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Discussion

Re-framing deer herbivory as a natural disturbance regime with ecological and socioeconomic outcomes in the eastern United States

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HIGHLIGHTS

- Large herbivores, particularly deer, are viewed as overabundant and forest threats.
- We reviewed effects of deer on forest ecosystems and society.
- Mass extinctions downsized herbivores, which shaped plant communities for epochs.
- Deer provide critical ecosystem services.
- Deer are a fundamental natural disturbance process from a historical perspective.

GRAPHICAL ABSTRACT
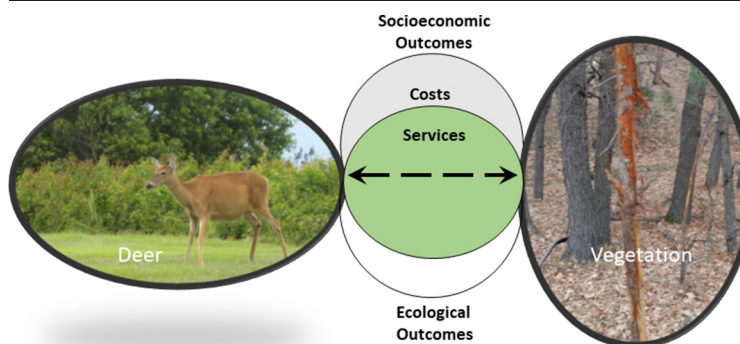
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ABSTRACT

Natural disturbances are critical ecosystem processes, with both ecological and socioeconomic benefits and disadvantages. Large herbivores are natural disturbances that have removed plant biomass for millions of years, although herbivore influence likely has declined during the past thousands of years corresponding with extinctions and declines in distributions and abundances of most animal species. Nonetheless, the conventional view, particularly in eastern North America, is that herbivory by large wild herbivores is at unprecedented levels, resulting in unnatural damage to forests. Here, we propose consideration of large herbivores as a natural disturbance that also imparts many crucial ecological advantages, using white-tailed deer (Odocoileus virginianus), the only wild large herbivore remaining throughout the eastern U.S., as our focal species. We examined evidence of detrimental effects of browsing on trees and forbs. We then considered that deer contribute to both fuel reduction and ecological restoration of herbaceous plants and historical open forests of savannas and woodlands by controlling tree and shrub densities, mimicking the consumer role of fire. Similarly to other disturbances, deer disturbance 'regimes' are uneven in severity across different ecosystems and landscapes, resulting in heterogeneity and diversity. In addition to biodiversity support and fuel reduction, socioeconomic benefits include >$20 billion dollars per year by 10 million hunters that support jobs and wildlife agencies, non-consumptive enjoyment of nature by 80 million people, cultural importance, and deer as ecological ambassadors, whereas costs include about $5 billion and up to 450 human deaths per year for motor vehicle accidents, along with crop damage and disease transmission. From a perspective of historical ecology rather than current baselines, deer impart a fundamental disturbance process with many ecological benefits and a range of socioeconomic effects.

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1. Introduction

Natural disturbances of herbivory, fire, flooding, drought, and strong winds are integral processes of ecosystems that influence biomass, ecosystem structure, composition, and ecological function (Peterken, 1996). Both ecological and socio-economic benefits and disadvantages may arise from disturbances, depending on the perspective and values of the observers. Disturbance regimes operate at a range of spatial scales, severities, and durations and remove vegetation from different locations in the vertical and horizontal vegetation profile, creating openings and growing space, which is particularly important in forests (Oliver and Larson, 1996; Peterken, 1996). Disturbances may affect primarily either the overstory layers of larger diameter trees (e.g., windstorms, insect outbreaks, ice and snow) or understory layers of small diameter trees, shrubs, and herbaceous plants (e.g., surface fires, low severity flooding, and ungulate herbivory; Peterken, 1996); alternatively, disturbances, when severe, may remove biomass throughout the vegetation profile (e.g., crown fires, volcanoes, Peterken, 1996).

Despite the fundamental role that vertebrate herbivores play in shaping ecosystems around the globe and through time (Bakker et al., 2016), intensive browsing by deer and other ungulate browsers at high densities is conventionally viewed as a forest health and management concern that is damaging forest ecosystems rather than an important ecological interaction and natural disturbance in forests (e.g., Côté et al., 2004; Horsley and Stout, 2004; Carson et al., 2014; Beguin et al., 2016). Browsing effects at current deer densities often are described as an impact where 'damages', or decreased provisioning services, are assessed relative to human demands and expectations; moreover, as human pressures on ecosystems increase, greater damage or overabundance may be assessed for stationary deer effect levels or populations (Reimoser and Gossow, 1996; McCabe and McCabe, 1997). In North America, perceptions of deer as primarily an ecosystem health problem rather than a natural disturbance process may be traced back to Aldo Leopold during the 1930s and 1940s. Leopold, who profoundly influenced the development of wildlife management, environmental ethics, and wilderness conservation, used terms such as 'destruction' and 'devastated' to describe effects of high deer browsing severity on vegetation after extirpation of wolves (*Canis lupus*; Leopold, 1943).

The absence of two top predators (wolves and mountain lions, *Puma concolor*) in eastern North America is frequently mentioned as a principal driver of deer 'overabundance' and assessed damaging impacts (Côté, 2005; Estes et al., 2011). However, the eastern coyote (*Canis latrans × Canis lycaon*) has emerged as a new top carnivore (i.e., >15 kg body weight; Way, 2007; Ripple et al., 2014) in the eastern U.S., consuming similar amounts of deer as the eastern wolf and potentially causing greater effects than wolves to deer populations because of the greater flexibility of coyote diets (Benson et al., 2017). The eastern coyote has not completely replaced the wolf ecologically, but it has filled the niche of a large deer-consuming canid, leaving only the large felid niche left by the extirpated mountain lion unfilled. Additionally, in landscapes where top predators are present, intensive herbivory by wild ungulate species still occurs (Kuijper et al., 2010; Churski et al., 2017; Fløjgaard et al., 2022). In the Bialowieza forest in Poland, fenced areas contained over three times the number of saplings >50 cm compared to control areas exposed to herbivores, wolves, and Eurasian lynxes (*Lynx lynx*; Kuijper et al., 2010). Indeed, contemporary Bialowieza and the once great Pleistocene megafauna in eastern North America and Northwestern Europe reveal that multiple ungulate species was the typical ecological condition in northern temperate forests (Gill, 2006). When top predators are present, variations in carnivore presence and density result in a range of browsing severity from low to high, which appears to be the normal range of variation rather than an aberration (McLaren and Peterson, 1994; Callan et al., 2013; Flagel et al., 2016; Martin et al., 2020).

