

Experimental evaluation of four protocols for assessing white-tailed deer browse intensity

Brendan R. Quirion¹, Bernd Blossey^{*}

Department of Natural Resources and the Environment, Cornell University, Ithaca, NY 14853, United States

ARTICLE INFO

Keywords:

White-tailed deer
AVID Ten-Age
Ten-Tallest
Sentinel
Browse intensity

ABSTRACT

Native and introduced deer populations have expanded on many continents and are now considered primary drivers of ecosystem degradation. Large herbivore management can be controversial, requiring appropriate tools to gauge impacts and guide management decisions. While many different protocols have been proposed to measure deer impacts to vegetation, few have been experimentally validated to assess whether they respond reliably to changes in deer browse intensity.

Here we used a network of large (2 ha) long-term deer exclosures in New York State to assess utility and reliability of AVID (Assessing Vegetation Impacts of Deer), the Ten-Tallest, and Twig-Age protocols to capture changes in white-tailed deer (*Odocoileus virginianus*) browse intensity. We also assessed whether three herbaceous species: blue-stemmed goldenrod (*Solidago caesia*), white wood aster (*Eurybia divaricata*), and zigzag goldenrod (*Solidago flexicaulis*) could expand upon a red oak (*Quercus rubra*) Sentinel protocol. Finally, we evaluated whether these four protocols adhered to criteria defined for ecological indicator selection.

AVID, Ten-Tallest, and Twig-Age protocols rely on existing vegetation to measure deer browse intensity, which limited their ability to adhere to basic sampling principles and be standardized across different forest types, especially in areas with little vegetation remaining in browse height. The Ten-Tallest protocol did not consistently detect differences in deer browse intensity, calling into question its scientific validity. The Sentinel protocol utilizes propagated and planted species, which standardizes impact assessments across sites and captures annual changes in deer browse intensity. Sentinel met nearly all criteria required to function as a reliable deer browse indicator. Validation and selection of additional sentinel species is necessary to build out a portfolio of regionally relevant species that can gauge deer browse intensity across vegetation and habitat types. Of the herbaceous species evaluated, *S. caesia* showed promise as a new sentinel species, but further evaluations are necessary. Evidence-based deer management will require scientifically rigorous and validated impact monitoring approaches and metrics. We caution against adopting protocols that have not been thoroughly vetted to avoid misguided deer management and policy.

1. Introduction

Habitat loss, biological invasions, pollution, climate change and their interactions threaten biodiversity globally and challenge the ability of societies to effectively respond (Malhi et al., 2020; Tylianakis et al., 2008). Correctly identifying which stressors are main drivers of ecosystem degradation is essential for developing appropriate ecosystem management and policy (MacDougall and Turkington, 2005). Ideally, societies use sophisticated long-term monitoring approaches that measure changes in conditions, processes, and biota that characterize

ecosystem composition, structure, and function, but financial and logistical constraints continue to delay progress (Siddig et al., 2016; Tylianakis et al., 2008). An increasingly popular approach is deployment of ground-based or remote monitoring techniques that detect ecological changes using indicators (Siddig et al., 2016; Xu et al., 2019). Such monitoring ideally incorporates simple and efficient measurements that facilitate evidence-based but cost-effective management (Siddig et al., 2016).

Despite their increasing popularity, many proposed indicators are developed using vague selection criteria, lack experimental evaluation

^{*} Corresponding author.

E-mail addresses: brendan.quirion@dec.ny.gov (B.R. Quirion), bb22@cornell.edu (B. Blossey).

¹ Present address: Division of Fish & Wildlife, New York State Department of Environmental Conservation, 625 Broadway, Albany, NY 12233-4754.

to confirm whether they respond appropriately to environmental change, and do not account for co-occurring stressors that are difficult to recognize (Siddig et al., 2016). Failure to use clearly defined and scientifically rigorous selection processes when developing ecological indicators can result in misguided management and policy (Brice et al., 2022; Dale and Beyeler, 2001). The challenge then is to develop and validate a set of ecological indicators that are: (1) easily measured, (2) sensitive to stresses, (3) respond to stress in a predictable manner, (4) signify an impending change in the ecosystem under consideration that (5) can be averted by management interventions, (6) provide coverage of key ecosystem conditions and resources that could be compromised, (7) have a known response through time, and (8) have low variability of that response (Dale and Beyeler, 2001).

Here we focus on validation of indicators proposed to assess deer (family *Cervidae*) browse intensity (henceforth “deer browse indicators”). Predator extirpations, intercontinental introductions, changes in land use and hunting regulations, shifts in societal norms and values, and climate change have allowed deer populations to flourish, mostly in the Global North. Early warnings of threats posed by increasing deer populations were raised in Europe and North America decades ago (Hare et al., 2021; Leopold et al., 1947) but to no avail. Deer populations have now increased to historically unprecedented levels and become major drivers of ecosystem degradation on multiple continents (Côté et al., 2004; Nishizawa et al., 2016; Nopp-Mayr et al., 2020; Wardle and Bardgett, 2004; Wright et al., 2012).

High deer populations not only exert strong selective top-down consumptive effects on vegetation, but their non-consumptive, indirect effects have cascading impacts on biological invasions (Dávalos et al., 2015a; Dávalos et al., 2015b), spread of tick-borne diseases (Kilpatrick et al., 2014), and abundance of birds, small mammals, and invertebrates (Kalisz et al., 2014; Nuttle et al., 2011; Parsons et al., 2013). Legacies of altered plant reproduction and recruitment, soil structure and chemistry, and nutrient dynamics can allow these degraded systems to persist for decades, even after deer populations have been reduced (Harada et al., 2020; Nuttle et al., 2014; Wright et al., 2012). In eastern North America, deer browse impacts are now so pervasive that forest regeneration is largely prevented, creating a regeneration debt that will affect forest food webs, biodiversity, and the ability of forests to store carbon for decades to come (Miller et al., 2019).

Scientists around the world have recognized the need and urgency to develop more sophisticated deer impact assessment protocols and have promoted a diversity of monitoring approaches and metrics. These have often focused on deer abundance, health, and condition, and economically valuable agricultural or timber species, largely ignoring herbaceous species, conservation interests, or indirect impacts until recently (Bachand et al., 2014; Chevrier et al., 2012; Frerker et al., 2013; Iijima and Nagaike, 2015; Morellet et al., 2007). However, despite these developments, no European country has implemented a formal program to assess deer impacts to agriculture, forestry or conservation (Putman et al., 2011). The United States’ National Forest Inventory and Analysis program has yielded important regional data on deer impacts to forest regeneration (Miller et al., 2019; Patton et al., 2018), but has limited utility to inform local deer management decisions due to low spatial and temporal sampling resolution.

In North America, state wildlife agencies have primary responsibility for wildlife management, and retaining abundant populations of ungulates for recreational hunting continues to be a primary focus (Freyfogle and Goble, 2009). Agency funding is largely derived from hunting and fishing licenses and excise taxes on hunting and angling equipment (Jacobson et al., 2007), which can create a conflict of interest for agencies to reduce ungulate populations despite legal obligations to conserve wildlife in the interest of all current and future members of the public (Hare and Blossey, 2014). Surveys gauging support for deer population reductions indicate that a majority of residents support increased efforts to reduce deer populations to benefit other plants and animals, human health, and economic interests, or to increase forest

carbon capture (Hare et al., 2021). Since lethal large herbivore management is controversial (Frye, 2006; Sterba, 2012), the scientific validity of proposed deer impact assessment protocols meant to inform management is of utmost importance. However, many proposed protocols have not been experimentally evaluated for their ability to meet defined selection criteria of an ecological indicator (Dale and Beyeler, 2001).

Here we evaluated whether three deer browse impact assessment protocols, Twig-Age (Waller et al., 2017), Ten-Tallest (Rawinski, 2018), and AVID (Assessing Vegetation Impacts from Deer) (Sullivan et al., 2020) met criteria of a deer browse indicator. We utilized a network of paired 2-ha plots (one fenced, one adjacent unfenced) established in 2013 in five northern hardwood forests to test whether each could detect differences in deer browse intensity across the fence. Treefalls created occasional fence breaches, allowing deer access for short periods of time until repairs were made. Therefore, we investigated greatly reduced deer browse intensity since 2013 rather than complete deer exclusion. The three protocols measure different aspects of existing vegetation, and predictions in their primary response metrics vary accordingly. In areas under reduced deer browse intensity (here fenced plots), AVID and Ten-Tallest predict (1) taller tree seedlings/saplings and herbaceous plants; and (2) increased flowering of herbaceous plants compared to areas with higher deer browse intensity (here unfenced plots). Twig-Age predicts (3) older twig ages in fenced compared to unfenced plots.

