly poor (Lashley et al. 2015b). Thus, deer may be sensitive to shifts in resource pulse phenology. As evidence of this nutritional burden, a relatively large portion of neonates starve on the site, regardless of fire timing, as compared to similar studies in more productive soil regions (Chitwood et al. 2014, 2015b). Likewise, diet selection is relatively narrow and concentrated on obtaining exceedingly limited quantities of phosphorus (Lashley et al. 2015b, 2016). Moreover, predation risk is relatively high (Chitwood et al. 2014, 2015b, 2017) and may limit female selection of the highest quality resources during lactation (Lashley et al. 2015c). Importantly, this population does not have access to anthropogenic subsidies as is common in other parts of their range, so changes in starvation should be related to available nutrition in the native plant community.

Field experiment study design

In a randomized block design, we selected four upland longleaf pine forest stands in each of 3 separate watersheds (blocks), averaging ~8 km apart, with similar soil types (Candor Sands complex) and similar basal area (45–60 m^2 ha^{-1}). We randomly assigned stands to each of four fire phenologies relative to our plant sampling period (see next section): fires ignited in June of the previous year (1 year-since-fire), and fires ignited in the same year in February (i.e. early anthropogenic phenology), April (i.e. late anthropogenic phenology) and June (lightning phenology). The February fire phenology was meant to represent the onset of the anthropogenic fire season (Brennan et al. 1998, Cox and Widener 2008). The April fire phenology was intended to represent the end of the anthropogenic fire season (Platt et al. 1988, Robbins and Myers 1992, Streng et al. 1993, Glitzenstein et al. 1995, Kirkman et al. 1998, Hiers et al. 2000, Knapp et al. 2009). The June fire phenology was meant to represent the peak in lightning fires for this region (Knapp et al. 2009). Each block contained a replicate from each treatment, and 1 year-since-fire was intended to be the control for comparison to fires ignited in the same year because previous reports suggested that any nutritional benefits would be lost after a single growing season (Dills 1970, Wood 1988, Carlson et al. 1993, Van de Vijver et al. 1999, Long et al. 2008, Nichols et al. 2021).

Plant sampling and analysis

We selected 4 native plant species that occurred in every replicate of each fire treatment. Because deer eat plants of several growth forms, we selected 2 trees, 1 shrub and 1 forb to ensure the plants represented responses across functional groups. The trees collected were common persimmon *Diospyros virginiana* and sassafras *Sassafras albidum*, the shrub was dwarf huckleberry *Gaylussacia umosa* and the forb was fragrant goldenrod *Solidago odora*. We selected these species because they are common in the study area and commonly consumed by white-tailed deer (Lashley et al. 2015b, 2016).

In each month of the growing season (i.e. May–September), we remotely established a plot center in each replicate of each treatment using a geographic information system. We navigated to the a priori selected plot center and collected the foliage of the nearest 10 plants of each species that were in the understory strata (i.e. < 1.5 m tall), separately bagging young leaves and the mature plant parts not typically eaten by this herbivore (Lashley et al. 2014a). We used previous data collected on site to determine that 10 plant samples was robust to the expected variation in intraspecific plant nutritional value (Lashley et al. 2015b). We separated physiologically mature and immature plant parts because plant maturity affects quality, and we were interested in how fire affects relative maturity of plant tissue, quality of young leaves, as well as quality of the whole plant. We assumed that secondary plant compounds were not significantly affecting nutritive quality based on results presented in Jones et al. (2010) that demonstrated tannin defensive compounds in forages consumed by herbivores in this region were generally low. If a plant was discolored, malformed or damaged (by herbivory or otherwise), we did not collect the plant tissues and instead sampled the next nearest plant. To avoid biases associated with forage handling, we followed the protocol presented by Lashley et al. (2014a) by transporting samples within 3 hours to a convection oven and drying forages to constant mass at 47°C. After drying samples, we measured weight to the nearest 0.01 g of the young and mature plant parts and shipped samples to the Clemson University Agricultural Service Laboratory, which was certified by the United States National Forage Testing Association.