The last remaining free-ranging, wild ungulate that occurs throughout the eastern United States is the white-tailed deer (*Odocoileus virginianus*), consisting of about 21 million animals in the 3 million km² region (Hanberry and Hanberry, 2020; Fig. 1). Notwithstanding claims to the
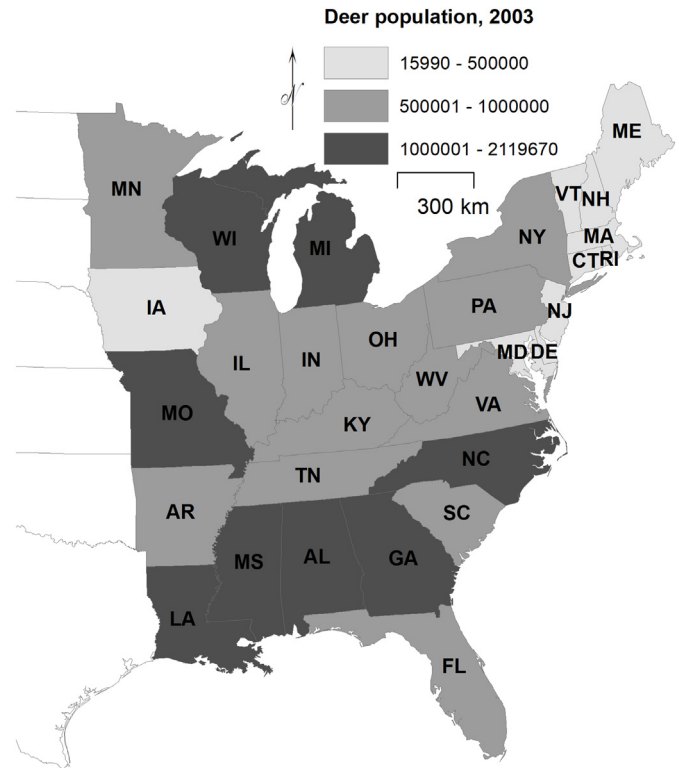

Fig. 1. Deer populations by state, totaling about 21 million, during 2001 to 2005 in the eastern United States, an area of 3 million km².

contrary, the current population appears to be within the bounds of historical population estimates, if not lower, albeit some of the land base has been lost to other land uses, perhaps resulting in higher local densities in some areas (McCabe and McCabe, 1997). Historical deer densities were estimated by Seton (1927) at around 8 deer per km² in eastern North America, which would total 24 million deer in the eastern U.S., where white-tailed deer are most abundant. However, these density estimates were conservative and white-tailed deer had a range of approximately 7.8 million km² in North America (McCabe and McCabe, 1984), so the maximum historical deer population in North America may have been much greater than the current North American population. Moreover, historical accounts report localized areas that contained 20 to 40 or more deer per km², similar to other accounts of plentiful wildlife before Euro-American settlement (McCabe and McCabe, 1984). These localized areas with extremely high densities also occurred when deer populations were reduced during the early 20th century (Leopold et al., 1947). Deer populations reached a low of 300,000 to 500,000 individuals between years 1850 to 1900 (McCabe and McCabe, 1984), a time when they were extirpated from large parts of their range due to overexploitation. However, estimation of wildlife numbers remains a challenge, resulting in inaccurate quantification of abundance, while herbivore effect on ecosystem functioning is not a linear function of population number.

Despite a large volume of work, evidence is limited for some ecological effects of deer browsing, with potential for bias of positive findings for deer effects (Habeck and Schultz, 2015). A disproportional number of study locations occur in the northern U.S. and were selected to study known deer browsing effects (Russell et al., 2001; Murray et al., 2013). Spatially imbalanced stand studies of localized effects may not be representative of the range of deer effects across landscapes (Gill, 2006; Murray et al., 2013). Publication bias for positive or uni-directional results generates the 'file drawer problem' of outcome reporting bias (Fanelli, 2012; Nissen et al., 2016) and facilitates one-dimensional narratives of deer effects, resulting in positive findings becoming accepted as fact unless negative or null findings also are published to provide balance through divergent results

(e.g., Brockway and Lewis, 2003; Rutherford and Schmitz, 2010; Fox et al., 2014; Hanberry et al., 2014a, 2014b).

Here, our objective was to pose that deer, and other large wild herbivores, are long-standing natural disturbances of varying intensity that generate a range of ecological and socioeconomic outcomes. We examine ecological effects on trees, forbs, other species, and ecosystem function, including the magnitude of influence, and offer that any perceived disadvantages are often advantages when considered from a different perspective (e.g., an historical perspective of disturbances and ecosystems). We then develop characteristics of the herbivore disturbance regime. Lastly, we focus on socioeconomic costs and benefits, for which deer overabundance is a value judgement. Thus, our aim was to compile a range of deer herbivory effects and highlight the potential benefits, which typically are not considered, from a viewpoint of the eons when megaherbivores were integral components of forested ecosystems. We rely on published systematic reviews and meta-analyses, stand and landscape studies, and conceptual papers in this synthesis about deer as a natural disturbance.

2. Large herbivores and historical vegetation structure

Large mammalian herbivores are a component of ecosystems that have co-evolved with trees and herbaceous plants for millions of years (Fløjgaard et al., 2018) In the eastern U.S. (Fig. 1), megafauna included species of llama, peccary, horse, tapir, pronghorn, ground sloth, muskox, zebra, another bison, and proboscideans (i.e., mammoth, mastodon, gomphothere; Means, 2006). Ten species weighed at least 1000 kg, including the four ground sloths.

Megaherbivore extinctions and extirpations have downscaled native herbivore assemblages in terms of reduced number of species, number of individuals, size of species, and overall biomass (Fløjgaard et al., 2022). In the eastern U.S., extinctions primarily may have occurred about 13,000 to 10,000 years ago, following arrival and establishment of humans (details of which are not well-known). Euro-American exploration and settlement and concurrent rapid resource overexploitation resulted in extirpation or range decreases for the remaining few large herbivores. Only white-tailed deer (a large herbivore at 57 kg (Sauer, 1984), albeit relatively small) now occur throughout the eastern U.S. Elk (*Cervus elaphus*; also known as red deer) were extirpated from the eastern U.S. during 1740 to 1880, reaching a range-wide population low of 70,000 in the U.S. and 20,000 in Canada (Seton, 1927). Seton (1927) estimated an historical total population of about 10 million elk. Thus, the eastern elk population may have ranged from 2 to 5 million, depending on proportionate density throughout the range (Seton, 1927; Means, 2006). Extirpation of American bison (*Bison bison*) occurred from about 1770 to 1830 in the eastern U.S., with a range-wide population low of 800 during 1895 (Seton, 1927). Seton (1927) proposed a widely accepted historical estimate of 60 million American bison, of which about 2 to 4 million may have occurred in the eastern U.S. (Gates et al., 2010). However, it is unclear if bison were present in the eastern U.S. for centuries or millennia (Mueller et al., 2021). Moose (*Alces alces*, also known as elk) were present in the northern region of the eastern U.S. as far south as Pennsylvania, and currently their southern range limit has contracted modestly northward to central New York and northern Connecticut (Seton, 1927; Karns, 1997; Wattles and DeStefano, 2011). Woodland caribou (*Rangifer tarandus caribou*) historically ranged the northern third of New England and northern sections of New York and the Upper Great Lake states, but were extirpated from these regions by the early 1900s and have not returned (McLoughlin et al., 2003). Feral non-native hogs (*Sus scrofa*) have an estimated U.S. population size of 6.3 million animals, of which 2.5 million are in Texas (Lewis et al., 2019; Fig. 1, we did not include Texas as part of the eastern U.S.). However, hog populations may have been much greater during Euro-American settlement when free-ranging hogs were raised deliberately as a food source (Whitney, 1996).

