

Defining deer overabundance and threats to forest communities: From individual plants to landscape structure¹

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Abstract: Changes in habitat and reduction in predation and hunting pressure are two primary causes of high-density populations of white-tailed deer (*Odocoileus virginianus*) in many areas of eastern North America. Despite increasing recognition of the major effects deer exert on forest communities, deciding when deer are overabundant remains a major challenge to managers charged with conserving native plant communities. In this context, we define overabundance as a condition where deer are causing the local extinction of a native plant species. Because this definition is difficult to apply from a management perspective, we outline an approach using native understory forbs. Indicator species are selected based on combined criteria of palatability to deer, leaf and flower morphology, and demographic characteristics. Four indices related to plant population viability are derived from understory survey data: flowering rate, mean stem height, stage-class distribution, and deer browsing pressure. We apply this analysis to *Trillium* populations from forests in Minnesota (highly fragmented agricultural landscape with varying deer densities), Pennsylvania (forested and fragmented landscape with long-term high deer densities), and New York (forested and fragmented landscape with long-term low deer densities). We observed two distinct types of deer-affected plant populations. In sites with moderate or recent increases in deer density, *Trillium* populations were characterized by low mean plant size, high browsing rates, intermediate flowering rates, and a size class distribution lacking large, reproductive plants. Sites affected by long-term high deer densities exhibited low browsing rates on *Trillium*, low *Trillium* flowering rates, a population structure lacking both large and small plants, and high summer browsing pressure on woody saplings. We suggest these combined indices be used to assess deer browsing impact, and we discuss the role of landscape structure and deer density in defining deer overabundance.

Keywords: forest fragmentation, *Odocoileus*, old-growth forest, plant community conservation, *Trillium*, understory indicators.

Résumé : Les modifications des habitats ainsi que la diminution de la prédation et de la chasse sont les deux principales causes des fortes densités de population de cerf de Virginie (*Odocoileus virginianus*) dans plusieurs régions de l'est de l'Amérique du Nord. Bien que l'impact du cerf sur les communautés forestières soit de plus en plus connu, il est toujours difficile pour les gestionnaires chargés de conserver les communautés de plantes indigènes de statuer à quel moment il y a surabondance de cerfs. Dans ce contexte, nous estimons qu'il y a surabondance de cerfs lorsque ces derniers causent l'extinction locale d'espèces végétales indigènes. À cet égard, nous proposons une approche qui utilise les plantes indigènes du sous-bois comme indicateurs. Les espèces choisies ont été retenues en fonction d'une combinaison de critères tenant compte des préférences des cerfs, de la morphologie des feuilles et des fleurs et des caractéristiques démographiques. Quatre indices associés à la viabilité des populations de plantes sont issus des inventaires réalisés dans les sous-bois : le taux de floraison, la hauteur moyenne de la tige, la répartition des individus au sein des classes de vie et la pression de broutement des cerfs. Nous avons testé notre méthode avec les populations de trilles (*Trillium* spp.) des forêts du Minnesota (où les paysages sont agricoles et fortement fragmentés et où les densités de cerfs sont variables), de la Pennsylvanie (où les paysages sont forestiers ou fragmentés et où les densités de cerfs sont élevées depuis longtemps) et de l'état de New York (où les paysages sont également forestiers ou fragmentés mais où les densités de cerfs sont faibles depuis longtemps). Nous avons observé deux types distincts de populations de plantes affectées par les cerfs. Dans les sites où les densités de cerfs sont modérées ou en croissance récente, les populations de trilles se caractérisent par une taille moyenne faible, des taux de broutement élevés, des taux de floraison intermédiaires et par l'absence d'individu reproducteur. Dans les sites affectés depuis longtemps par des densités élevées de cerfs, on observe chez les trilles des taux de broutement faibles, des taux de floraison peu élevés, l'absence d'individus de petites et de grandes dimensions ainsi qu'une pression de broutement élevée sur les arbres à l'état de gaules au cours de l'été. Nous suggérons que cette combinaison d'indices soit utilisée pour évaluer l'envergure des impacts du broutement par les cerfs. Ils pourraient également servir dans toute discussion portant sur les rôles de la structure du paysage et de la densité des cerfs lorsque vient le moment de décider s'il y a surabondance de cerfs.