The lab performed a standard full nutrient array with chemical determination methods to yield the percent of each sample of young and mature plant parts that was crude protein (i.e. nitrogen × 6.25; CP), acid detergent fiber (ADF) and neutral detergent fiber (NDF). For the same samples, we obtained measurements for macro-nutrients phosphorus (P), potassium (K) and calcium (Ca), and micro-nutrients magnesium (Mg), zinc (Zn), copper (Cu), manganese (Mn), iron (Fe), sulfur (S) and sodium (Na). After obtaining the nutritional parameters for physiologically young and mature plant parts, we calculated the whole plant nutritional value by weighting each sample by the relative proportion of physiologically young and mature plant parts and their associated nutritional values.

For the purposes of understanding the effects of fire phenology mismatch on available nutrition for white-tailed deer, we calculated the phosphorus requirements of a lactating white-tailed deer conservatively based on the minimum concentration needed to obtain adequate phosphorus assuming forage abundance was not limiting maximum possible physiological intake. We used this nutrient specifically because it was formerly deemed the limiting nutrient on this study site (Lashley et al. 2015b). However, we recorded the array of nutrients because it was part of a standard analysis at the lab. We assumed a maximum daily intake for a 45 kg animal (i.e. average adult female on site (Lashley et al. 2015b)) was 4.8% of the body weight or 2.16 kg day^{-1} (dry matter), which is the reported physiologically limited possible dry matter intake for female white-tailed deer during peak lactation (National Research Council 2007). Our intention with this calculation was simply to compare the forage quality in terms of phosphorus availability in the plants following each respective fire phenology to determine if those plants would meet the phosphorus requirement for an average size female with one fawn in the study area. We estimated the phosphorus concentration of the plants would need to be a minimum of 0.025% for a lactating female which is consistent with previous estimates (McEwen et al. 1957, Barnes et al. 1990).

In JMP Pro 11.0 (SAS Corporation, Cary North Carolina, USA), we fit general linear mixed models with restricted maximum likelihood to evaluate the effects of fire treatments on the proportion of biomass contributed by young leaves, the nutritional quality of young leaves and the nutritional quality of the whole plant. We included random effects of drainage (i.e. block) and plant species to control for influences on nutritional quality not related to fire.

Influence of fire phenology on deer reproductive success

To determine the influence of fire phenology on deer reproductive success, we radiotagged pregnant female white-tailed deer in winter to identify birth site locations relative to burned areas on the landscape and measure the subsequent survival of the neonates. Each female was fitted with a vaginal implant transmitter (VIT) to aid in the discovery of birth sites and hours-old neonates. We fitted each neonate with an expandable, breakaway VHF collar that had a 4-hr motion-sensitive mortality switch. We monitored neonates intensively (i.e. every 4–8 hrs) for the first month of life via VHF and continued monitoring survival at reduced time intervals until fawns reached 16 weeks (Chitwood et al. 2015a). Thus, survival of neonates was our proxy for reproductive success in this study. When we detected a mortality signal from the collar, we tracked to the collar to determine cause of mortality using field evidence and, when predation was evident or suspected, DNA swabs for residual predator saliva on the carcass and/or radiotag (Chitwood et al. 2015a). We necropsied all carcasses to finalize cause of mortality; individuals with no signs of predation that had lost body mass since capture and had empty digestive tracts were classified as starvation (Chitwood et al. 2015a). We used the birth site location of each neonate to calculate a straight line distance to the nearest area burned during the lightning season (i.e. June in the study area). This allowed us to determine if proximity to areas burned in the lightning season affected the likelihood of neonate starvation. Using a binary logistic regression in JMP Pro 11.0, we used the straight line distance from each birth site to the nearest area burned during the lightning phenology to predict the probability of starvation. Our rationale for using straight line distance to areas burned in lightning season was that in this resource limited environment, which does not contain anthropogenic subsidies or agriculture, the predicted pulse in available nutrients following fire would serve as the highest quality foraging opportunity for lactating females in this system and thus, serve as a primary means to meet the demands of lactation (Chitwood et al. 2015a, 2017, Lashley et al. 2015b, Nichols et al. 2021). All protocols presented herein were approved by the North Carolina Wildlife Resources Commission and the NCSU IACUC (no. 10-143-O).