The influence of large herbivores on vegetation has diminished in correspondence with extinctions and extirpations of large herbivores (Vera, 2000; Bakker et al., 2016). Megaherbivores before extinction probably

were abundant enough to maintain relatively low tree densities (Gill et al., 2009). Following megafauna extinction and the end of the last ice age, paleoecological evidence suggests that forests in Europe and North America that re-organized after glacier recession were more closed than previously, consistent with removal of megaherbivores like proboscideans (Sandom et al., 2014; Bakker et al., 2016).

However, as the megafauna declined (measured in dung fungal spores in sediment cores), reduced browsing pressure resulted in increased importance of fire in the eastern U.S. and other regions (as measured in charcoal; Robinson et al., 2005; Gill et al., 2009; Ripple et al., 2015). Open oak and pine forests covered much of the eastern region south of the northern forest zone at the time of Euro-American settlement (Bragg et al., 2020), and oaks and pines were the most abundant tree species in non-boreal eastern forests before megaherbivore extinction (Delcourt and Delcourt, 1987). Remaining megafauna of elk, bison, and deer likely contributed to maintaining these open forests (Scholes and Archer, 1997; Vera, 2000), but bison and elk ranges did not overlap completely with savannas and woodlands (defined by open midstories and an herbaceous groundlayer). They were not present in all or parts of longleaf pine (*Pinus palustris*) woodlands in the Coastal Plain and in southern New England during the early Holocene; thus, savannas and woodlands occurred in the absence of large herbivores, except deer (Faison et al., 2006; Means, 2006). Large herbivore densities occurred in a range of severities, creating heterogeneity in the vegetation of ecosystems that have been consumed by large herbivores for eons.

3. Ecological disadvantages or advantages?

3.1. Browsers: the disturbance mechanism

Advantageous or disadvantageous outcomes of a particular disturbance are dependent on the values and priorities of the observer, as well as the organism, biotic community, or habitat being considered. Herbivores decrease biomass of vegetation, similar to other disturbances. Herbivory may reduce survival of plants in early life stages, particularly through nipping terminal buds, or reduce growth by removing photosynthetic tissue (Bakker et al., 2016). In addition to reducing plant survival and growth, consumption of fruit and seeds may diminish regeneration, although some seeds benefit from acid scarification.

Browsers such as deer feed preferentially on woody plants and forbs, including fruits and seeds, rather than grasses. Deer particularly favor young tree stems greater than about 30–50 cm in height (Rooney et al., 2000; Kuijper et al., 2010), often greatly reducing young tree numbers. Below this stem height, ungulate effects on seedling density and diversity are often minimal (Horsley et al., 2003; Kuijper et al., 2010). According to Bradshaw and Waller (2016), during winter and early spring, white-tailed deer consume tree seeds, seedlings, and the buds, flowers, leaves, and sometimes bark and branches of saplings, while during spring and summer, deer graze on forbs and graminoids. Deer and moose may strip and eat bark, sometimes leading to girdling, if other forage is not available (Miquelle and Van Ballenberghe, 1989; Gill, 1992; Faison et al., 2010). Large mammalian herbivores also trample or pull down small trees and shrubs and rub various size trees, with the possibility of girdling or breaking trees (Gill, 1992; Miquelle and Van Ballenberghe, 1989; Faison et al., 2010; Fig. 2).

3.2. Tree density and diversity

Reduction in tree density due to deer browsing is typically interpreted as ecological degradation and a forest health problem (Rooney, 2009; Estes et al., 2011; Tanentzap et al., 2011). In a meta-analysis of North American forests, Habeck and Schultz (2015) detected positive responses of woody vegetation abundance, cover, and richness to deer exclusion. Likewise, in a meta-analysis of temperate and boreal forests, Bernes et al. (2018) determined that native herbivores reduced woody plant abundance and richness. Deer may damage future forest products by suppressing growth rates, reducing abundance of some timber trees, and altering stem architecture (Tilghman, 1989; Bergeron et al., 2011). Browsing by deer

Fig. 2. Small and large diameter trees that have been damaged by large mammals (particularly by bison in these photos, but deer and elk also are present; photos courtesy of B. Hanberry).

and other ungulates also may reduce carbon stocks (Tanentzap and Coomes, 2012). Syntheses showed that ungulates in temperate zones reduce tree regeneration at a threshold equivalent to about 5 to 7 white-tailed deer per km^2 (Russell et al., 2017; Ramirez et al., 2018). Browsing of woody plants may reduce structural diversity in some stands through reductions in tall shrub and mid-story tree layers (Hester et al., 2006).

Over time, some heavily browsed stands may begin to show characteristics of open forests, which contain sparse mid-story tree layers and graminoid-dominated understories (Rooney, 2009; Tanentzap et al., 2011; Faison et al., 2016a; Reed et al., 2022). When interacting with other disturbances, great browsing intensities may maintain vegetation in a woodland or shrubland state for an extended period of time (Bergquist et al., 1999; Faison et al., 2016b; MacSween et al., 2019). Nevertheless, there is also an element of over-reporting of deer effects, in which heavily browsed sites that are reported as having woodland-like qualities still have tree densities that fall well within the definition of forests (e.g., ≥250 larger diameter trees/ha; Healy, 1997; Tanentzap et al., 2011; Hanberry et al., 2014a, 2014b; Faison et al., 2019).

Despite the potential for deer to reduce tree densities, particularly at local scales, deer have relatively minor effects on resulting midstory and overstory forest structure at broad scales in the eastern U.S. (Hanberry and Abrams, 2019; Hanberry et al., 2020; but see Russell et al., 2017 for reductions in the tree seedling understory). Deer densities during the past decades were not related significantly to current tree stocking at landscape scales in the eastern U.S. for all but one ecological province, which was heavily forested (Hanberry and Abrams, 2019). Severe and sustained browsing by deer that results in long-term shifts in vegetation structure to open forests of savannas and woodlands at landscape scales has not occurred in the eastern U.S. (Hanberry et al., 2020), which is consistent with the fact that almost 90 % of the eastern U.S. is characterized as being browsed at low to moderate rather than high intensity (McWilliams et al., 2018). Indeed, forest density has increased from historical open forest of savannas and woodlands to current closed woodlands coincident with the rise in deer numbers, rather than the reverse (Hanberry et al., 2020).