Mots-clés : conservation des communautés végétales, forêt ancienne, fragmentation de la forêt, indicateurs de sous-bois, *Odocoileus*, *Trillium*.

Nomenclature : Gleason & Cronquist, 1991.

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Introduction

Deer overabundance and related environmental impacts throughout much of eastern North America have been a major focus of research and debate for decades. Problems associated with white-tailed deer populations range from direct effects on humans such as vehicle collisions and crop damage to potentially negative ecological effects such as development of a browse line, reproductive or regenerative failure of plant species, and alteration of habitat for other vertebrates. Caughley (1981) outlined four categories of overabundant animal populations: 1) when animals threaten human life or livelihood, 2) when animals depress densities of favoured species, 3) when animals are too numerous for their own good, and 4) when animals cause ecosystem dysfunction. All of these categories apply to the relationships between deer, plant communities, and humans in eastern North America. All depend to some degree on human values or objectives. In categories (2) and (3) we must define favoured species and the animal's own good from a human perspective. In category (4), we must somehow define proper ecosystem function.

In this paper, we examine a combination of categories (2) and (4) by evaluating situations where deer seem to have untoward impact on co-evolved plant species in eastern North America. We chose to evaluate this perspective on overabundance because many parks and preserves managed by national, state, and county agencies are struggling to conserve native plant communities affected by deer. Defining and monitoring deer overabundance in terms of an imbalance between deer and native plant communities is exceedingly difficult because baseline information on the historic dynamics of deer and native plant communities does not exist; deer occur across many forest and savanna community types; deer forage on hundreds of different plant species; and native plant communities in eastern North America have already been strongly altered by other post-settlement forces, such as altered disturbance regimes, forest fragmentation, and introduced insect herbivores, plants, and plant pathogens.

The first objective of this paper is to define ecological deer overabundance in terms of deer impacts on understory herbaceous species. Our second objective is to outline an approach to selecting understory species to use as indicators of deer overabundance based on three basic criteria. Using these criteria, we identify *Trillium* spp. as a useful genus for monitoring deer impacts in many forest communities of eastern North America. Our third objective is to test whether measures of *Trillium* population structure reflect variation in deer density and previously documented impacts to forest communities in Minnesota, Pennsylvania, and New York. Specifically, we focus on measures of *T. cernuum* in Minnesota forests and *T. undulatum* in Pennsylvania and New York. Finally, we discuss how landscape structure may modify the relationship between deer populations and native plant communities.

ECOLOGICAL OVERABUNDANCE

Much debate on deer overabundance has been driven by observations of deer populations that achieved and in some cases persisted at densities of 20-60 deer·km⁻²

(Redding, 1995; Palmer *et al.*, 1997; Underwood & Porter, 1997). Debate has also focused on deer population irruptions and long-term density dynamics (McCullough, 1997; Porter & Underwood, 1999). Although factors regulating deer abundance are central to plant-deer interactions, our understanding of population regulation provides only limited insight into the question of whether deer are exerting significant negative effects on plant species. On one hand, deer populations below ecological carrying capacity could still have severe impacts on particular plant species (Augustine & Frelich, 1998). On the other hand, deer populations that regularly fluctuate and reach densities well above carrying capacity may have no significant effect on the plant community's productivity or long-term ability to support rapid deer population growth (McCullough, 1997). Thus, animal malnutrition and plant community impoverishment may not necessarily be associated with one another. Severe deer effects on plant populations could occur due to two basic changes in deer-plant relations: 1) relaxation of predation and hunting pressure, allowing deer to persist at long-term densities that exceed pre-settlement densities (Crête, 1999) and 2) changes in the landscape's disturbance regime, which alters the abundance and distribution of forage and allows deer to operate as an edge effect in native plant communities (Alverson, Waller & Solheim, 1988).