Results

Regional fire

We collected data on 4541 lightning-generated fires and 5224 anthropogenic fires over the 36-year data set. Over that time period, a peak in lightning-ignited fires occurred during June and July, with 44% of lightning fires occurring in those two months (Fig. 1A). Also, a peak occurred in human-ignited fires, but the peak was three months earlier than lightning fires, with 45% of fires occurring in the months of March and April. On average, 66% of prescribed fires occurred between January and April whereas only 16% of lightning fires occurred during those months.

Field experiment

Leaf phosphorus, which was previously identified as the limiting nutrient to herbivores in this study area (Lashley et al. 2015b), on average across the four plant we sampled, did not meet the nutritional requirements of an adult female white-tailed deer to support lactation for a single fawn when burned a year prior (Fig. 1B). Anthropogenic fire phenology, lit in February or April, both increased leaf P concentrations relative to plants burned the year prior (Fig. 1C–D), but only during May, before peak lactation of white-tailed deer in the study area. Lightning fire phenology caused a pulse in leaf P relative to plants burned the year prior, which coincided with peak lactation in July and August and surpassed the minimum level needed to meet lactation requirements for a single fawn (Fig. 1E). Similar patterns were observed in many other plant nutritional qualities both in the young plant tissues selected by deer and in the whole plant in general (Supporting information).

Fire timing affected the proportion of available biomass comprised of young leaves ($p < 0.01$, $r^2 = 0.3$; Fig. 2). In particular, plants contained a greater proportion of young leaves in the 3 months following lightning phenology (i.e. June-lit fire) as compared to the control (i.e. 1 year-since-fire; $\beta = 0.14$, $p < 0.01$). The early anthropogenic fire phenology (i.e. February-lit fire; $\beta = -0.02$, $p = 0.5$) and late anthropogenic fire phenology (i.e. April-lit fire; $\beta = -0.06$, $p = 0.06$)