We previously demonstrated the utility and sensitivity of annually planted red oak (*Q. rubra*) seedlings to gauge changes in deer browse intensity using a Sentinel protocol (Blossey et al., 2019; Blossey et al., 2017). The proportion of browsed *Q. rubra* seedlings was a function of the size of the local deer population, but there is a need to expand the protocol to include more sensitive sentinel species. Use of purposefully selected, propagated, and planted seedlings has distinct advantages because it allows for standardization of assessments across habitats with different plant communities, and in areas heavily impacted by deer with little remaining understory vegetation. The particular species selected and planted as sentinels may differ based on species distributions, conservation purposes, and habitat type, but require experimental validation before widespread use. Therefore, we used the same fenced and unfenced 2 ha plots to assess whether transplanted seedlings of three widespread herbaceous species (*Solidago caesia*, blue-stemmed goldenrod; *Eurybia divaricata*, white wood aster; and *Solidago flexicaulis*, zigzag goldenrod) could be used to complement *Q. rubra* as useful sentinels of deer browse intensity. To be reliable sentinels, planted individuals protected from deer should (4) have greater survival rates; (5) achieve greater height; and (6) show increased flowering frequency. Using long-term fenced and unfenced plots also allowed us to assess the potential presence of non-consumptive, indirect deer impacts (Dávalos et al., 2015b; Dobson et al., 2015). To reliably indicate differences in deer browse intensity, attack by other organisms that can affect sentinel species survival and performance (rodents, insects, diseases, etc.) should be similar regardless of whether individuals are protected by fences.

2. Methods

2.1. Study sites

We established paired 2 ha rectangular plots in 2013 in five closed-canopy forests in central New York State (Bobolink Hill, Ellis Hollow, Polson, Ringwood, and Sapsucker Woods). All sites have a diverse overstory of mature seed producing trees dominated by maples (*Acer* spp.), and less frequent American beech (*Fagus grandifolia*), ash (*Fraxinus* spp.), birch (*Betula* spp.), red oak (*Q. rubra*), shagbark hickory (*Carya ovata*), American hornbeam (*Carpinus caroliniana*), black cherry (*Prunus serotina*), tulip tree (*Liriodendron tulipifera*), eastern white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*). All sites are on protected or private lands dedicated to conservation (Ellis Hollow is owned by the Finger Lakes Land Trust, Bobolink Hill is in private ownership, the

Table 1
Specifications to perform AVID, Ten-Tallest, Twig-Age, and Sentinel protocols.

Specifications	Assessment protocol			
	AVID	Ten-Tallest	Twig-Age	Sentinel
Target vegetation	Saplings <i>Trillium</i> spp. <i>M. virginiana</i> <i>A. triphyllum</i>	Saplings Shrubs Herbs	Deciduous saplings	<i>Q. rubra</i> validated species
Vegetation height	15–152 cm	≤122 cm	20–180 cm	≥10 cm
Key metric(s)	Plant height Flowering	Plant height Flowering	# of bud scale scars (on 2 twigs/ sapling)	Deer browse Rodent attack Invertebrate attack Plant growth Survival Flowering Transect
Sampling unit	Circle	Circle	Transect or arc	
Sampling dimensions	1.8 m radius	5.6 m radius	≥1 m between stems	100 + m
# Sampling units/site	6	Unbounded	1 to 3	1 (per 10–100 ha)
# Plants measured/unit	4 to 6	10	50 to 60/ species	20/species
Selection of sampling units	Non-random	Non-random	Random	Random
Selection of plant species	Based on availability	Based on availability	Based on availability	Planted
Selection of individuals	Random	10 tallest	Random	Planted

others are unique natural areas owned by Cornell University), and all have active deer management programs (recreational hunting and/or culling). Within a site, we established paired plots in areas with similar slope, aspect, elevation, canopy cover, and species composition. In each plot, we established a spatial grid (20×20 m cells marked by PVC stakes) and randomly selected one plot to be fenced (Trident extruded deer fence, 2.3-m-high fence, DeerBusters.com, Maryland, USA).

2.2. Twig-Age, Ten-Tallest, & AVID protocols

Twig-Age requires counting terminal bud scale scars from tips of lateral twigs back to the nearest branching point to record age. This protocol measures time (in years) that a twig has grown without tip removal or death that would lead to a branching event. Tip death is assumed to occur primarily from deer browse. We recorded twig ages on two twigs/sapling on 50 to 60 saplings/species (height: 20–180 cm) in randomly established 100 m × 2 m belt transects (one/plot) before leaf-out in April/May 2020 (Table 1).

Ten-Tallest measures heights (≤122 cm) of the 10 tallest woody or herbaceous stems/species using temporary or permanent circular sampling locations (5.64 m radius; with no specified number of sampling units). Sampling locations are typically established subjectively based on availability of vegetation. To avoid sampling bias and meet assumptions for statistical analyses, we randomly selected six sampling locations in each plot using a random number generator assigned to the spatial grid in each plot. However, we reverted to subjective selection of sampling locations if the first five random locations did not contain enough stems/species. We used a center stake and tape measure to delineate sampling area circumference and selected species based on availability of ≥10 stems. We measured height of every stem of a target species to select the 10 tallest, and documented evidence of flowering or fruiting (Table 1).

AVID recommends establishment of six permanent sampling locations/site (1.8 m radius) and then tracks growth (heights 15.3–152.4 cm) of five to six permanently marked tree seedlings/species or stems of

Trillium spp., *Medeola virginiana*, or *Arisaema triphyllum*, and the proportion flowering through time. Similar to Ten-Tallest, sampling locations for AVID are selected subjectively based on availability of vegetation. We nested all AVID sampling locations within Ten-Tallest locations since they already contained at least 10 stems/species and implemented both protocols between May and November 2020 (Table 1).

We recorded time required for a data collector and recorder to implement each protocol (excluding travel time and initial set-up) using a stopwatch.

2.3. Sentinel protocol expansion

Sentinel requires propagation of seedlings that are then planted in spring and tracked individually to assess survival, growth, deer browse, rodent or invertebrate attack, and overwinter mortality (Blossey et al., 2019; Blossey et al., 2017). Typically, *Q. rubra* cohorts are planted annually to assess changes in deer browse intensity (Table 1). We propagated *Q. rubra*, *S. caesia*, *E. divaricata*, and *S. flexicaulis* from seed collected in fall 2019 near Ithaca, New York. All four species are widespread, favored by deer, simple to collect and propagate, and fast growing. For oaks we followed established propagation procedures (Blossey et al., 2017). We cold-stratified seeds of herbaceous species to break dormancy before sowing into flats of potting soil (BX Mycorrhizae General Purpose Pro-mix; Premier Brands, Riviere-du-Loup, Quebec, Canada) in March 2020. We maintained flats in a greenhouse (12:12 day:night, 20° C) until seedlings produced 2 – 3 true leaves before transplanting into 72-cell flats. We moved flats outdoors in late May to allow for hardening and stratified seedlings by height/species before planting to ensure unbiased initial height distributions across study sites.

Within each plot, we selected a starting point, picked a cardinal direction, and established a 100 – 150 m transect using a measuring tape. We used a cordless impact driver (Milwaukee M18 series, milwaukee.com) with a wood-boring bit (Speedbor Max 3.175 cm × 15.24 cm, irwin.com) to create planting holes at 1 m increments along the transect, excluding unsuitable planting locations (e.g., boulders, blow-downs, wet depressions, dense vegetation, etc.) that could potentially negatively affect plant performance or prevent deer access. We planted 20 individuals/species from 15 to 24 June 2020 in a repeating pattern (i. e. *Q. rubra*, *S. caesia*, *E. divaricata*, *S. flexicaulis*; repeat) for a total of 80 individuals per plot. We firmly planted each seedling, adding surrounding soil to planting holes as needed to ensure adequate root contact and avoid desiccation. We recorded the position of each seedling along transects, initial height, and marked seedlings using a 10 cm long nail inserted through a 3 or 4 cm steel washer adjacent to each plant. This allowed for relocation using a metal detector (ACE 350, Garret Electronics Inc., Garland, Texas, USA). We revisited all transects after two weeks and replaced eight individuals that had died due to transplant shock (two *Q. rubra*, two *E. divaricata*, three *S. caesia*, and one *S. flexicaulis*). Thereafter, we recorded presence, height, type of attack, and flowering monthly through October 2020. We did not record invertebrate attack (insects and diseases combined) in October as plant tissues started to senescence. We recorded overwinter survival (defined as live aboveground plant tissue) in June 2021 and second season height by end of August 2021.

We recorded time required to establish and plant transects (typically three individuals) and for follow-up data collection (a data collector and a recorder) using a stopwatch (excluding travel time and initial set-up). This did not include time required for seed collection and propagation.

2.4. Statistical analyses

We analyzed data in R and considered $P < 0.05$ statistically significant (R Core Team, 2020). For Twig-Age, Ten-Tallest, and AVID, we fitted linear mixed effects models (GLMs) for twig age and plant heights,

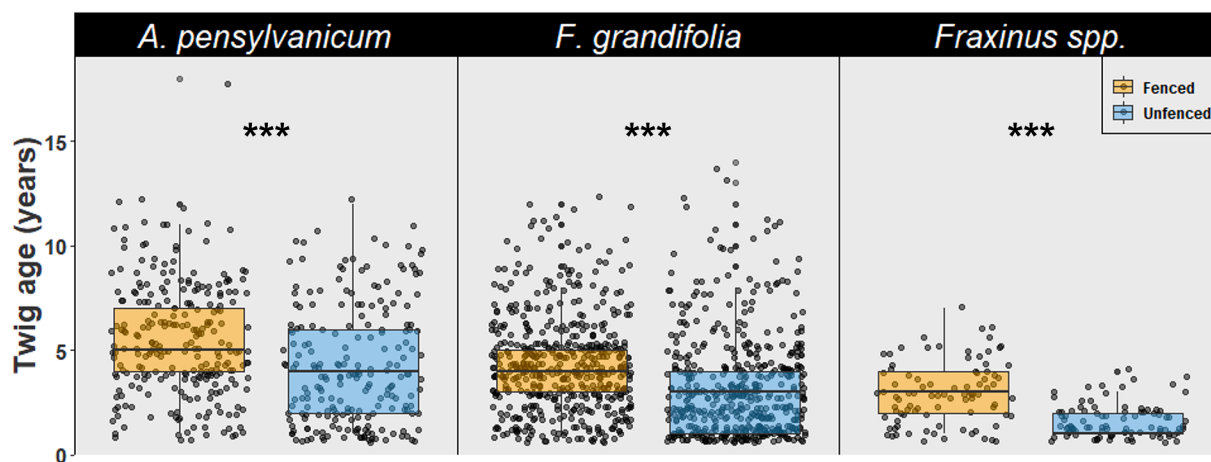


Fig. 1. Boxplots of *A. pensylvanicum*, *F. grandifolia*, and *Fraxinus* spp. twig ages (years) in fenced and unfenced plots at two, four, and one site respectively. Boxplots show medians, ranges, and error bars representing 95% confidence intervals. Data points represent individual twig ages ($N = 90 - 500$ per species/plot combination). Asterisks indicate statistically significant differences (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) between fenced and unfenced plots.