Localized areas of intensive herbivory are typical for deer, even when deer populations are low (Leopold et al., 1947). Nonetheless, eastern forest stands that appear to have regeneration failures often exhibit remarkable resilience to intensive browsing after deer densities decline or part or all of the canopy is removed by disturbance. For instance, tree saplings >1 m in height were absent beneath a forest canopy and exposed to 27 deer/km^2; but under a partial canopy, 3200 saplings/ha grew above 1 m when exposed to the same deer density (Tilghman, 1989; Gill, 2006).

The legacy effects of deer browsing at these same study sites revealed long-term reductions in tree basal area, density, and diversity in the areas with the highest deer densities, but also relatively high canopy rugosity (i.e., canopy structural complexity), canopy gaps, and tree height in areas with the greatest browsing pressure (Reed et al., 2022). Canopy rugosity is strongly correlated with net primary production (Gough et al., 2019), and canopy gaps are important determinants of biodiversity. This highlights the fact that strong deer impacts that appear only detrimental at small spatial and temporal scales may have unexpected benefits if examined at broader spatial and temporal scales.

Even when deer do limit tree densities at smaller scales, reduced tree densities often have beneficial effects on other flora or fauna (McInnes et al., 1992; Côté et al., 2004; Peterson and Reich, 2008; Royo et al., 2010; McShea, 2012; Faison et al., 2016b; Webster, 2016; Haffey and Gorchov, 2019). Currently abundant closed forests have an understory dominated by trees and shrubs and leaf litter, which limit herbaceous layers and slow the development of large spreading trees. Many historical ecosystems of the eastern U.S., south of the northern forest zone, were open forests with low tree densities, which allowed greater diversity and abundance of the herbaceous layer (Bragg et al., 2020). Increased growing space in savannas and 'wood pastures' also results in a greater occurrence of large, spreading trees, which provide numerous and unique conservation benefits (Hartel et al., 2013; Plieninger et al., 2015). Restoration and management for now rare open forests involve control of small diameter trees to allow

growing space for herbaceous species, which deer browsing helps provide (Ritchie et al., 1998; Bragg et al., 2020). In addition to supporting greater herbaceous plant diversity, open forests benefit distinctive guilds of vertebrates such as birds and bats that require open foraging space, invertebrates such as pollinators that use floral resources, and even fungi (Tanentzap et al., 2011; Dey et al., 2017; Hanberry and Thompson, 2019).

Reduction of tree and shrub densities by deer also serve as a provision of ecosystem services by reducing fuel loads and mitigating wildfires (Gill, 2006; Bakker et al., 2016). This service currently is more beneficial in the western part of the range because severe wildfires are uncommon in the eastern U.S., due to humid climate and limited number of extreme fire weather days. Nevertheless, extreme fire weather days are expected to increase with climate change (Hanberry, 2020).

Regarding damage to forest products, several countering points are important to consider. In current successional forests, growing space is not available for every seedling to become a canopy tree and many tree seedlings will not survive density-dependent competition (i.e., self-thinning), regardless of herbivory (Peet and Christensen, 1987). A common silvicultural treatment is thinning to decrease competition for resources, and some evidence for thinning benefits by deer and moose include increased growth rates of young trees (Thompson and Curran, 1993) and overstory trees (Lucas et al., 2013) and reduced competition from non-desirable tree species (De Vriendt et al., 2020). Indeed, loblolly pine (*Pinus taeda*) is the most abundant tree species in the southeastern U.S. due to plantations, and most pine species typically are avoided by deer (Hanberry and Abrams, 2019); loblolly pine plantations receive herbicide applications to control broadleaf tree species (Hanberry et al., 2012). Browsing by deer and moose can in some cases also increase the abundance of valuable timber species such as spruce and black cherry (*Prunus serotina*; Tilghman, 1989; Thompson and Curran, 1993).

Paralleling deer influence on forest structure, deer preference for certain tree species may alter species composition in some stands (e.g., Nuttle et al., 2013). Deer cause declines in oak regeneration under a closed forest canopy at local scales (Healy, 1997; Gill, 2006). Additionally, deer have caused declines in other tree species at local scales including eastern hemlock (*Tsuga canadensis*), northern white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*) and pin cherry (*Prunus pensylvanica*), as well as increases in spruce, black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), white pine (*Pinus strobus*), and striped maple (*Acer penylvanicum*; Augustine and McNaughton, 1998; Côté et al., 2004; Faison et al., 2016c).

However, cumulative effects of deer on tree species composition are generally much less common at landscape to regional scales (Hanberry and Abrams, 2019). Browse preferences, or assignments of browse preferences, are not consistent spatiotemporally (Wakeland and Swihart, 2009; Hanberry and Abrams, 2019). Therefore, black cherry, American beech, and white pine, which were not preferred by deer in local studies that documented increases (e.g., listed above), are preferred in some locations during some seasons (Wakeland and Swihart, 2009; Hanberry and Abrams, 2019). Changes in species composition at landscape and regional scales occur regardless of browse preference. Species browsed heavily by deer at local scales have, in many cases, increased at broader scales since Euro-American settlement (e.g., northern white cedar, balsam fir; Thompson et al., 2013; Hanberry and Abrams, 2019). Tree species, such as oaks and eastern hemlock, that have declined at landscape scales since Euro-American settlement, can be attributed primarily to land use history and changes in disturbance regimes (Whitney, 1996; Thompson et al., 2013). The late-successional hemlock has decreased in northern forests since Euro-American settlement due to frequent harvesting and more recently from infection by an invasive insect (*Adelges tsugae*). Oaks are generally tolerant of and benefit from frequent surface fires that are much reduced in today's forests compared to pre-Euro-American landscapes (Whitney, 1996). Historically, oaks were about 55 % of all trees in the central eastern U.S., an area of 1.2 million km^2, and about 35 % of all trees in the northern southeastern U.S., an area of 0.5 million km^2, but oaks have declined greatly relative to other tree species since Euro-American

settlement (e.g., Whitney, 1996; Thompson et al., 2013; Bragg et al., 2020). Oaks regenerated and recruited well under historical herbivory pressure that included 3 to 4 large herbivores (deer, elk, bison, and in northern areas, moose). At least in more open forest conditions, oaks can regenerate effectively under moderate herbivory (Vera, 2000; Bobiec et al., 2011).