Sinclair (1997: 389) defined overabundance as "more deer than the original prehistoric plant community evolved to tolerate". Specifically, we suggest that a plant-deer disequilibrium occurs when the deer population is causing the local extinction of a native plant species. This definition avoids ambiguity associated with deer merely altering the relative abundance of plants within a community (*e.g.*, do we prefer more deer or more maple biomass?) or changing species diversity. Although changes in forest canopy composition due to deer (Tierson, Patric & Behrend, 1966; Tilghman, 1989) may conflict with commercial or cultural goals, such changes could certainly have occurred in the presettlement landscape. The historic strength and pattern of deer-plant interactions likely fluctuated due to disturbance patterns, predation and parasitism of deer, winter weather, and canopy masting events. However, long-term persistence of extant native plant species under the presettlement herbivory regime implies that coexistence with deer was possible. Extinction indicates a disruption of deer-plant interactions to a degree that did not occur during the evolutionary history of the species. Sinclair's definition focuses debate on the population ecology of specific plant species and away from ambiguous measures such as plant community diversity or richness. A similar definition informed research that linked deer-induced recruitment failure of tree species such as hemlock-*Tsuga canadensis* (Anderson & Katz, 1993; Alverson & Waller, 1997), white cedar-*Thuja occidentalis* (Verme & Johnston, 1986; Van Deelen, 1999; Cornett *et al.*, 2000), and red oak-*Quercus rubra* (Healy, 1997) to the need to re-evaluate deer management practices in light of ecosystem conservation (Alverson, Kuhlmann & Waller, 1994; deCalesta, 1997).

Three problems limit application of a simple extirpation-based definition to research and management. First,

complete extirpation of a species is difficult to measure, particularly over large management units and the short time frame of much research and monitoring. Even in heavily browsed landscapes, small refugia facilitate persistence and occasional recruitment of sensitive plant species (Rooney, 1997; Borgmann, Waller & Rooney, 1999). A second problem involves the scale of an extirpation. Even if a species is eliminated or recruitment is suppressed in specific stands within a defined management area (*i.e.*, the population within a specific stand is not viable due to deer herbivory), the species could persist in other stands or continually recolonize the management unit from external sources. This dynamic is especially important for tree species, which can persist in the canopy layer for decades to centuries, whose seeds can disperse over large distances, and for which deer have no effect on seed production. Finally, if extirpation results from current deer densities, we are already too late from a conservation standpoint; reintroduction of the plant species may be possible, but it is expensive and local adaptations may have been lost.

One approach that addresses these difficulties is the use of understory species to gauge the severity of deer effects on forest communities. Long-term enclosure studies show that severe effects of deer on tree species typically occur in mid or late-successional forests (Anderson & Katz, 1993; Alverson & Waller, 1997; Healy, 1997), even though seed-producing individuals in tree populations are never consumed. More severe effects may occur for coexisting understory species that never exceed the browsing height of deer. We examine use of understory species, particularly those characteristic of late-successional forest communities, to index where deer are sufficiently abundant that extirpation of sensitive plant species is imminent.

DEER AND UNDERSTORY FORB COMMUNITIES

Anderson (1994) first suggested use of an understory forb, *Trillium grandiflorum*, to monitor deer impacts in fragmented forests of Illinois. His recommendations based on *Trillium* stem height reflected the criterion of local extinction because grazing by deer at densities $> 20 \cdot \text{km}^{-2}$ eliminated *Trillium* reproduction in his study area and was obviously unsustainable. In contrast, sites with $\sim 5 \text{ deer} \cdot \text{km}^{-2}$ exhibited population characteristics (stem height, flowering rate) similar to those of an enclosure population, indicating long-term coexistence of low-density deer populations and *Trillium* is possible. The utility of the indicator approach lies in the ease of measuring *Trillium* compared to the difficulties of measuring summer deer densities.