modeling each species separately and including fencing treatment as a fixed effect. We included sapling on which twigs were measured as a random effect for twig age. We included the Ten-Tallest/AVID sampling location as a random effect for plant heights. For all GLMs, we included site as a random effect if a species was assessed at $\geq$ four sites, and as a fixed effect if at $\leq$ three sites. For Ten-Tallest, we fitted a linear model for total number of flowering plants per sampling location, including fencing and site as fixed effects. For AVID, we fitted a GLM with binomial errors for flowering of *Trillium* spp., *M. virginiana*, or *A. triphyllum*, including fencing and site as fixed effects, and sampling location as a random effect.

For Sentinel, we applied data exclusions to restrict our analyses to

plants available to deer, rodents, and invertebrates, and to plants that were still present to evaluate second-year growth. We excluded dug up plants or those with unverifiable attack causing premature death from all analyses. We excluded plants browsed by deer inside fenced plots due to fence breaches from all analyses except one-year survival. For deer browse, we excluded individuals that remained below browse height ($< 5\text{cm}$) for the entire 2020 growing season, were absent after planting, or had compromised leaf tissue that did not recover by the end of the 2020 growing season. For invertebrate attack, we excluded individuals absent after planting or without leaves, or that lacked vegetative regrowth by the end of the 2020 growing season. For rodent attack, we excluded plants absent after planting, or that lacked vegetative regrowth

Table 2

Results of linear mixed models for effect of fencing on twig age, plant height, and flowering under four different protocols assessing deer browse intensity (Twig Age, Ten-Tallest, AVID, and Sentinel). Site is included as a fixed effect if a plant species could be evaluated by a protocol at three or fewer sites and as a random effect if at four or five sites.

Response	Predictors	df_{Num}	df_{Den}	Sum sq	Mean sq	F	P
Twig-Age (years)							
<i>F. grandifolia</i> ¹	Fencing	1	493	82.8	82.8	33.77	<0.001
<i>A. pensylvanicum</i> ²	Fencing	1	228	42.9	42.9	16.44	<0.001
	Site	1	228	20.4	20.4	7.83	0.006
<i>Fraxinus</i> spp. ²	Fencing	1	119	43.4	43.4	46.66	<0.001
Ten-Tallest							
<i>F. grandifolia</i> Height (cm) ³	Fencing	1	46	180.0	180.0	0.68	0.414
<i>Trillium</i> spp. Height (cm) ⁴	Fencing	1	17	136.9	136.9	17.16	0.001
	Site	1	17	27.8	27.8	3.49	0.079
<i>Trillium</i> spp.	Fencing	1	116	1125.0	1125.0	11.44	0.004
Fertile stems (N)	Site	1	116	45.6	45.6	0.46	0.505
<i>S. caesia</i> Height (cm) ⁴	Fencing	1	10	15.8	15.8	0.27	0.616
AVID							
<i>F. grandifolia</i> ³	Fencing	1	46	6106.8	6106.8	8.21	0.006
Height (cm)							
<i>Trillium</i> spp. ⁴	Fencing	1	18	260.2	260.2	29.89	<0.001
Height (cm)	Site	1	17	70.8	70.8	8.14	0.011
Sentinel							
August 2021 height (cm) ⁵	Fencing	1	1206	254.6	254.6	6.59	0.010

¹ Sapling and sapling within site as random effects.

² Sapling as random effect.

³ Sampling location and sampling location within site as random effects.

⁴ Sampling location as random effect.

⁵ Site as a random effect and species, planting height, and days since planting as fixed effects.

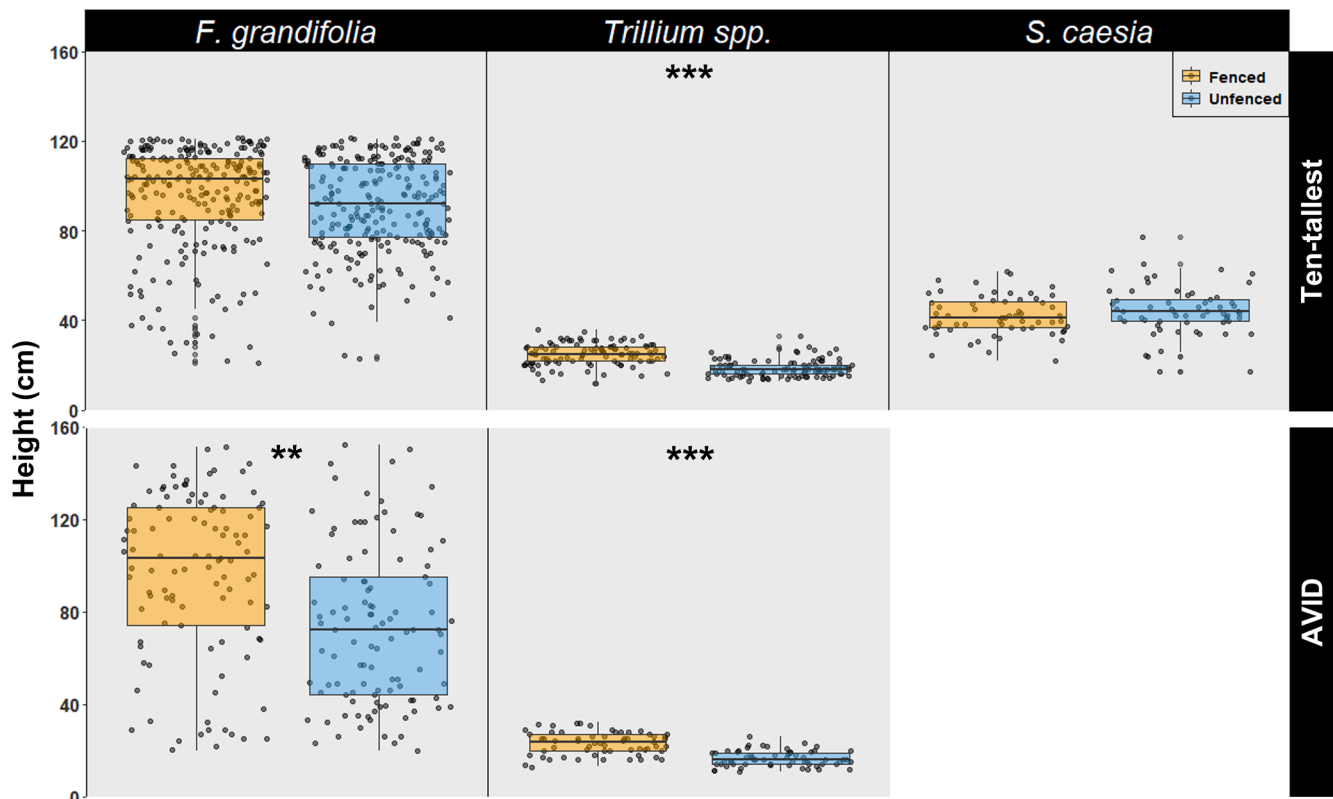


Fig. 2. Boxplots of *F. grandifolia*, *Trillium* spp., and *S. caesia* heights (cm) in fenced and unfenced plots at four, two, and one site, respectively, using Ten-Tallest and/or AVID. Boxplots show medians, ranges, and error bars representing 95% confidence intervals. Data points represent individual plant heights (N = 60 – 240 per species/plot combination). Asterisks indicate statistically significant differences (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) between fenced and unfenced plots.

by the end of the 2020 growing season. For plant heights by the end of August 2021, we excluded plants that did not survive to the end of the 2020 growing season or that did not survive to spring 2021.

We fitted a GLM with binomial errors for deer browse of unfenced plants, including species as a fixed effect and site as a random effect. We fitted GLMs with binomial errors for rodent and invertebrate attack, one-year survival, and flowering, including fencing and species as fixed effects, and site as a random effect. We included initial height of each plant at planting as a fixed effect for one-year survival. For plant growth by August 2021, we fitted a linear mixed effects model including fencing, species, planting height, and days since planting as fixed effects and site as a random effect.

We used “lmerTest” (Kuznetsova et al., 2017) for linear models and “brglm2” (Kosmidis and Firth, 2021) for GLMs. We examined effects of experimental variables by conducting type III analyses of variance, applying Benjamini-Hochberg corrections to Sentinel models to account for multiple comparisons and control the false discovery rate. For Sentinel models we report Benjamini-Hochberg-corrected P -values. We visually inspected the modeled data and residuals to ensure model assumptions had been met.