3.3. Herbs

Increases and decreases in herb richness from browsing may occur in recently disturbed and undisturbed forests across a broad range of deer densities (Royo et al., 2010; Urbanek et al., 2012; Faison et al., 2016b; Haffey and Gorchov, 2019; Averill et al., 2018). Deer herbivory in some stands causes declines in height and abundance of taller-statured forbs characteristic of interior forests but a corresponding increase in the abundance of shorter-statured and more disturbance-adapted species (Frerker et al., 2014; Faison et al., 2016a; Webster, 2016). Overall herbaceous vegetation is tolerant to herbivory, based on a meta-analysis of North American deer effects that found no effect of deer exclusion on herbaceous vegetation cover and diversity (Habeck and Schultz, 2015). Correspondingly, herbaceous vegetation did not display a negative response to native herbivores in a meta-analysis of boreal and temperate forests (Bernes et al., 2018). Bernes et al. (2018:26) stated that forest vegetation is more sensitive to novel herbivory regimes than to native herbivores. Habeck and Schultz (2015) added the caveat that lack of herbaceous response may be due to inadequate diversity indices, non-native species replacement, or legacy effects of chronic deer overabundance.

The effects of deer may depend on the density, type, and distribution of browse, along with timing of herbivory (Gerhardt et al., 2013). Thus, even densities of 20 deer per km^2 may affect forbs minimally where browse is plentiful (Augustine and Jordan, 1998). If browse is limited or unpalatable, declines in herb richness is more likely to occur and effects are much greater than expected from a given deer density (Goetsch et al., 2011; Averill et al., 2018). Indeed, forest forbs can decline in response to deer densities as low as 4 deer per km^2 under closed canopy conditions (Alverson et al., 1988). Under current conditions in some previously logged areas stands, intensive herbivory by deer may shift composition of forest understories from forb-dominated to less palatable and browse-tolerant species, such as graminoids and ferns (Rooney, 2009; Rooney and Waller, 2003; Côté et al., 2004). It follows that herbaceous layers in open forests are more resilient to high deer densities than the more sparse and ephemeral herb layers in closed forests (Urbanek et al., 2012). For example, very high deer densities (20–30 deer per km^2) had little effect on savanna plant diversity and had notably higher plant diversity than nearby closed forests with low deer densities (6 deer per km^2; Urbanek et al., 2012). Plant tolerance to tissue loss also depends on timing of herbivory relative to the growing season and the amount of time in between foraging in which growth can occur (Augustine and McNaughton, 1998; Gill, 2006).

One of the reasons for this tolerance is that deer browsing may maintain balance between trees and herbaceous plants by reducing woody plants that compete for growing space with forbs (Hester et al., 2006). In fact, deer browsing often has contrasting effects of depressing richness of the woody plant layer and promoting the herbaceous layer (Hegland et al., 2013; Faison et al., 2016a; Webster, 2016). Typically, disturbances intrinsic to an ecosystem interact with vegetation to generate positive feedbacks that help maintain the ecosystem. For example, herbivores and fire control tree densities, maintaining herbaceous cover, which also supports consumption by herbivores and fire. Graminoids in particular are able to recover to full stature quickly after removal of aboveground biomass, unlike the tall life form of trees (Galetti et al., 2018). In addition, bryophytes and other plant species are adapted to areas of reduced plant biomass and competition (Chollet et al., 2014; Hegland and Rydgren, 2016).

Forests of the eastern U.S. historically were abundant in forb species when exposed to herbivory from multiple ungulate species and frequent surface fire that reduced tree densities (Noss et al., 2015). Longleaf pine forests in particular are a temperate plant biodiversity hotspot and longleaf pine remnant forests still contain >1500 endemic plant species (Noss et al., 2015).

Although reductions in tree and shrub densities from browsing generally promote herbaceous plants, ecological disadvantages of large herbivores include additional pressure on rare and declining herbaceous plant species (Gregg, 2004; McGraw and Furedi, 2005). Once populations have become rare, historical natural disturbances such as herbivory and fire may be too harmful in the short term to be beneficial in the long term.

3.4. Animals

Deer may have indirect cascading effects, positive, negative, or neutral, on other animals depending on the magnitude of changes in vegetation structure and composition (Waller and Alverson, 1997; Rooney and Waller, 2003). As with any disturbance, localized effects that are severe enough to change vegetation may change species abundances. Negative effects associated with deer browsing include declines in aboveground insect abundance and diversity (Chips et al., 2015) and declines in abundance of low and intermediate canopy birds (McShea and Rappole, 2000; Rushing et al., 2020). Deer also may affect other species through competition for mast, primarily oak acorns (Waller and Alverson, 1997), and in one extreme case are hypothesized to have caused the extirpation of black bears (*Ursus americanus*) on Anticosti Island, Quebec as a result of removal of berry-producing shrubs (Côté, 2005). At the same time, where deer browsing creates more open forest conditions, positive effects include increased (1) open understory birds and open canopy birds in browsed areas (DeGraaf et al., 1991; McShea and Rappole, 2000; Rushing et al., 2020), (2) species that prefer relatively warm and dry microclimates and high light levels (e.g., ground-dwelling and litter invertebrates; Greenwald et al., 2008, Chips et al., 2015; Record et al., 2018); (3) predators of ground invertebrates (e.g., salamanders and snakes; Greenwald et al., 2008); and (4) consumers of animal dung (e.g., dung beetles and camel crickets; Ripple et al., 2015; Galetti et al., 2018).

As deer effects on forest structure and composition decline at broad scales (Hanberry and Abrams, 2019; Hanberry et al., 2020), then indirect effects of deer on other animals likely decline in correspondence at broader scales. Animal species were abundant under pressure from multiple large herbivores before Euro-American settlement. Many animal species in the eastern U.S. are declining, particularly species that are associated with herbaceous vegetation, whether in grasslands or forests (Hanberry and Thompson, 2019). Chollet and Martin (2013) identified that both the greatest bird declines and greatest large herbivore biomass occurred in the eastern U.S.; they state that deer are a pressure added to human activities of land use change, fragmentation, resource extraction, and non-native species. Overall, the effects of sustained and high deer densities on other animals are small relative to land use disturbance, such as timber harvesting (DeGraaf et al., 1991; Brockway and Lewis, 2003; IPBES, 2019; Hanberry et al., 2020). Equally, shortages of mast resources can be more readily traced to declines in mast-producing tree species (e.g., oaks and American beech) resulting from land use history, insects and pathogens, and past management rather than deer (Whitney, 1996; Thompson et al., 2013). Generally, changes in species and ecosystems have occurred due to unprecedented human activities of land use and disturbance change, overexploitation, chemical pollution, and introduction of non-native species, rather than native deer browsing (IPBES, 2019; Hanberry et al., 2020). However, further research is needed to provide evidence concerning the effect of deer herbivory on wildlife abundance and richness, including publication of negative results.