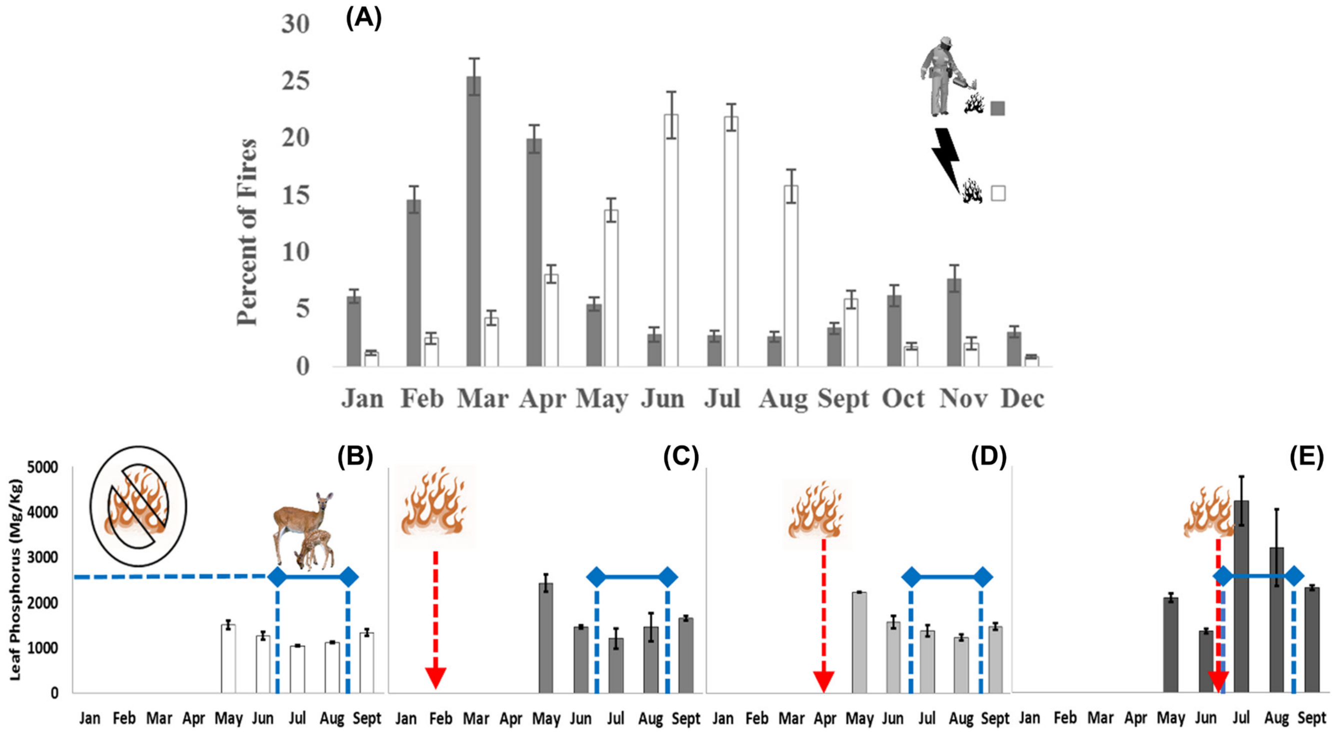

Figure 1. Temporal distribution (panel A; mean, SE) of fires actually caused by lightning (n = 4541) and human ignition (n = 5224) in 11 southeastern states, USA, 1980–2015. Leaf phosphorus does not meet the requirement (horizontal blue lines) of a female white-tailed deer to successfully feed a single fawn during the period (blue triangles and vertical blue broken lines) of heightened nutritional demand when the area is not burned (panel B), burned in the early anthropogenic phenology (panel C), or in the late anthropogenic phenology (panel D). Leaf phosphorus does meet minimum requirements in areas burned during the peak lightning phenology (panel E). We downloaded wildland fire occurrence data for all fires that occurred in 11 states in the southeastern United States for the time period of 1980–2015 from the federal fire occurrence database (<https://wildfire.cr.usgs.gov/firehistory/data.html>). The states chosen included Alabama, Arkansas, Georgia, Florida, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, Virginia and West Virginia. We extracted all fires known to be caused by lightning and all fires that were known to be prescribed, along with their respective dates. Note: P requirements were conservatively calculated based on the minimum concentration needed to obtain adequate phosphorus with maximum possible physiological intake.

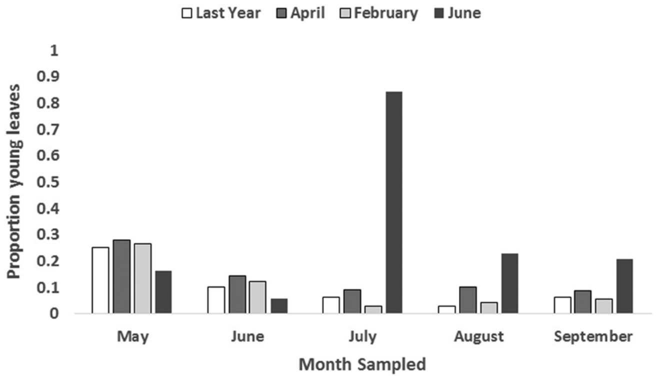

Figure 2. Proportion of available biomass that consisted of young leaves averaged across 4 species (*Diospyros virginiana*, *Sassafras albidum*, *Gaylussacia dumosa*, *Solidago odora*) following fires lit in the previous year and in February, April and June of the same year at Fort Bragg Military Installation, North Carolina, USA, sampled May–September 2014. The legend refers to the timing of fire and the x-axis represents the timing of sampling. Note that May and June samples were collected before the June fires occurred and represent 3 years-since-fire.

had similar proportions of young leaves as the control in all months measured. The watershed, month of collection and the plant species had no effect on the proportion of young leaf biomass ($p > 0.22$). No young leaves were available for persimmon, sassafras and dwarf huckleberry in August and September following the early and late anthropogenic phenology, or control.