3. Results

3.1. Twig-Age, Ten-Tallest, & AVID protocols

A fence breach at Ellis Hollow in late winter 2019/2020 resulted in deer browse damage to understory woody vegetation. Therefore, we only implemented the herbaceous species components of Ten-Tallest and AVID at this site after fence repairs. For AVID and Ten-Tallest, we immediately confronted difficulties associated with establishing sampling locations randomly due to a lack of species and stems in appropriate size classes, even in fenced plots that had been protected from

deer herbivory for seven years. In only one instance (unfenced plot at Polson) could we establish all six sampling locations for woody species from the first six random locations we visited. All Ten-Tallest/AVID sampling locations for herbaceous species had to be selected subjectively. Conversely, we were able to perform Twig-Age through randomly selected transects in every plot.

Despite a diverse overstory, only *F. grandifolia* was present in sufficient abundance at all sites to implement AVID, Ten-Tallest and Twig-Age, while *A. pensylvanicum* and *Fraxinus* spp. were also present in sufficient abundance at two sites and one site, respectively, to implement Twig-Age. We were able to implement Ten-Tallest for *S. caesia* and *Trillium* spp. at one and two sites, respectively. The only herbaceous species that AVID targets that was present in sufficient abundance was *Trillium* spp. at two sites. However, we could only identify four Ten-Tallest/AVID sampling locations with sufficient *Trillium* spp. at Ringwood.

Twig ages were significantly older in fenced compared to unfenced plots for all species: *F. grandifolia* ($F = 33.77$, $P = < 0.001$), *A. pensylvanicum* ($F = 16.44$, $P = < 0.001$), *Fraxinus* spp. ($F = 46.66$, $P < 0.001$) (Fig. 1, Table 2). AVID detected significantly taller *F. grandifolia* in fenced compared to unfenced plots ($F = 8.21$, $P = 0.006$), but Ten-Tallest did not ($F = 0.68$, $P = 0.414$) (Fig. 2, Table 2).

Both AVID ($F = 8.14$, $P = 0.011$) and Ten-Tallest ($F = 17.16$, $P = 0.001$) detected significantly taller *Trillium* spp. in fenced compared to unfenced plots (Fig. 1, Table 2). Ten-Tallest detected significantly more ($F = 11.44$, $P = 0.004$), and AVID a significantly greater proportion ($z = -2.88$, $P = 0.004$), of *Trillium* spp. flowering in fenced compared to unfenced plots (Fig. 3, Table 2, Table 3). We found no significant difference in *S. caesia* heights ($F = 0.27$, $P = 0.616$) between fenced and unfenced plots using Ten-Tallest (Fig. 2, Table 2) and no *S. caesia* flowered.

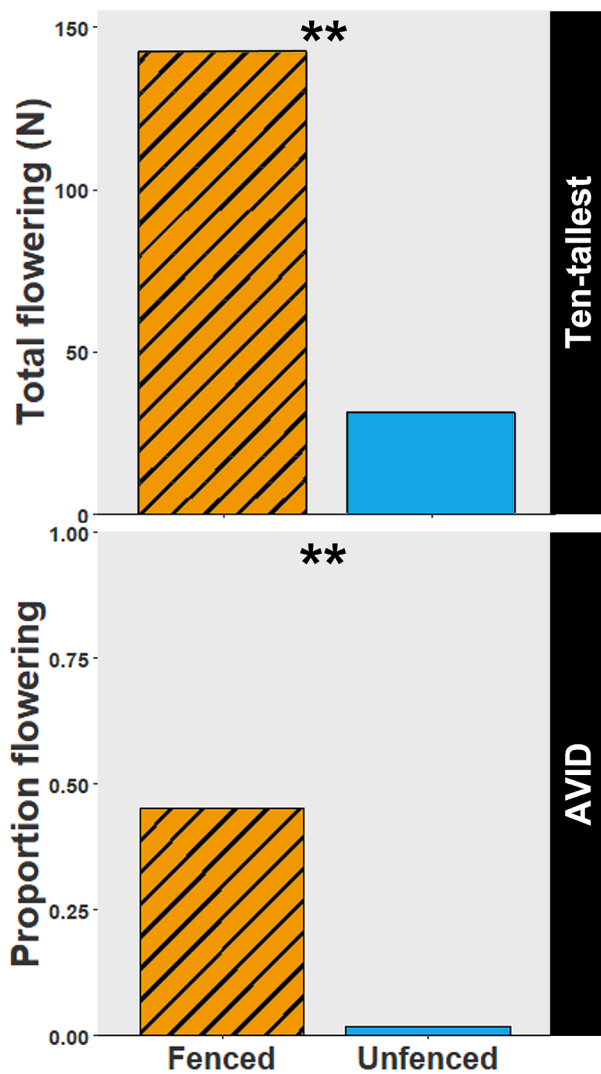


Fig. 3. Barplots of number and proportion of flowering *Trillium* spp. in fenced and unfenced plots at two sites using Ten-Tallest and AVID. Asterisks indicate statistically significant differences (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) in number and proportion of *Trillium* spp. flowering between fenced and unfenced plots.

3.2. Sentinel protocol expansion

Tree falls allowed deer access at Ellis Hollow and Ringwood in 2020 and 2021, resulting in deer browse on three *S. caesia*, 12 *S. flexicaulis*, and one *E. divaricata* (Ellis Hollow) and 11 *S. caesia*, nine *S. flexicaulis*, four *E. divaricata*, and 10 *Q. rubra* (Ringwood). We excluded these individuals from analyses, except for one-year survival, as they represent a treatment failure. We did not observe evidence of recent deer browse in fenced plots when performing Twig-Age, Ten-Tallest, or AVID because data collection for these protocols occurred prior to these fence breaches.

Deer showed preferences among our planted herbaceous species with a significantly greater proportion of *S. caesia* browsed compared to *Q. rubra* in unfenced plots ($z = 2.72$, $P = 0.007$). Neither *S. flexicaulis* ($z = -0.27$, $P = 0.789$) nor *E. divaricata* ($z = 1.66$, $P = 0.098$) were browsed significantly more than *Q. rubra* in unfenced plots (Fig. 4, Table 3). Rodent attack on *S. flexicaulis* was significantly greater in fenced compared to unfenced plots ($z = 2.92$, $P = 0.014$) but was similar irrespective of fencing for other species (Fig. 5, Table 3). Invertebrates attacked a significantly greater proportion of *E. divaricata* in unfenced compared to fenced plots ($z = -3.53$, $P = 0.002$), but patterns of

Table 3

Results of GLMs with binomial errors on proportion of *Q. rubra*, *S. caesia*, *S. flexicaulis*, and *E. divaricata* browsed by deer, attacked by rodents or invertebrates, one-year survival, and flowering in fenced and unfenced plots at five sites using Sentinel, and proportion of flowering *Trillium* spp. using AVID. Site is included as a fixed effect if a plant species was evaluated at three or fewer sites and as a random effect if at four or five sites.

Response	Predictors	Estimates	SE	z	P
Sentinel					
Deer browse ¹	Intercept (<i>Q. rubra</i>)	-2.22	0.43	-5.22	<0.001
	<i>S. caesia</i>	1.18	0.44	2.72	0.007
	<i>S. flexicaulis</i>	-0.14	0.51	-0.27	0.789
	<i>E. divaricata</i>	0.83	0.50	1.66	0.098
Rodent attack ¹	Intercept (Fenced, <i>Q. rubra</i>)	-2.84	0.74	-3.84	<0.001
	Unfenced	-17.29	40.48	-0.43	0.669
	<i>S. caesia</i>	0.76	0.45	1.68	0.094
	<i>S. flexicaulis</i>	1.15	0.45	2.57	0.010
	<i>E. divaricata</i>	1.70	0.44	3.90	<0.001
	Unfenced *	16.39	40.48	0.41	0.686
	<i>S. caesia</i>				
	Unfenced *	15.89	40.48	0.39	0.695
	<i>S. flexicaulis</i>				
	Unfenced *	16.57	40.48	0.41	0.682
	<i>E. divaricata</i>				
Invertebrate attack ¹	Intercept (Fenced, <i>Q. rubra</i>)	-2.45	0.56	-4.41	<0.001
	Unfenced	0.54	0.46	1.16	0.245
	<i>S. caesia</i>	-0.67	0.56	-1.21	0.228
	<i>S. flexicaulis</i>	2.33	0.43	5.43	<0.001
	<i>E. divaricata</i>	1.99	0.43	4.59	<0.001
	Unfenced *	-0.69	0.79	-0.87	0.383
	<i>S. caesia</i>				
	Unfenced *	-1.04	0.57	-1.83	0.068
	<i>S. flexicaulis</i>				
	Unfenced *	0.71	0.58	1.22	0.222
	<i>E. divaricata</i>				
One-year survival ¹	Intercept (Fenced, <i>Q. rubra</i>)	1.12	0.49	2.27	0.023
	Unfenced	-0.32	0.39	-0.84	0.401
	<i>S. caesia</i>	0.27	0.47	0.56	0.576
	<i>S. flexicaulis</i>	-0.49	0.38	-1.31	0.192
	<i>E. divaricata</i>	-1.33	0.36	-3.69	<0.001
	Planting Height	0.06	0.03	2.13	0.033
	Unfenced *	-0.80	0.58	-1.39	0.164
	<i>S. caesia</i>				
	Unfenced *	0.06	0.50	0.12	0.903
	<i>S. flexicaulis</i>				
	Unfenced *	-0.51	0.49	-1.04	0.297
	<i>E. divaricata</i>				
<i>S. caesia</i> flowering ¹	Intercept (Fenced)	-0.01	0.40	-0.03	0.973
	Unfenced	0.25	0.31	0.82	0.413
AVID					
<i>Trillium</i> spp. flowering ²	Intercept (Fenced, Bobolink Hill)	-1.38	1.05	-1.31	0.190
	Unfenced	-4.65	1.62	-2.88	0.004
	Ringwood	1.34	1.30	1.03	0.301

¹ Site as random effect.