3.5. Non-native species

Deer may both increase and decrease richness and abundance of non-native plants (Urbanek et al., 2012; Faison et al., 2016a; Averill et al., 2018). Native vertebrate herbivores overall may suppress non-native plants rather than promote them (Levine et al., 2004; Parker et al., 2006). For examples of increased non-native plant species, deer promote the abundance of the unpalatable shrub Japanese barberry (*Berberis thunbergii*), the herbaceous Japanese stilt grass (*Microstegium vimineum*), and garlic mustard

(*Allaria petiolata*; Eschtruth and Battles, 2009; Faison et al., 2016a; Shen et al., 2016). Dense layers of Japanese barberry and stilt grass can become dominant species in forest understories, inhibiting tree regeneration (e.g., Flory and Clay, 2010). Thick, non-native shrub layers can also provide important, even preferred, habitat for uncommon and globally rare species such as New England cottontail (*Sylvilagus transitionalis*; Cheeseman et al., 2019). While increasing the cover of several invasive species, deer reduce the abundance of many other palatable invasives such as oriental bittersweet (*Celastrus orbiculatus*), multi-flora rose (*Rosa multiflora*), honeysuckle (*Lonicera* spp.), and burning bush (*Euonymus alatus*; Rossell et al., 2007; Faison et al., 2016a; Averill et al., 2018; Peebles-Spencer et al., 2018).

Because of widespread, numerous non-native species, any type of disturbance, including deer, creates opportunities for non-native plants to establish. The increase of non-native plant abundance with browsing disturbance parallels the response of non-native plants to other common forest disturbances such as windstorms, insect outbreaks, and fire (Eschtruth and Battles, 2009; Alba et al., 2015; Daniels and Larson, 2020). At landscape scales, some studies have shown a positive relationship between elevated deer densities and non-native plants in some forest types (Russell et al., 2017), while others found no relationship between deer densities and number of non-native species (Hanberry, 2022).

4. Characteristics of disturbance regimes

4.1. Herbivory as a disturbance

Herbivores consume vegetation, reducing the amount of biomass while decomposing biomass back into nutrients (via excrement) available to plants (Pausas and Bond, 2020). Given enough browsing pressure, deer may maintain balance between trees and herbaceous plants by reducing woody plants that compete for growing space with forbs, thereby supporting open conditions (Hester et al., 2006). Conversely, if forbs become increasingly available, deer may proportionately switch to foraging on forbs. Herbivores select highly edible and digestible plants to consume, promoting tolerance, escape, or chemical or physical defenses in plants (Galetti et al., 2018). Although deer, and other herbivores, may modify the vegetation, the modifications do not completely remove their source of food. Because herbivory has been so prevalent for millions of years, herbivory has filtered plant species for tolerance to herbivores, with some particular physiological specialists, such as grasses and ruderal forbs (Fløjgaard et al., 2018; Galetti et al., 2018).

4.2. Location of effect on vegetation

Browsing primarily occurs in the understory, similar to surface fire, and potentially can affect composition, structure, conditions, and function, as detailed above. Herbivores select plants encompassed within the height zone of animal reach (Gerhardt et al., 2013), a browse trap similar to the fire trap when young trees are vulnerable to consumption. Herbaceous plants, such as graminoids that have basal meristems and greater resources allocated belowground, can recover quickly after aboveground biomass loss compared to woody plants, which are a slower-growing and taller life form with resources devoted to aboveground growth (Galetti et al., 2018). When herbaceous plants, sometimes in coexistence with large overstory trees, can hold the growing space, then resources for tree establishment are limited.

4.3. Severity, return interval, and seasonality

Herbivory effects on vegetation generally is sustained and suppressive rather than episodic like abiotic disturbances of fire and windstorms, at least for herbivory by non-migratory species that may exert year-round pressure (Peterken, 1996; Augustine and McNaughton, 1998). Herbivory tends to consist of short return intervals and effects that accumulate over time compared to disturbances with longer return intervals (Peterken, 1996). Nonetheless, browsing severity may vary temporally, by season

and year, or be spatially patchy due to selection for seasonally variable resources, such as forbs. Browsing severity depends on the amount of available biomass (Gerhardt et al., 2013). Because deer densities and vegetation suppression by deer are rarely uniform across the landscape, a range of browsing severity may result in greater landscape and habitat diversity than in the absence of herbivory (Gill, 2006).

Deer density is a proxy for browsing severity, with the transition between low severity, or no evidence of ecological effects, and high severity, or evidence of ecological effects, delineated at about 5 to 7 white-tailed deer per km^2 (Ramirez et al., 2018). Deer are present throughout all counties of the eastern U.S., but deer may be absent at local spatial scales, depending on resources such as forage and cover, and predators may drive spatiotemporal distributions, resulting in deer densities that likely range from 0 to >40 deer per km^2, with extreme examples of 100 deer per km^2 (Averill et al., 2018; Martin et al., 2020). At regional scales, U.S. states varied in density from 2.4 to 14.6 deer per km^2 and deer densities were greatest during 2001 to 2005 in the Southeast, southern New England, and in the Upper Midwest (Bradshaw and Waller, 2016; Hanberry and Hanberry, 2020).

Due to constant and frequent tree removal, deer may be powerful stabilizers of the open forest state of savannas and forests, particularly when extended fire-free intervals occur (e.g., Tanentzap et al., 2011). Additionally, because deer prefer grazing in forests with herbaceous resources, patterns of deer disturbance will reflect and reinforce these conditions. However, at least at current deer densities, deer herbivory is not strong enough to force transition from a closed to open state in forest vegetation.

4.4. Soil disturbance and ecological function

Deer can disturb soil by trampling, pawing, rolling, bedding, and removing plant cover. Bioturbation is soil mixing by biological means. This exposes mineral soil, which is necessary for germination of some plants. For example, layers of organic matter may be barriers to emergence of germinants. Additionally, removal of established vegetation breaks up growing space monopolies by dominant species and allows entry of diverse plant species (Mueller et al., 2021). Bison, in particular, create wallows, or small depressions that capture more water than surrounding areas and supply important moisture gradients for plants and insects (Fig. 3; Nickell et al., 2018; Mueller et al., 2021). Moose create similar depressions of heterogeneity in beddings in forested areas (Olmsted et al., 2021).

Deer also may affect nutrient, light, and moisture environments. Because herbivores decompose plant matter and remove biomass from trees, they release inputs to biogeochemical cycling while generally increasing decomposition rates. However, changes to nutrient cycling rates may depend on nutrient availability and use of less digestible species (e.g., spruce) that return nitrogen more slowly to the soil (Pastor et al., 1988; Popma and Nadelhoffer, 2020). Deer also directly move nutrients in their waste, concentrating nutrients in non-uniform patterns, which may be linked to increased heterogeneity of herbaceous plant communities in areas of high winter deer use (Jensen et al., 2011). If herbivores are able to reduce tree densities, then consequently, herbivores reduce tree leaf litter, which may result in changed litter quality, decomposition rates, and soil inputs (Popma and Nadelhoffer, 2020). Disturbance by browsing on tall woody plants may create more open conditions, increasing solar radiation and wind flows, with consequent boosting of heating and drying, or reduced relative humidity.