Of the 28 neonates used in the analysis, 10 of those neonates starved, all within 48 hours of parturition. The other 18 neonates either survived the study or were depredated outside the initial threat of starvation. Neonates that died of starvation were born on average more than three times as far from lightning season fires that occurred in the same season than neonates surviving the starvation window (i.e. 408–128 m, respectively; Fig. 3A–B). Logistic regression indicated the probability of starvation increased as a function of distance to lightning-season fire ($r^2 = 0.38$, $p = 0.006$).

Models had substantial predictive power in explaining the variation in fiber and nutrients within young leaves (r^2 0.63–0.92). The exception again was Fe, which was predicted poorly by the variables included ($r^2 = 0.03$). Overall, fire phenology was an important predictor for CP ($p = 0.01$), P ($p = 0.01$), K ($p = 0.01$), Mg ($p < 0.01$), Zn ($p < 0.01$), S ($p = 0.02$) and Na ($p = 0.02$) but not for Ca ($p = 0.98$), Cu ($p = 0.07$), Mn ($p = 0.07$), Fe ($p = 0.64$), ADF ($p = 0.21$) and NDF ($p = 0.91$). The early and late anthropogenic fire phenology did not affect any macro-nutrients or fiber content within young leaves (i.e. CP, P, K, Ca), but lightning phenology resulted in greater CP, P and K than control (Supporting information). The early and late anthropogenic fire phenologies did not affect any micro-nutrients within young leaves except that the late anthropogenic phenology resulted in less Mg than control (Supporting information). Lightning phenology resulted in greater concentrations of Mg, Zn and S in young leaves than control but did not affect other micronutrients (Supporting information). Nutrient concentrations increased substantially in the month following lightning phenology and remained greater (all the way through September) than control. Similar relationships were evident in each plant species and with all macro- and micro-nutrients surveyed except Ca and Fe (Supporting information). No relationships were evident for ADF or NDF (Supporting information).

Models had substantial predictive power in explaining the variation in whole plant nutritional value for fiber