² Sampling location as random effect.

invertebrate attack for other species were inconsistent and nonsignificant (Fig. 5, Table 3).

Survival of *S. caesia* ($z = 2.62$, $P = 0.018$) and *E. divaricata* ($z = 2.78$, $P = 0.018$) was significantly greater in fenced compared to unfenced plots, but nonsignificant for *Q. rubra* or *S. flexicaulis* (Fig. 5, Table 3). Only *S. caesia* flowered in sufficient numbers for analysis, but we found no significant difference in proportion flowering between fenced and

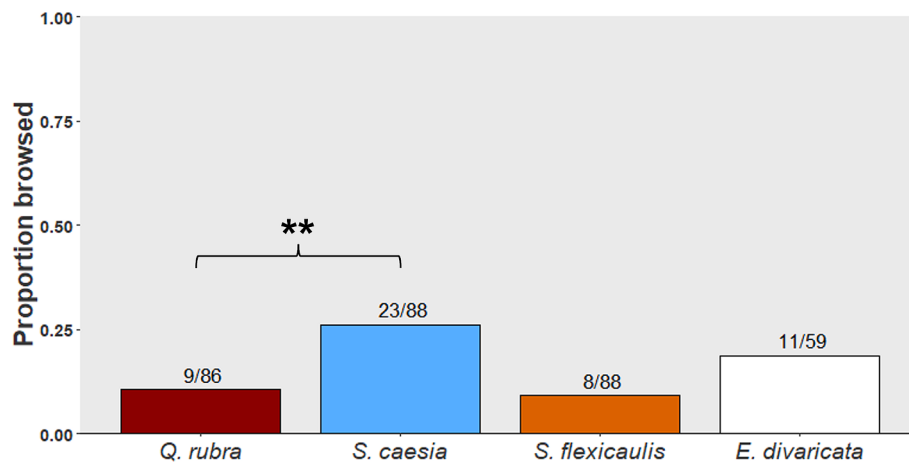


Fig. 4. Proportion of browsed *Q. rubra*, *S. caesia*, *S. flexicaulis*, and *E. divaricata* in unfenced plots at five sites. Numbers of plants browsed out of the pool of available individuals (see text for details) are indicated above bars. Asterisks indicate statistically significant differences (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) in browse rates between herbaceous species and *Q. rubra*.

unfenced plots ($z = 0.82$, $P = 0.413$) (Fig. 6, Table 3). By the end of August 2021, *S. caesia* were significantly taller in fenced compared to unfenced plots ($t = 4.50$, $P = < 0.001$), but we found no significant differences in second-year growth between fenced and unfenced plots for the other species (Fig. 7, Table 2).

Twig-Age required the least amount of time to implement (91 min on average/plot for two species; 59 min on average/plot for a single species), followed by AVID (62 min on average/plot for a single species), and Ten-Tallest (110 min on average/plot for a single species). Planting and four follow-up assessments to experimentally evaluate four species under Sentinel required on average 449 min/plot.

4. Discussion

The future of deer management and its social acceptability is intimately linked to the availability of reliable, timely, and scalable evidence of deer impacts (Hare et al., 2021). Such information presently does not exist, thus development, validation, and implementation of protocols to assess deer impacts is paramount to informing management decisions. When we evaluated the four protocols for their ability to function as reliable deer browse indicators using expanded sub-selection criteria ($N = 17$) defined by Dale and Beyeler (2001), Ten-Tallest met four, AVID met six, Twig-Age met eight, and Sentinel met 16 (Table 4). Our results offer reason for caution when landowners or management agencies select particular protocols to assess deer browse intensity.

To be easily measured (first criterion, Table 4), deer browse indicators should be easy to understand, simple to apply, scientifically sound, and cost effective. While each protocol required some initial familiarization and set-up, we found all were easy to understand and cost effective to implement (Table 4). We could readily implement Twig-Age and Sentinel at all sites, but it was difficult or impossible to implement AVID for *Trillium* spp., *M. virginiana*, or *A. triphyllum* due to low abundance of these species at our study sites. This is not unique to our study area, but is reflective of chronic deer browse impacts in forests throughout the Northeast and Mid-Atlantic regions of North America (Kelly, 2019; Miller et al., 2019). We could also implement Ten-Tallest at all sites, but had to measure numerous stems/species to identify the 10 tallest when vegetation height was uniform. This became very tedious, especially for herbaceous species when there could be hundreds of stems/species in each Ten-Tallest sampling area.

Both Twig-Age and Sentinel adhered to basic scientific sampling principles, but neither AVID nor Ten-Tallest could be readily implemented through random sampling due to low stem densities at our study sites. In partial recognition of this issue, AVID recommends sampling woody vegetation in forests with $< 50\%$ canopy closure. Such forests are

often associated with recent timber harvests or large-scale disturbances (i.e., wind or ice storms, insect outbreaks, etc.) where increased light availability favors regrowth that can be randomly sampled. But this is not representative of regional forest conditions and does not resolve the challenges we faced with implementing AVID for the herbaceous species the protocol recommends in closed canopy forests. These challenges will likely limit AVID's usefulness to gauge deer browse intensity and inform deer management decisions over large spatial scales. Ten-Tallest measures the tallest rather than a random sample of stems. This is an example of sampling bias and can undermine the scientific validity and interpretation of data. For example, Brice et al. (2022) found that such sampling greatly overestimated strength of a trophic cascade involving wolves, elk and *Populus tremuloides* in Yellowstone National Park.

Sentinel was the only protocol validated for its sensitivity (second criterion, Table 4) to changes in deer browse intensity using *Q. rubra* (Blosssey et al., 2019) until recently when Twig-Age was shown to be sensitive as well (Sample et al., 2023). Previous assessments of AVID and Twig-Age used deer exclosures to confirm the responsiveness of proposed metrics to drastic differences in deer browse intensity (Curtis et al., 2021; Waller et al., 2017). However, use of exclosures alone is not sufficient to evaluate a protocol's sensitivity to variations in deer browse intensity as such manipulations only create deer presence/absence treatments and fencing influences factors other than deer browse intensity that may affect growth of woody and herbaceous species (Dávalos et al., 2015a; Dávalos et al., 2015b; Heckel et al., 2010).

Ten-Tallest was the only protocol that did not consistently respond (third criterion, Table 4) to our experimental manipulation of deer browse intensity. Our fencing treatments created strong differences in deer browse intensity despite occasional fence breaches. However, Ten-Tallest failed to detect differences in *F. grandifolia* and naturally occurring *S. caesia* heights between our fenced and unfenced plots. In contrast AVID, which records heights from a random sample of stems, detected significant differences in *F. grandifolia* heights across the fence using the same sampling locations. This finding further calls into question the scientific validity of the Ten-Tallest protocol. Twig-Age consistently detected highly significant differences in twig ages across the fence for all species. Since Twig-Age accounts for small changes in horizontal twig expansion, such as in response to sunflecks on the forest floor, it is likely more sensitive than AVID and Ten-Tallest in closed-canopy forests where light limitations delay vertical growth of seedlings. However, only Sentinel has articulated a known deer browse intensity response threshold ($< 15\%$ annual browse rate for red oaks; Blosssey et al 2019) that should not be exceeded. Neither AVID, Ten-Tallest, nor Twig-Age have yet defined or validated annual growth, flowering rates, or twig ages that are unacceptable and would require interventions by