Use of herb-based indicators has recently been examined for several late-successional forest communities in eastern North America (Table I). Collectively, these studies document a consistent correlation between deer density and indices of forb size or reproductive rate across a broad geographic region. In particular, strong correlations between deer density, indicator species height, and condition of understory communities in Indiana (Webster & Parker, 2000; Webster, Jenkins & Parker, 2001) and Illinois (Anderson, 1994) suggest the utility of this approach.

However, experimental evidence linking deer herbivory and population persistence of native forbs is limited. Studies in maple-basswood (*Acer saccharum*-*Tilia americana*) forests of Minnesota identified sites where deer removed 50% to 100% of reproductive individuals annually from unexclosed *Trillium* spp. and *Laportea canadensis* populations. This level of browsing reduced leaf area and probability of flowering in subsequent growing seasons, indicating future deer-induced extirpations of both species (Augustine & Frelich, 1998; Augustine, Frelich & Jordan, 1998). Enclosure comparisons also

TABLE I. Studies examining the use of understory forbs as indicators of deer overabundance in forests of eastern North America. Studies that correlated understory forb indices with measures of deer density included density estimates based on hunter kill per unit area (H), hunter kill per unit effort (H/E), aerial deer counts, and classification of sites as high versus low deer density based on the absence or presence of hunting.

Community	State	Indicator species	Index	Correlated with:	Source
Mesic maple forests	IL	<i>Trillium grandiflorum</i>	Mean height	Grazing pressure; overall herb reproduction	Anderson, 1994
Northern hardwood/hemlock	WI	<i>Clintonia borealis</i>	Scape height	Deer density (H); <i>Clintonia</i> abundance	Balgooyen & Waller, 1995
Mesic hardwood forests	IN	<i>Osmorhiza claytonii</i>	Mean height	Deer density (H/E); adjusted % herb cover	Webster & Parker, 2000
		<i>Arisaema triphyllum</i>	Mean height	Deer density (H/E); adjusted % herb cover	Webster, Jenkins & Parker, 2001
		<i>Actaea pachypoda</i>	Mean height	Deer density (H/E); adjusted % herb cover	Webster, Jenkins & Parker, 2001
Riparian forests	PA	<i>Chelone glabra</i>	Mean height	No significant correlations	Williams, Mosbacher & Moriarity, 2000
		<i>Chelone glabra</i>	% Grazed	Overall grazing pressure	
Oak-hickory forests	VA	<i>Smilacina</i> spp.	% Reproductive	Deer density (high versus low)	Fletcher <i>et al.</i> , 2001
		<i>Uvularia</i> spp.	% Reproductive	Deer density (high versus low)	Fletcher <i>et al.</i> , 2001
		<i>Arisaema triphyllum</i>	% Reproductive	Deer density (high versus low)	Fletcher <i>et al.</i> , 2001
Maple - basswood forests	MN	<i>Trillium</i> spp.	% Reproductive	Deer density (aerial counts)	Augustine & Frelich, 1998; this study

showed nearly complete elimination of *Uvularia* spp. reproduction by deer in Virginia (Fletcher *et al.*, 2001). Ideally, indicator species should not only serve as proxy measures of understory condition, but also identify situations where current deer densities are driving native species to local extinction. We suggest that understory forbs are especially useful provided three criteria are carefully evaluated when selecting species to study and monitor. These criteria were formulated to identify species likely to be extremely sensitive to deer browsing in terms of reproduction and yet to have persisted through years of negative deer effects due to demographic characteristics of the plant species.