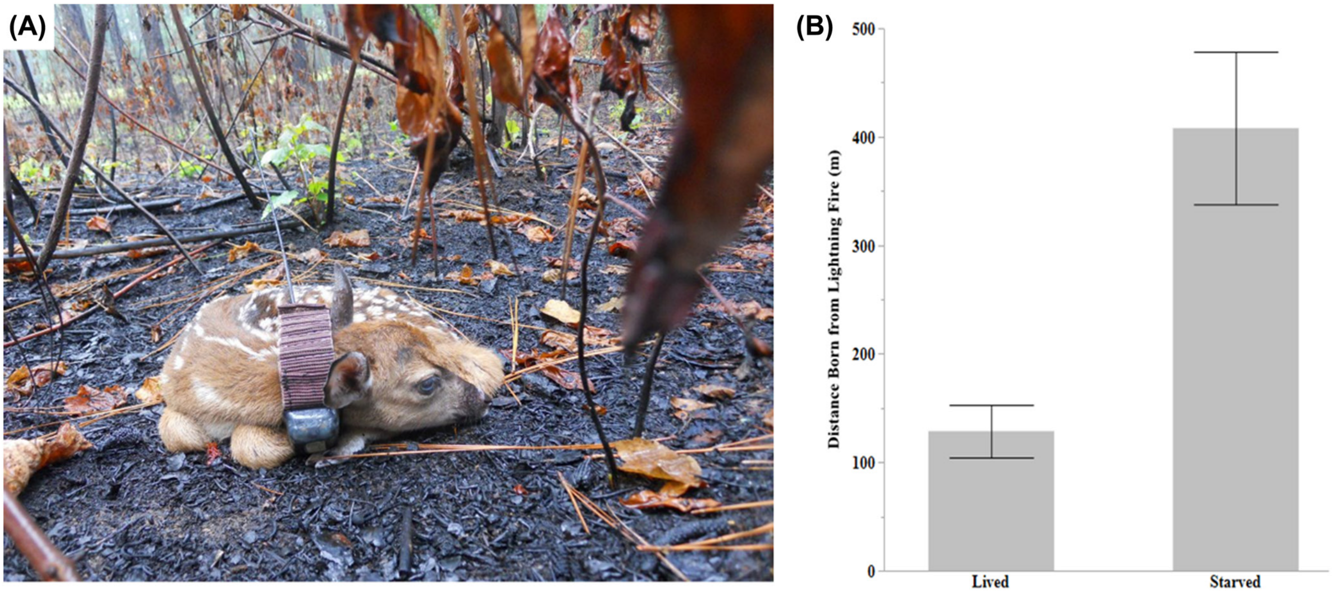

Figure 3. Neonatal white-tailed deer (panel A) bedding in an area burned a couple of weeks previous during June, consistent with the peak of lightning phenology for the study area. Fawns that starved were born on average more than three times as far from areas burned during the peak lightning season phenology (binary logistic regression, $r^2 = 0.37$, $p = 0.006$, panel B). Photo credit: Amanda Stickles.

and nutrients (r^2 0.67–0.93). The exception was Fe, which was predicted poorly by the variables included ($r^2 = 0.33$). Overall, fire phenology was an important predictor for CP ($p < 0.01$), P ($p < 0.01$), K ($p < 0.01$), Ca ($p = 0.02$), Zn ($p < 0.01$), Cu ($p < 0.01$), Mn ($p < 0.01$), Fe ($p = 0.01$) and S ($p < 0.01$) but not for Mg ($p = 0.08$) and Na ($p = 0.90$). The early and late anthropogenic fire phenology did not affect any macro-nutrient value for the whole plant (i.e. CP, P, K, Ca), but lightning phenology resulted in greater CP, P and K and less Ca than control (Supporting information). Early anthropogenic phenology resulted in less whole plant nutritional value for Cu, and late anthropogenic phenology resulted in less whole plant nutritional value of Mg and greater whole plant nutritional value of Mn and Fe than control (Supporting information). Lightning phenology resulted in greater whole plant nutritional values of Zn, Cu and S than control but did not affect other micro-nutrients (Supporting information). Macro-nutrient concentrations in the whole plant increased substantially in the month following lightning phenology. Also, whole plant nutritional value of each macro-nutrient remained greater through September following lightning phenology than control. Similar relationships were evident with whole plant nutritional value of all macro- and micro-nutrients surveyed except Ca and Fe (Supporting information). No relationships were evident for ADF or NDF (Supporting information).

Discussion

We provide evidence that anthropogenic fire timing may shift or weaken pulses in resource availability which could result in a trophic mismatch. As a result of that mismatch, plants we sampled did not contain the required nutrients to meet the nutritional demands of reproductive females which likely explains the positive relationship between neonate starvation probability and distance to areas burned in the lightning season. To our knowledge, no previous empirical data have been presented to suggest that humans induce phenological trophic mismatches, but our results provide key evidence that humans may do so commonly across much of the terrestrial landscape by manipulating the phenology of fire.