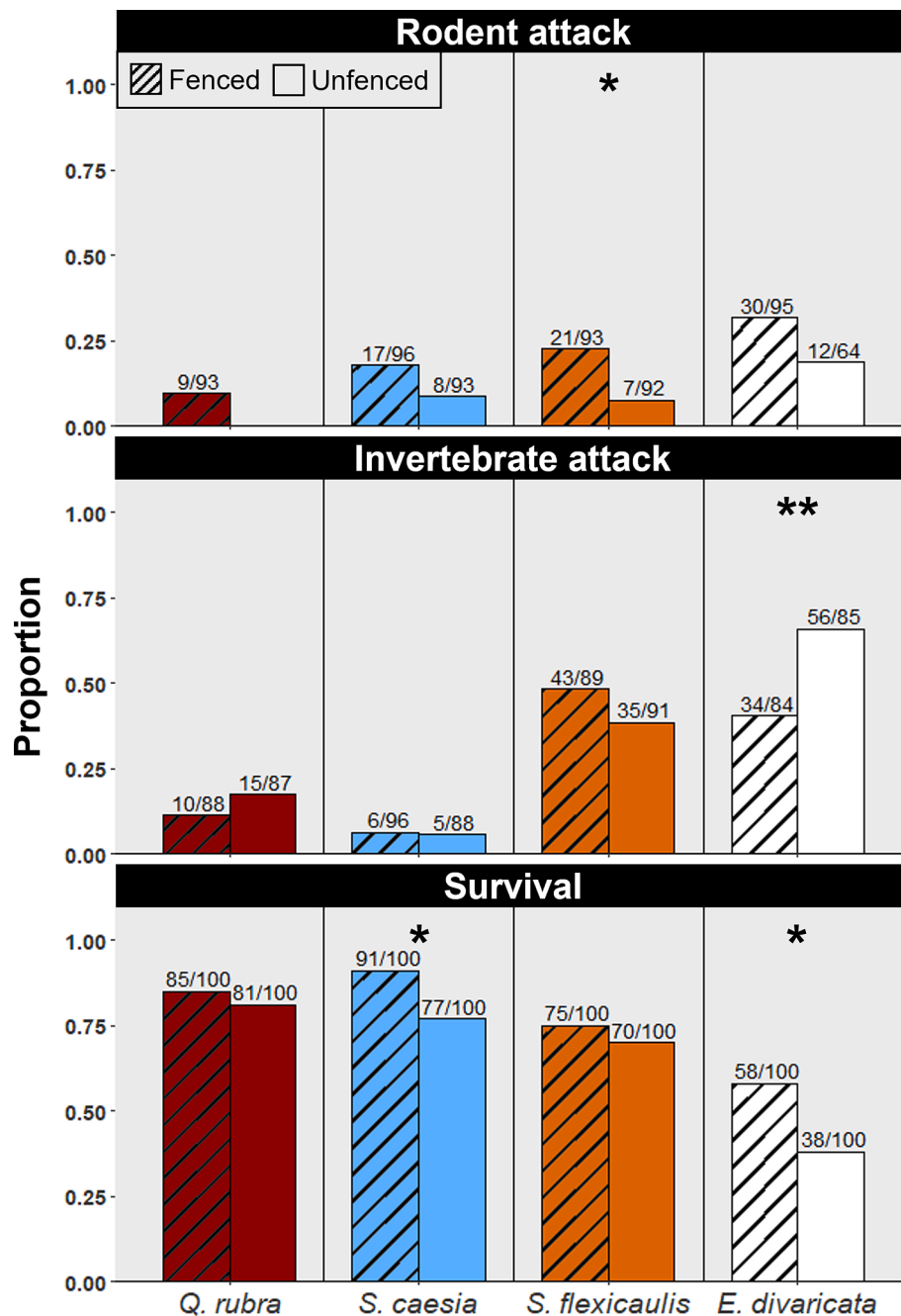


Fig. 5. Proportion of *Q. rubra*, *S. caesia*, *S. flexicaulis*, and *E. divaricata* attacked by rodents or invertebrates and that survived for one year in fenced and unfenced plots at five sites. Number of individuals attacked or surviving out of the pool of available individuals (see text for details) are indicated above bars. Asterisks indicate statistically significant differences (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) between fenced and unfenced plots.

managers.

None of the protocols we assessed have been evaluated for their ability to be anticipatory (fourth criterion, Table 4) of deer browse intensity before changes in ecological integrity occur. Deer browse impacts at our study sites were chronic rather than incipient, limiting our ability to evaluate this criterion. Future studies could focus in areas where deer are expanding their ranges due to climate change (Dawe and Boutin, 2016) to determine whether these protocols meet this criterion. However, Sentinel could theoretically incorporate more highly preferred species to gauge deer browse intensity before impacts to other species occur. For example, in areas where deer populations have been drastically reduced, red oak browse rates are $<5 - 10\%$, while browse rates on flowering *Trillium grandiflorum* still exceed 30% (Blossey,

unpublished data), twice the known threshold for population persistence (Knight et al., 2009). Our results indicate that *S. caesia* has potential to serve as a more sensitive sentinel of deer browse intensity, but further evaluations are necessary.

Deer browse indicators should be able to predict changes to ecosystem integrity that can be averted by management interventions (fifth criterion, Table 4) over both the near- and long-term. Since the response metrics used by AVID, Ten-Tallest, and Twig-Age accumulate over multiple growing season (as plants increase in height, twigs extend, or plants transition to reproductive stage) these protocols are limited to informing deer management over the long-term. Since Sentinel measures deer browse intensity through annually planted seedlings, it is the only protocol we evaluated that can inform rapid response, and timely

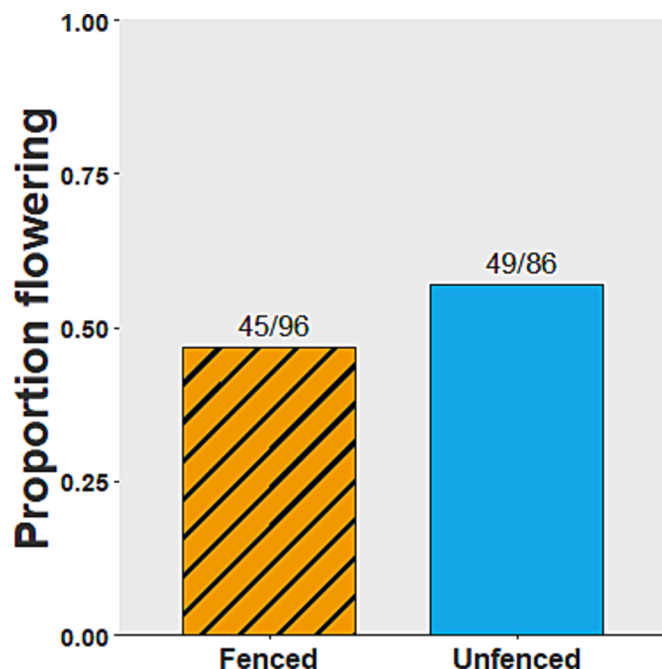


Fig. 6. Proportion of *S. caesia* flowering in fenced and unfenced plots at five sites. Number of plants flowering out of the pool of available individuals (see text for details) are indicated above bars. Asterisks indicate statistically significant differences (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) between fenced and unfenced plots.

adaptive management. Landowners or management agencies who desire substantial reductions in local deer populations also require rapid outcome monitoring approaches that can help gauge deer management success real-time, for example after culls, winterkills, or disease outbreaks (Christensen et al., 2021). This is critically important to maintain societal support, especially when deer management in principle, or the chosen methods, are contested by special interest groups for example recreational hunters or those opposed to lethal management (Sterba, 2012). Requesting that stakeholders be patient until success can be assessed years or even decades after deer management has been implemented will be unacceptable by those opposed to significant deer reductions and may prolong ecological deterioration.

To be integrative (sixth criterion, Table 4) deer browse indicators should incorporate information on woody and herbaceous vegetation and have the ability to be implemented and standardized across habitat

types. Twig-Age is the only protocol that is inherently limited in its ability to meet this criterion since it cannot assess deer browse intensity on herbaceous vegetation, reducing its utility in a broader conservation context. Previous assessments of AVID have only evaluated woody species (Curtis et al., 2021) and our results indicate that the herbaceous species that AVID targets are suspect. *Trillium grandiflorum* and *M. virginiana* are highly preferred by deer and locally uncommon in our area, calling into question whether these species could be readily monitored by AVID elsewhere. Conversely, *Arisaema triphyllum* is not browsed by deer, but responds indirectly to high deer browse pressure (Heckel et al., 2010). Our study expands the portfolio of Sentinel to include herbaceous species, particularly *S. caesia*. Since Sentinel utilizes propagated and planted seedlings, it is the only protocol we evaluated that could be implemented in all habitat types, including in unforested areas, but further research is needed to develop a portfolio of sentinel species that could be utilized in other regions and habitat types.

Chronic deer browse has sorted understory plant communities over the past century, reducing or removing highly preferred species and restricting protocols that rely on existing vegetation to species that remain (Augustine et al., 1998; Royo et al., 2017). This makes standardization of such protocols across spatial scales difficult and compromises the reliability and relevance of the inferences they generate. For example, *F. grandifolia* was the only species we were able to monitor across all sites using Twig-Age, AVID, and Ten-Tallest. Deer typically avoid *F. grandifolia*, the species is undesired and often managed against by foresters, is impacted by multiple forest pests and pathogens, regenerates through prolific root sprouting, and can reduce the regeneration potential of commercial timber species (Nyland et al., 2006). Measuring deer browse intensity on such species is likely of little relevance to deer or forest management. Sentinel, on the other hand, can be readily standardized across sites and can incorporate species previously lost or reduced as a result of chronic deer browse.