4.5. Seed dispersal

Deer play a critical role in seed dispersal (animal dispersal is termed zoochory), similar to seed dispersal by wind (termed anemochory). Seed dispersal occurs primarily through digestion, or endozoochory, but also surface attachment in fur, or epizoochory. In fact, seed dispersal by deer is hypothesized to have promoted the rapid migration north of forest forbs at the end of the last ice age, as well as their rapid recolonization of forests once cleared for agriculture in the 19th century (Vellend et al., 2003). Fruits dispersed by deer matched those of megafauna-dispersed fruits, with large size and numerous seeds; dry pods with fibrous pulp may remain available on the forest floor for long intervals (Jara-Guerrero et al., 2018). Seed dispersal by deer is likely a non-replaceable service, considering deer are the last wide-ranging animal capable of providing local recruitment and long-distance (5 km) dispersal (Jara-Guerrero et al., 2018).

4.6. Interaction with other disturbances

Deer remove smaller diameter trees. In targeting small trees, deer are similar to low severity fire and flooding disturbances, which also reduce understory trees, but dissimilar to high severity fire and flooding. Deer also are unlike invertebrates, such as bark beetles, foliage feeders, and sap

Fig. 3. Bison wallow (photo courtesy of P. Hanberry).

feeders, which are well-known for causing mortality of overstory trees (Potter et al., 2020).

Mammalian herbivory interacts with previously disturbed areas such as burns, timber harvests, insect outbreaks, and windthrows (Fuhlendorf et al., 2009; Kuijper et al., 2009; Royo et al., 2010; Gerhardt et al., 2013). Vegetation regrowth, particularly in response to fire, attracts more intensive grazing, resulting in a fire-grazing linkage that produces differential grazing severity. This interaction results in vegetation heterogeneity across landscapes ('pyric herbivory'; Fuhlendorf et al., 2009).

Landforms that are convex or with high terrain roughness are preferred by deer, along with valley bottoms (Gerhardt et al., 2013), where fire may be less likely to spread due to encountering roughness or wetness. Deer avoid snow cover, which may increase energy demand and hide forage (Gerhardt et al., 2013). Weather and climate appear to affect deer densities with some preference to warmer and drier sites (Gerhardt et al., 2013), similarly to fire that also responds to weather and climate, albeit fire occurrences may respond more immediately to altered conditions, whereas deer populations may lag behind altered weather and climate conditions.

Deer have some overlap with land cover and land use variables that favor fire spread and fire breaks. Deer prefer broadleaf forests, with ready access to herbaceous forb resources (Gerhardt et al., 2013), whereas fire occurrences are greatest in herbaceous land cover rather than forests (Hanberry, 2021). Deer densities typically are reduced in crop and pasture landscapes, which also limit fire occurrences due to reduced fuel loads. Other deer 'breaks' that deer avoid are locations without hiding cover or where traffic and hunting increase, such as along roads and settlements (Gerhardt et al., 2013), which also act as fire breaks.

5. Ecosystem services

5.1. Benefits

Animals may be considered overabundant to society when their socioeconomic disadvantages are greater than their advantages, by threatening human lives or livelihoods.

or depressing densities of economically or aesthetically important species (Côté et al., 2004). However, in the eastern U.S., deer are the most economically valuable wildlife species, after accounting for commodity costs of damage to cars, crops, forest products, and household gardens and benefits to the hunting industry and wildlife watchers (Conover, 1997). Deer supplied an estimated net annual monetary value of >$12 billion in 1997, or >$20 billion in 2020 (U.S. dollars, Conover, 1997).

White-tailed deer are the most popular game animal in the U.S. About 80 % of hunters, or 9.5 million Americans, hunted white-tailed deer during 2017 in their primary range of the eastern and central U.S. (QDMA, 2018). About 5.7 million deer were harvested during 2017 in the primary range (although no available data for Alabama, QDMA, 2019). During 2017, estimates for the entire hunting sector, of which about 80 % is deer hunting, include approximately $27.4 billion or about $22 billion if deer hunting proportionately is 80 % of expenses, and 195,000 jobs, which may result in economic multipliers (OIA, 2017). Licenses and taxes on equipment are the primary source of funding for state wildlife agencies. In contrast, during 2019, net income for the entire farm sector was $84.4 billion (ERS, 2020).

Deer are important culturally as a visible, tangible large wild mammal, one of the few remaining at historical populations and distributions. Cultural importance is evidenced through designation as state animals, depiction in flags and wildlife agency logos, illustration in a variety of images, and even symbolization for a professional basketball team (i.e., the Milwaukee Bucks). Deer are a highly observable representative and ambassador of eastern ecosystems.

Deer also connect humans to nature, which is valuable to mental and physical health and well-being. Wildlife viewing is enjoyable to humans and around-the-home wildlife watchers increased from 68.6 million during 2011 to 81.1 million participants during 2016 in the U.S. (DOI, 2017). In surveys, deer are the favorite wildlife mammal and most residents wanted deer levels to stay the same (64 %) or increase (27 %; Conover, 1997).

Instead of a cost, society may in some cases consider removal of tree biomass by deer a benefit. For the forest products industry, deer can provide control of stem densities, which are treated by expensive chemical and mechanical treatments. In some cases, intensive and selective browsing may result in a more commercially valuable forest stand if the less palatable tree species are more commercially valuable than then the preferred species (Thompson and Curran, 1993). For both commercial forests and agricultural lands, hunting activities can supply an additional income stream to offset any losses. Deer also add value to the price of land (Henderson and Moore, 2006).

Reduction of surface understory trees and ladder midstory trees is the primary method used by forest managers to prevent severe fires (Jain et al., 2021). Treatment expenses may be as high as $2500 and $6000 per ha (Jones et al., 2017). Browsing is a natural thinning 'treatment' that mimics, and therefore obviates, these mechanical treatments. Wildfires do occur in the eastern U.S. even though the humid climate and limited number of extreme fire weather days greatly reduce fire risk compared to the western U.S.; moreover, extreme fire weather days are expected to increase with climate change (Hanberry, 2020).

Additionally, reduction of small diameter trees is the primary requirement for ecological restoration and management of open forests. Open forests support a range of biodiversity not supported by closed forests (e.g., herbaceous plants and early successional bird species, Hanberry and Thompson, 2019; Bragg et al., 2020). Closed forests have trees throughout the vertical profile, without the shared coexistence with herbaceous plants that occurs when small diameter trees and tall shrubs are controlled (Bragg et al., 2020).