Interestingly, the synchrony and phenology of ungulate reproduction is governed by resource availability (Sinclair et al. 2000, Stoner et al. 2016) and relative birthing synchrony and phenology affect neonate survival (Michel et al. 2020). Given that our data demonstrate that fire timing regulates the timing of resource pulses, the anthropogenic mismatch in fire phenology could invoke strong selective pressure on the timing of ungulate reproduction if birth timing is a heritable trait and individuals not born during the fire-induced resource pulse do not subsequently successfully reproduce. Although this selective pressure of fire on the timing of ungulate reproduction has not been reported elsewhere, climate-driven shifts in resource availability reportedly do affect the timing of reproduction in ungulates (Post and Forchhammer 2008, Moyes et al. 2011, Paoli et al. 2018, 2019). Our fawn survival data support this notion given that proximity to areas burned in the lightning season was a strong predictor of fawn fate. Moreover, the effect of proximity to those areas on fawn starvation may have been exacerbated by the poor productivity on site (Lashley et al. 2015b). It is important to note that other global changes connected to human activities simultaneously may dampen or counteract the selective pressure of fire phenology, particularly in this species. First, the studied population did not have access to anthropogenic subsidies such as agriculture and supplemental feeds which all are commonly accessible by white-tailed deer across their range otherwise. Thus, the resource pulse provided by fire may be particularly important to this population, and historically to all populations, but contemporary access to human subsidies now may dampen the effects of environmental and resource variability otherwise (Oro et al. 2013, Ruffino et al. 2013). Second, humans facilitated the range expansion of coyotes *Canis latrans* and although starvation was an important cause of mortality in this population, depredation of fawns by coyotes was the leading cause of mortality in this study area (Chitwood et al. 2015b). Although, the high predation rates may be confounded by distress vocalizations of starving neonates making them more vulnerable to predation (Chitwood et al. 2014). Thus, if selective pressure by coyotes counteracts that of fire, coyotes may limit deer from shifting reproductive phenology to match fire phenology. Multiple forces of global change may confuse the expectation of shifting reproductive phenology making it particularly important to consider fire phenology in conservation efforts for fiery ecosystems.

For this particular anthropogenic-induced trophic mismatch, corrective management actions may be difficult because of traditional fire management goals and policy (Ryan et al. 2013). That is, most prescribed fire is lit for the purpose of decreasing fuel loads to reduce the risk of wildfire (Stephens and Ruth 2005), and the traditional burn window with the most predictable and therefore safe prescribed fire conditions occur during the dormant season when historical lightning fires were rare (Ryan et al. 2013). And, phenology is only one of the understudied characteristics of anthropogenic fire regimes that are likely mismatched and could have consequences to trophic interactions. Spatial scale of anthropogenic fires also need to be studied simultaneously in this context (Mason and Lashley 2021). In fact, in the southeastern USA, the top two lightning season fire months meet the fire policy requirements to gain a permit based on weather conditions < 10% of the time (Chiodi et al. 2018). The limitations are often limited by smoke management guidelines, which are often a source of controversy near populated areas (Ryan et al. 2013). Thus, to shift anthropogenic fire to match that of lightning season fires may require legislative action that relaxes the weather parameters to be met to legally burn, while maintaining the necessary components for safety. Of course, relaxing the conditions may increase volatility of fires making planning and careful implementation even more important. While the increasing focus on ecosystem restoration with the use of prescribed fire has led anthropogenic fire regimes to match more accurately that of lightning fires in some areas (Knapp et al. 2009), our data and the work of others indicates there is still a large-scale phenological mismatch (Miller et al. 2019), and policy barriers to shifting phenology across the global terrestrial landscape will prove more difficult. Many systems have already begun a transition to less (Alexander et al. 2021) or more (Seidl et al. 2017) flammable plant communities because of fire suppression and climate change so expanding the burning window may be a necessary step to circumvent ecosystem shifts to lower quality habitat or more dangerous states. With so many global changes rapidly occurring concurrently, a deeper understanding of the collective net effects changes in fire regimes are needed to best inform conservation policy.

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sxksn034z> (Lashley et al. 2022).

Supporting information

Any supporting information associated with this article is available from the online version.

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