First, the morphology and physiology of individual plants will influence their capacity to tolerate herbivory. Based on surveys of old-growth understory communities in maple-basswood forests of Minnesota (Augustine, 1997), we separated the community of 26 early- and late-summer forb species along a tolerance gradient that reflects leaf area lost to a deer bite and capacity for regrowth within a growing season (Figure 1). The most intolerant growth form consists of a single central stem supporting all leaves and flowers at the same height; in these species (*e.g.*, *Trillium* spp.), reproductive and photosynthetic activity within a year can be eliminated by a single deer bite. Species with apical flowers but multiple leaf levels, or a single leaf layer with flowers produced at a lower level, may be less affected, but still can lose

either all reproduction or all photosynthetic capacity to a single bite. Greater morphological plasticity and multiple leaf levels will generally confer greater tolerance. For example, species such as *Viola sororia*, *Osmorhiza claytonii*, and *Hydrophyllum virginiana* lost upper leaves to deer but often retained > 50% of leaf area. Species such as *Laportea canadensis* also exhibited post-herbivory regrowth, such that individuals grazed in June could still flower and produce seeds in August. Prostrate growth and rhizomatous reproduction will also confer greater herbivory tolerance. An additional issue is plant allocation to chemical defences that deter herbivory, which can decrease the tolerance of plants to leaf loss if it does occur (Augustine & McNaughton, 1998). However, in the case of white-tailed deer foraging on forest understory communities, this factor is unlikely to influence plant tolerance to herbivory since deer are selective feeders and factors promoting defoliation of unpalatable plants (*e.g.*, trampling by large herds, phenological patterns of forage availability; Augustine & McNaughton, 1998) are generally weak. In our assessment of the Minnesota species, we have not considered responses of species to cumulative episodes of herbivory within a season because we rarely observed deer to re-browse marked plants, but this may be an additional component of tolerance in areas of extremely high browsing pressure. For any given forest understory community in eastern North America, a subset of the forb species possess intolerant growth forms (Figure 1), and these should be the focus of monitoring efforts.