Finally, deer browse indicators should have a known response (seventh criterion, Table 4) with low variability (eighth criterion, Table 4). All protocols we evaluated, except for Ten-Tallest and the herbaceous species targeted by AVID, have a known and clearly described pattern of response in the peer reviewed literature. AVID, Ten-Tallest, and Twig-Age assume that differences in plant performance (height increases, flowering, and twig expansion) are a function of variations in deer browse intensity. However, plant survival, growth and reproduction are determined by numerous factors, including light and other resource availability, natural disturbances, competition, attack by a suite of natural enemies including deer, and other introduced species such as earthworms (Dobson and Blossey, 2015). Sentinel is the only protocol that measures deer browse directly, allowing the influence of

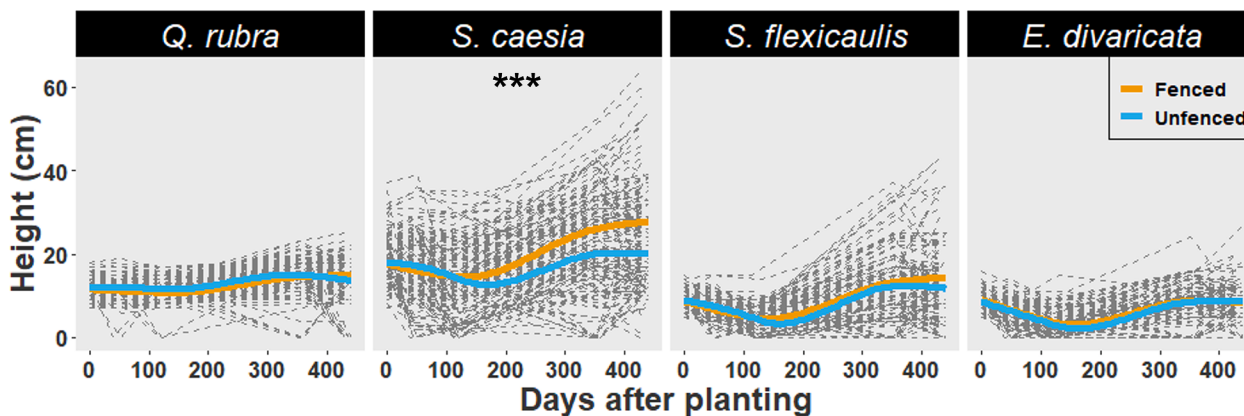


Fig. 7. Line plots of vertical *Q. rubra*, *S. caesia*, *S. flexicaulis*, and *E. divaricata* growth ($N = 249$ –336) in fenced and unfenced plots over two years at five sites. Dashed lines represent changes in height of individual plants. Solid, colored lines represent mean height changes for each species in fenced and unfenced plots. Asterisks indicate statistically significant differences (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) in mean height (cm) between fenced and unfenced plots for individual species by August 2021.

Table 4

Ability of AVID, Ten-Tallest, Twig-Age, and Sentinel protocols to meet criteria established for selecting ecological indicators (Dale and Beyeler, 2001). (✓) indicates criteria is met, (–) indicates criteria is not met, and (?) indicates criteria has not been evaluated.

Selection criteria	Sub-criteria for indicator of deer browse intensity	Assessment protocol			
		AVID	Ten-Tallest	Twig Age	Sentinel
Easily measured	Easy to understand	✓	✓	✓	✓
	Simple to apply	–	–	✓	✓
	Scientifically sound	✓	–	✓	✓
	Cost-effective	✓	✓	✓	✓
Sensitive	Sensitive to changes in deer browse intensity	?	?	✓	✓ ¹
Responsive	Unambiguous response	✓ ²	–	✓	✓
	Known threshold response level	–	–	–	✓
Anticipatory	Measurable before change in ecological integrity occurs	?	?	?	?
Predictive	Informs long-term deer management	✓	✓	✓	✓
	Informs rapid response deer management	–	–	–	✓
Integrative	Assesses woody and herbaceous vegetation	✓	✓	–	✓
	Can be implemented in all deer habitat types	–	–	–	✓
	Allows standardization	–	–	–	✓
Known response	Well documented and peer reviewed	✓ ²	–	✓	✓ ¹
Low variability in response	Independent of deer and land use legacy effects	–	–	–	✓
	Can discern influence of other stressors	–	–	–	✓
	Measures deer browse directly	–	–	–	✓
Number of sub-criteria met		6 ²	4	8	16 ¹

¹ Met for *Q. rubra*, other sentinel species require further assessment.

² Met for woody seedlings, *Trillium* spp., *Medeola virginiana*, and *Arisaema triphyllum* require further assessment.

deer browse on plant performance to be separated from natural background variability and deer or land use legacy effects. While both AVID and Ten-Tallest detected significant differences in height and flowering of *Trillium* spp. between fenced and unfenced plots, we have documented annual fluctuations in individual *Trillium* spp. plant presence and flowering that are independent of deer browse (Blossey and Nuzzo, unpublished data). Finally, *T. grandiflorum* and *T. erectum* cannot be reliably identified to species unless flowers or fruits are present, and as a result AVID potentially combines performance and demographic parameters for two species which may produce misleading results (Dávalos et al., 2014; Rooney and Gross, 2003). Unless marked individuals are assessed over time while recording what factors led to a plant's decline, generating inferences about drivers of plant performance is difficult, if not impossible, to do with certainty. Sentinel, for example, showed that

invertebrate or rodent attack could contribute significantly to differences in survival and growth for some species.

5. Conclusions

Among the protocols we evaluated, Sentinel met nearly all the criteria of a deer browse indicator (Table 4) (Dale and Beyeler, 2001). AVID and Twig-Age met some of these criteria but require further evaluation or have fundamental limitations related to protocol methodology. We cannot recommend Ten-Tallest as a deer browse indicator based on our evaluation. Sentinel also requires additional development to incorporate more browse sensitive species, such as *S. caesia*, to better gauge deer browse intensity on species that may remain vulnerable after deer populations have been reduced. Furthermore, to expand Sentinel beyond the Northeastern U.S., development of a portfolio of regionally relevant species is essential, as well as further evaluation of the spatial scaling of planting locations necessary to capture regional changes in deer browse intensity. Funding mechanisms for large-scale implementation of deer browse indicators also need to be developed but could potentially be supported by excise taxes on purchases of outdoor recreation related equipment, habitat/access stamps, or hunting license sales.

A primary criticism of Sentinel has been the time and effort required to propagate, plant, and assess seedlings annually (Curtis et al., 2021). Our results indicate that in closed-canopy forests, the effort required to implement Sentinel is comparable to the effort required to implement AVID, Ten-Tallest, and Twig-Age. Validation of new sentinel species also requires more effort than implementation using previously vetted species, which typically requires only two follow-up visits annually. While propagating seedlings may present challenges for individual land-owners, NGO's and management agencies could commission nurseries to produce and distribute seedlings in volume. All species we planted using Sentinel are commercially available at \$100–200/site. However, seedlings can also be propagated to reduce costs and limit the likelihood of spreading non-native species, such as earthworms, through soil substrate.

Viewing our results through the lens of an effective ecological indicator (Dale and Beyeler, 2001) magnifies the importance of validating any protocol meant to measure deer impacts before widespread implementation. The protocols we evaluated represent a small fraction of those that currently exist and are being utilized to inform deer and ecosystem management decisions. Many have been touted for their simplicity and effectiveness, and some have been incorporated into management plans without thorough evaluation. This is a major disservice to deer management which is under increasing pressure to incorporate additional scientific rigor into data collection processes and decision making (Curtis, 2020; Waller et al., 2017). We join others in cautioning management agencies to avoid hastily adopting deer impact assessment protocols that have not been thoroughly evaluated as this could result in misguided deer management and policy (Blossey et al., 2019; Curtis et al., 2021; Nuzzo et al., 2017; Waller et al., 2017). By allocating and prioritizing funding for additional experimental evaluations, management agencies could facilitate expanded use of deer impact assessment protocols while ensuring that products and information generated are accurate and relevant for deer management and conservation.

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.

Data availability

Data will be made available on request.

Acknowledgements

We thank Victoria Nuzzo, Audrey Bowe, and Ben Hopkins for assistance with implementation and data collection, and Erika Mudrak, Stacy Endriss, and Andrea Dávalos for recommendations on statistical analyses. Two anonymous reviewers provided valuable feedback on an earlier draft.