5.2. Costs

Drivers made insurance claims for about 1.2 million collisions with deer during July 2017 to June 2018 in the primary white-tailed deer range, at an average cost of $3875 per claim, totaling $4.65 billion (HLDI, 2019; QDMA, 2019). In the U.S., about 120 to 440 people per year are killed in motor vehicle collisions with deer (Williams and Wells, 2005; Conover, 2019), which is not appreciably >84 killed per year by lawnmowers and 74 killed per year by 'other mammals' such as horses and cattle during 2009 to 2018 (Forrester et al., 2018; CDC, n.d.). As a context for motor vehicle collisions with deer, about 35,000 human fatalities occur per year due to motor vehicles, of which about 7000 fatalities are pedestrians and cyclists (FHA, 2020). Car and motorcycle safety practices could reduce deaths due to deer-vehicle accidents, as 65 % of motorcyclists killed were not wearing helmets and 60 % of vehicle occupants killed were not wearing seatbelts; additionally, a majority of fatalities occurred due to drivers swerving into vehicles or objects such as trees (Williams and Wells, 2005). Other countermeasures include not planting desirable forbs, such as clover, along roadsides. In some locations, warning signs, fences, or road under- or overpasses would be worthwhile, not only to prevent damage to cars and humans but also to help numerous wildlife species safely cross roads.

One commodity cost of deer is the potential impact of browsing on future wood products. Conover (1997) estimated this cost conservatively at $750 million, or $1.2 billion in 2020 after inflation adjustment in the U.S. Deer browsing may directly kill small trees or reduce their growth; however, only a small percentage of small trees can physically gain space to become large enough to harvest. Thus, deer disturbance supplies a similar mechanism to herbicide application and mechanical thinning (Thompson and Curran, 1993), which can be expensive entries into stands to reduce competition among trees. Because plantations mostly are comprised of pine species, but with some spruce plantations located in northern locations, plantations do not carry the cost of protecting pine and spruce, which in general are not preferred by deer (Hanberry et al., 2012; Hanberry and Abrams, 2019).

Deer cause more agricultural damage than any other species of wildlife in the U.S. (Conover, 1997). Deer also consume non-commercial household gardens and landscaping plants. However, deer prefer forests and use agriculture where forests are not available; this is an ecological cost of land use

(Hanberry, 2021). Therefore, provision of natural herbaceous and woody resources will divert deer from non-forest land uses. Fencing, individual plant cages, odor repellents, and deterrents such as dogs, noise, motion, and lights are mitigation options.

Tick-borne diseases affect humans, specifically black-legged or deer tick (*Ixodes scapularis*) that transmits Lyme disease (*Borrelia* bacterium) to humans (VerCauteren and Hygnstrom, 2011). Deer can spread disease by being the primary host for the adult black-legged tick. However, deer densities are only one of many landscape variables (rodent density, acorn crop, predators, climate, forest cover) in a complex food web in temperate forests that predict tick infection and Lyme disease risk (Ostfeld et al., 2018). Different studies have generated conflicting results, for example, greater tick abundance within deer exclosures (Shelton et al., 2014), but overall tick densities, and consequently Lyme disease, likely increase with deer densities (Martin et al., 2020). Historically, frequent surface fires may have been able to control ticks, resulting in another complex interaction among ticks, deer browsing, and fires (Gallagher et al., 2022).

6. Conclusions

We are only beginning to appreciate in aggregate the ecological benefits of deer browsing from a viewpoint of historical disturbances and ecosystems. Numerous studies, over many years and locations, reveal the important effects of deer on plant and animal community structure and composition, primarily tree reduction. Perceived ecological problems caused by sustained and suppressive deer browsing may be based on recent ecosystem and disturbance norms, a concern over exponential but natural growth of deer populations during recovery from historical lows in the late 19th century, and extirpation of apex predators (wolves and mountain lions) that may suggest an unregulated ecosystem that is out of balance. However, ecosystems with apex predators and ungulates still demonstrate a range of browsing effects on vegetation.

Ecological benefits of reduced tree density from browsing include support of biodiversity, along with diminished risk of high severity fires and insect outbreaks, due to open conditions, herbaceous resources, and plant dispersal. Because deer browsing is chronic rather than episodic, deer may be a powerful stabilizer of the open forest state. With stabilization from deer and other ungulates, frequent surface fire-maintained grasslands and oak and/or pine open forests in many parts of the eastern U.S. against forest closure. Deer are the only species filling the ecological role of large herbivores south of the northern forest zone now, including responsibility for all the megaherbivore seed dispersal. Localized areas with poor tree regeneration due to chronic deer browsing may be viewed as opportunities for open forest restoration and structural heterogeneity rather than simply closed forest failures. Deer disturbances supply the soil mixing of trampling, digging, or wallowing that disrupts superior plant competitors, allowing diverse forbs into interspaces between grasses. Still, in most forest types and locations, browsing by a single herbivore, even at elevated densities, is unlikely to promote widespread open forest and woodland conditions. Although deer are considered by many to be overabundant, with socioeconomic and ecological costs, deer likely are within historical population levels and deer also provide abundant ecosystem services. As for socioeconomics, deer benefit human livelihoods and are culturally desirable. Deer are the most economically valuable wildlife species and the primary source of funding for state wildlife agencies. Deer, as the most visible large mammal, are prized by society. Costs include motor vehicle accidents, which can be minimized with safety precautions and wildlife crossings, along with disease transmission.

Based on this integration about deer effects, we recommend re-framing deer and herbivory as a fundamental natural disturbance that generates a range of ecological outcomes. Assessed impacts are ultimately minor when considered in the context of paleoecological disturbance regimes of megaherbivores and frequent surface fires that formerly controlled tree densities and promoted landscape heterogeneity in forest structure (i.e., grasslands, savannas, and woodlands defined by open midstories and an herbaceous groundlayer) but have been extirpated or greatly

reduced from the eastern U.S. Where there is a historical precedent for herbivory and the structural outcomes that emerge from it, browsing by deer and other ungulates is a fundamental ecological interaction that has been shaping the structure and composition of temperate forest ecosystems for millions of years. Given dynamics, extinctions, and extirpations of large herbivores, the current influence of mammalian herbivory on vegetation and ecosystems is less than historical influence, in that only one large herbivore's abundance and range is within historical bounds. Whether deer browsing that reduces tree densities is considered an unnatural forest health concern or an important ecological disturbance depends on the lens through which we view current ecosystem and disturbance norms and the paleoecological and historical context in which we place browsing by white-tailed deer.

CRediT authorship contribution statement

Brice Hanberry: Conceptualization; Roles/Writing – original draft; Writing – review & editing.
Edward Faison: Conceptualization; Roles/Writing – original draft; Writing – review & editing.

Data availability

No data was used for the research described in the article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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