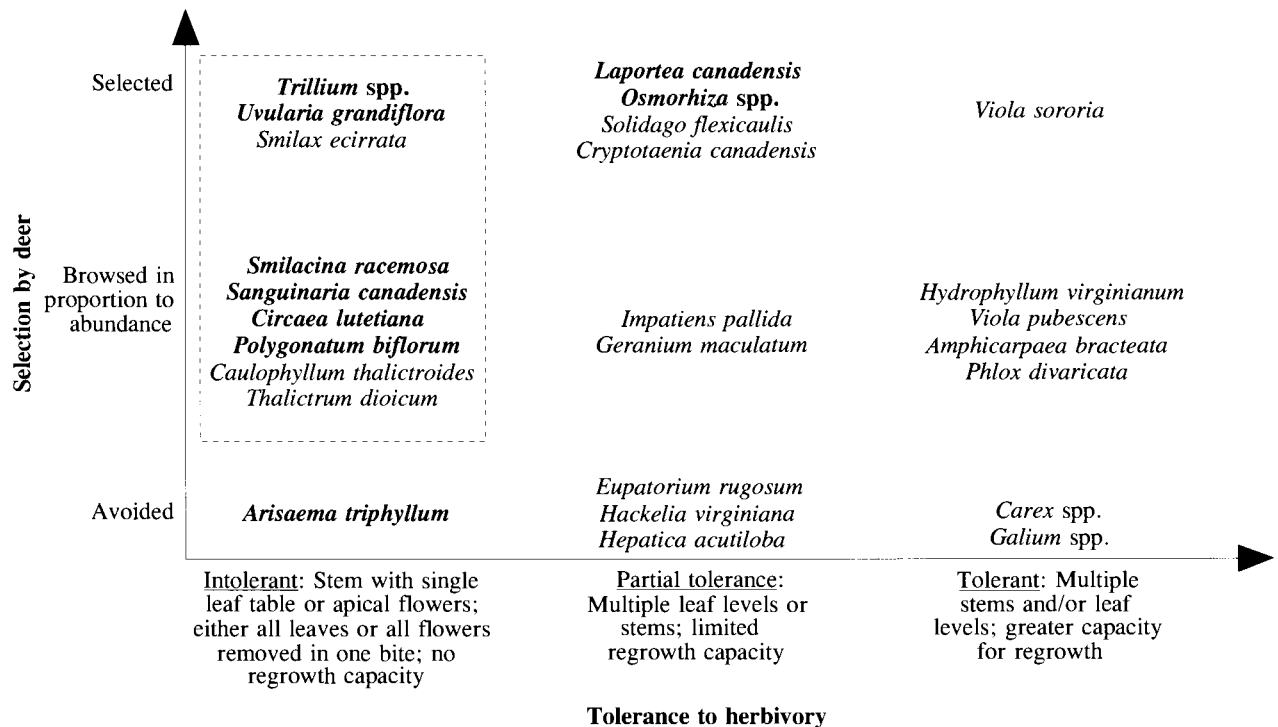


FIGURE 1. Ranking of understory forb species in maple-basswood forests of south-central Minnesota in terms of their selection by deer (based on surveys of four forests in 1995 and 1996; Augustine, 1997) and tolerance of different species to herbivory. The nine species in the dashed box are both regularly browsed by deer and possess intolerant growth forms, hence they are likely to be sensitive to high deer browsing pressure. Severely suppressed reproduction in response to high browsing pressure has been documented for six of these nine species (shown in boldface in the dashed box) in eastern North America (Anderson, 1994; Rockwood & Lobstein, 1994; Balgooyen & Waller, 1995; Augustine & Frelich, 1998; Fletcher *et al.*, 2001), and no known studies have examined the remaining three species. In addition, studies indicate deer can have significant negative effects on the three other species shown in boldface outside the dashed box (Augustine *et al.*, 1998; Webster & Parker, 2000).

A second obvious criterion is selection by deer (Strole & Anderson, 1992). We also ranked the 26 common understory species from maple-basswood forests as "selected", "browsed in proportion to abundance", or "avoided" based on surveys of four forests in Minnesota (Augustine, 1997). Combined with the classification of tolerance to herbivory, we identified nine sensitive forb species that were selected or browsed in proportion to abundance and possess intolerant growth forms (Figure 1, dashed box). Severely suppressed reproduction in areas with high deer densities has been documented for six of these species in eastern North America (Anderson, 1994; Rockwood & Lobstein, 1994; Balgooyen & Waller, 1995; Augustine & Frelich, 1998; Fletcher *et al.*, 2001); no known studies have examined the remaining three species (*Caulophyllum thalictroides*, *Smilax ecirrata*, and *Thalictrum dioicum*). Many Liliaceae species are both browse-intolerant and selected by deer, which may explain the high proportion of Liliaceae in Miller, Bratton, and Hadidian's (1992) survey of plants impacted by deer herbivory. Unfortunately, selection by deer can be site specific, and measurement will require pilot surveys or prior manager experience to adequately evaluate. For example, jack-in-the-pulpit (*Arisaema triphyllum*) has an intolerant growth form, but was avoided and unaffected by deer in Minnesota forests because more preferred forbs were available (Augustine & Jordan, 1998). However, studies in Virginia and Indiana suggest deer increase consumption of *A. triphyllum* and depress flowering rates where *A. triphyllum* is more available relative to other understory species (Fletcher *et al.*, 2001; Webster, Jenkins & Parker, 2001). Highly preferred but more tolerant species such as *Laportea canadensis* and *Osmorhiza claytonii* may be severely affected when deer density is extremely high or overall forage availability is low (Augustine, Frelich & Jordan, 1998; Webster & Parker, 2000), but such species can also persist at deer densities that are eliminating more sensitive species (Augustine & Frelich, 1998).