References

- Augustine, D.J., Frelich, L.E., Jordan, P.A., 1998. Evidence for two alternate stable states in an ungulate grazing system. *Ecol. Appl.* 8 (4), 1260–1269.
- Bachand, M., Pellerin, S., Cote, S.D., Moretti, M., De Caceres, M., Brousseau, P.M., Cloutier, C., Hebert, C., Cardinal, E., Martin, J.L., Poulin, M., 2014. Species indicators of ecosystem recovery after reducing large herbivore density: Comparing taxa and testing species combinations. *Ecological Indicators* 38, 12–19.
- Blossey, B., Dávalos, A., Nuzzo, V., 2017. An indicator approach to capture impacts of white-tailed deer and other ungulates in the presence of multiple associated stressors. *AoB PLANTS* 9, plx034. <https://doi.org/10.1093/aobpla/plx034>.
- Blossey, B., Curtis, P., Boulanger, J., Dávalos, A., 2019. Red oak seedlings as bioindicators to assess browsing pressure and efficacy of white-tailed deer management. *Ecol. Evol.* 9, 13085–13103.
- Brice, E.M., Larsen, E.J., MacNulty, D.R., 2022. Nonrandom sampling and untested assumptions exaggerate the strength of a classic trophic cascade. *Ecol. Lett.* 25, 177–188.
- Chevrier, T., Saïd, S., Widmer, O., Hamard, J.-P., Saint-Andrieux, C., Gaillard, J.-M., 2012. The oak browsing index correlates linearly with roe deer density: a new indicator for deer management? *European Journal of Wildlife Research* 58 (1), 17–22.
- Christensen, S.A., Williams, D.M., Rudolph, B.A., Porter, W.F., 2021. Spatial variation of white-tailed deer (*Odocoileus virginianus*) population impacts and recovery from epizootic hemorrhagic disease. *Journal of Wildlife Diseases* 57, 82–93.
- Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. *Ann. Rev. Ecol. Syst.* 35 (1), 113–147.
- Curtis, P., Sullivan, K., Smallidge, P., Hurst, J., 2021. AVID: A rapid method for assessing deer browsing of hardwood regeneration. *Forest Ecol. Manag.* 497.
- Dale, V.H., Beyeler, S.C., 2001. Challenges in the development and use of ecological indicators. *Ecological Indicators* 1 (1), 3–10.
- Dávalos, A., Nuzzo, V., Blossey, B., Wardle, D., 2014. Demographic responses of rare forest plants to multiple stressors: the role of deer, invasive species and nutrients. *J. Ecol.* 102 (5), 1222–1233.
- Dávalos, A., Nuzzo, V., Blossey, B., 2015a. Single and interactive effects of deer and earthworms on non-native plants. *Forest Ecol. Manag.* 351, 28–35.
- Dávalos, A., Simpson, E., Nuzzo, V., Blossey, B., 2015b. Non-consumptive effects of native deer on introduced earthworm abundance. *Ecosystems* 18 (6), 1029–1042.
- Dawe, K.L., Boutin, S., 2016. Climate change is the primary driver of white-tailed deer (*Odocoileus virginianus*) range expansion at the northern extent of its range; land use is secondary. *Ecol. Evol.* 6 (18), 6435–6451.
- Dobson, A., Blossey, B., Gilliam, F., 2015. Earthworm invasion, white-tailed deer and seedling establishment in deciduous forests of north-eastern North America. *J. Ecol.* 103 (1), 153–164.
- Frerker, K., Sonnier, G., Waller, D.M., 2013. Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. *Forest Ecol. Manag.* 291, 55–64.
- Freyfogle, E.T., Goble, D.D., 2009. *Wildlife law: a primer*. Island Press, Washington DC.
- Frye, B., 2006. *Deer Wars. Science, Tradition, and the Battle Over Managing Whitetails in Pennsylvania*. The Pennsylvania State University Press, University Park, Pennsylvania.
- Harada, K., Ang Meng Ann, J., Suzuki, M., 2020. Legacy effects of sika deer overpopulation on ground vegetation and soil physical properties. *Forest Ecol. Manag.* 474.
- Hare, D., Blossey, B., 2014. Principles of public trust thinking. *Human Dimensions of Wildlife: An International Journal* 19 (5), 397–406.
- Hare, D., Daniels, M.B.B., 2021. Public perceptions of deer management in Scotland. *Frontiers in Conservation Science* 2, 781546. <https://doi.org/10.3389/fcsc.2021.781546>.
- Heckel, C.D., Bourg, N.A., McShea, W.J., Kalisz, S., 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecology* 91 (2), 319–326.
- Iijima, H., Nagaike, T., 2015. Appropriate vegetation indices for measuring the impacts of deer on forest ecosystems. *Ecological Indicators* 48, 457–463.
- Jacobson, C.A., Decker, D.J., Carpenter, L.E., 2007. Securing alternative funding for wildlife management: insights from agency leaders. *The Journal of Wildlife Management* 71 (6), 2106–2113.
- Kalisz, S., Spigler, R.B., Horvitz, C.C., 2014. In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. *P. Nat. Acad. Sci. USA* 111 (12), 4501–4506.
- Kelly, J.F., 2019. Regional changes to forest understories since the mid-twentieth century: effects of overabundant deer and other factors in northern New Jersey. *Forest Ecol. Manag.* 444, 151–162.
- Kilpatrick, H.J., Labonte, A.M., Stafford, K.C., 2014. The relationship between deer density, tick abundance, and human cases of Lyme disease in a residential community. *Journal of Medical Entomology* 51 (4), 777–784.
- Knight, T.M., Caswell, H., Kalisz, S., 2009. Population growth rate of a common understory herb decreases non-linearly across a gradient of deer herbivory. *Forest Ecol. Manag.* 257 (3), 1095–1103.
- Leopold, A., Sows, L.K., Spencer, D.L., 1947. A survey of over-populated deer ranges in the United States. *J. Wildlife Manage* 11, 162–177.
- MacDougall, A.S., Turkington, R., 2005. Are invasive species the drivers or passengers of change in degraded ecosystems. *Ecology* 86 (1), 42–55.
- Malhi, Y., Franklin, J., Seddon, N., Solan, M., Turner, M.G., Field, C.B., Knowlton, N., 2020. Climate change and ecosystems: Threats, opportunities and solutions. *Philosophic Transactions of the Royal Society of London B* 375 (1794), 20190104.
- Miller, K.M., McGill, B.J., Frair, J., 2019. Compounding human stressors cause major regeneration debt in over half of eastern US forests. *J. Appl. Ecol.* 56 (6), 1355–1366.
- Morellet, N., Gaillard, J.M., Hewison, A.J.M., Ballon, P., Boscardin, Y., Duncan, P., Klein, F., Maillard, D., 2007. Indicators of ecological change: new tools for managing populations of large herbivores. *J. Appl. Ecol.* 44, 634–643.
- Nishizawa, K., Tatsumi, S., Kitagawa, R., Mori, A.S., 2016. Deer herbivory affects the functional diversity of forest floor plants via changes in competition-mediated assembly rules. *Ecological Research* 31 (4), 569–578.
- Nopp-Mayr, U., Reimoser, S., Reimoser, F., Sachser, F., Obermaier, L., Gratzner, G., 2020. Analyzing long-term impacts of ungulate herbivory on forest-recruitment dynamics at community and species level contrasting tree densities versus maximum heights. *Scientific Reports* 10.
- Nuttall, T., Yarger, E.H., Stoleson, S.H., Ristau, T.E., 2011. Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. *Ecosphere* 2:art 4. <https://doi.org/10.1890/ES1810-00108.00101>.
- Nuttall, T., Ristau, T.E., Royo, A.A., 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understories reflect past deer density treatments for at least 20 years. *J. Ecol.* 102, 221–228.
- Nuzzo, V., Dávalos, A., Blossey, B., 2017. Assessing plant community composition fails to capture impacts of white-tailed deer on native and invasive plant species. *AoB PLANTS* 9, plx026. <https://doi.org/10.1093/aobpla/plx026>.
- Nyland, R.D., Bashant, A.L., Bohn, K.K., Verostek, J.M., 2006. Interference to hardwood regeneration in northeastern North America: Controlling effects of American Beech, striped maple, and hobblebush. *North. J. Appl. For.* 23, 122–132. <https://doi.org/10.1093/njaf/23.2.122>.
- Parsons, E.W.R., Maron, J.L., Martin, T.E., Pelletier, F., 2013. Elk herbivory alters small mammal assemblages in high-elevation drainages. *Journal of Animal Ecology* 82 (2), 459–467.
- Patton, S.R., Russell, M.B., Windmuller-Campione, M.A., Frelich, L.E., Apollonio, M., 2018. Quantifying impacts of white-tailed deer (*Odocoileus virginianus* Zimmerman) browse using forest inventory and socioenvironmental datasets. *PLoS One* 13 (8). <https://doi.org/10.1371/journal.pone.0201334>.
- Putman, R., Watson, P., Langbein, J., 2011. Assessing deer densities and impacts at the appropriate level for management: a review of methodologies for use beyond the site scale. *Mammal Review* 41, 197–219.
- R Core Team, 2020. *R: A Language and Environment for Statistical Comput-ing*. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>.
- Rawinski, T.J., 2018. *Monitoring white-tailed deer impacts: the ten-tallest method*. US Department of Agriculture, Forest Service, Northeastern Area State and Private Forestry, 11 Campus Boulevard, Suite 200, Newtown Square, PA. 19073.
- Rooney, T.P., Gross, K., 2003. A demographic study of deer browsing impacts on *Trillium grandiflorum*. *Plant Ecology* 168, 267–277.
- Royo, A.A., Kramer, D.W., Miller, K.V., Nibbelink, N.P., Stout, S.L., 2017. Spatio-temporal variation in foodscapes modifies deer browsing impact on vegetation. *Landscape Ecol.* 32 (12), 2281–2295.
- Sample, R.D., Delisle, Z.J., Pierce, J.M., Swihart, R.K., Caudell, J.N., Webster, C.R., Jenkins, M.A., 2023. Predicting and indexing ungulate browse intensity from local to regional scales. *Ecological Indicators* 154.
- Siddig, A.A.H., Ellison, A.M., Ochs, A., Villar-Leamand, C., Laub, M.K., 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in *Ecological Indicators*. *Ecological Indicators* 60, 223–230.
- Sterba, J., 2012. *Nature wars; the incredible story how wildlife comebacks turned backyards into battlegrounds*. Crown Publishers, New York.
- Sullivan, K.L., Smallidge, P.J., Curtis, P.D., 2020. AVID. Assessing vegetation Impacts from Deer. A rapid assessment method for evaluating deer impacts to forest vegetation. Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA.
- Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351–1363.
- Waller, D.M., Johnson, S.E., Witt, J.C., 2017. A new rapid and efficient method to estimate browse impacts from twig age. *Forest Ecol. Manag.* 404, 361–369.
- Wardle, D.A., Bardgett, R.D., 2004. Human-induced changes in large herbivorous mammal density: the consequences for decomposers. *Front. Ecol. Environ.* 2 (3), 145–153.
- Wright, D.M., Tanentzap, A.J., Flores, O., Husheer, S.W., Duncan, R.P., Wiser, S.K., Coomes, D.A., 2012. Impacts of culling and exclusion of browsers on vegetation recovery across New Zealand forests. *Biol. Conserv.* 153, 64–71.
- Xu, H., Wang, Y., Guan, H., Shi, T., Hu, X., 2019. Detecting ecological changes with a remote sensing based ecological index (RSEI) produced time series and change vector analysis. *Remote Sensing* 2019 (11), 2345.