A third criterion is the use of long-lived, shade-tolerant forb species. For example, individuals of *Trillium grandiflorum* in a Michigan population lived for > 30 y, the mean age of flowering individuals was 23 y, and age to first reproduction was 17 y (Hanzawa & Kalisz, 1993). Although individuals of such species may be severely affected by leaf removal, demographic inertia and occasional reproduction at low rates may allow the population to persist for decades (albeit at decreasing abundance) despite high deer densities. Seedlings that established prior to increased deer densities will take decades to mature, and older plants may persist in smaller, non-reproductive size classes. In addition, many understory forbs are ant-dispersed at local spatial scales (*e.g.*, *Trillium*, *Uvularia*, and *Sanguinaria*), and most *Trillium* seeds disperse only 0.5-2.4 m from the parent plant (Kalisz *et al.*, 1999). Thus, plant population dynamics operate at local spatial scales (within forest stands) that can be easily measured, and the long generation times provide managers with time to detect problems and decide upon management directions. We suggest 10- to 100-ha forest stands as an appropriate scale at which to measure forb popula-

tions and monitor potential plant extirpations because smaller scales do not capture the variation in canopy structure typically present in late-successional forests, while at larger scales the dynamics of understory forb populations in different portions of the landscape may be independent due to their limited dispersal ability.

UNDERSTORY FORBS AS INDICATORS OF OVERABUNDANT DEER: APPLICATION

The previous discussion suggests *Trillium* species could be particularly useful and sensitive for identifying deer-induced plant extinctions. Other genera must be identified in forests where *Trillium* are rare or absent (Webster & Parker, 2000), but *Trillium* spp. occur throughout most mesic forest communities in eastern North America (Case & Case, 1997). Our approach to using *Trillium* as an indicator of deer impact was developed from observations of *T. cernuum* population structure in maple-basswood forests of south-central Minnesota, which we present in this paper. We then tested the application of this approach by sampling populations of *T. undulatum* and *T. grandiflorum* in the forests of Pennsylvania and New York. The regions we studied contained fragmented old-growth forests with varying deer density in an agricultural landscape (Minnesota), hardwood and beech (*Fagus grandifolia*)-hemlock stands with long-term high deer densities in a forested landscape (Allegheny National Forest, Pennsylvania), and hardwood and beech-hemlock stands with long-term low deer densities in a forested landscape (Hoxie Gorge and Adirondack State Park, New York). Pennsylvania study sites were selected because the region has supported high deer densities (10-20·km⁻²) since the 1970s (Redding, 1995) and deer have affected forest regeneration in the region (Marquis, 1974; 1981; Horsley & Marquis, 1983; Tilghman, 1989). In contrast, long-term studies in the Adirondacks show deer have persisted at relatively low densities (< 10·km⁻²) since the 1960s (Underwood, 1990). We analyzed *Trillium* population indices and size-class distributions from these sites in relation to deer density and landscape structure within and among states.

Methods

STUDY AREAS

We sampled four sites in south-central Minnesota (44-45° N, 93° 25' W), four sites in the Allegheny National Forest of Pennsylvania (ANF; 41° 39' N, 78° 57' W), one site in Hoxie Gorge of central New York (42° 33' N, 76° 05' W), and three sites in the Huntington Wildlife Forest within the Adirondack State Park of New York (ASP; 44° 00' N, 74° 13' W; see Figure 2). The Minnesota sites consisted of two old-growth, maple-basswood forests with high deer densities (HD-1, HD-2), one old-growth forest with moderate deer densities (MD-2), and one mature, second-growth maple-basswood forest where we sampled *Trillium* populations both inside a 7-y deer enclosure (E) and outside the enclosure, where moderate deer densities occurred (MD-1; see below for measurements of deer density).

In Pennsylvania, the first site (ANF-1) was a contiguous landscape of old-growth beech-hemlock forest and

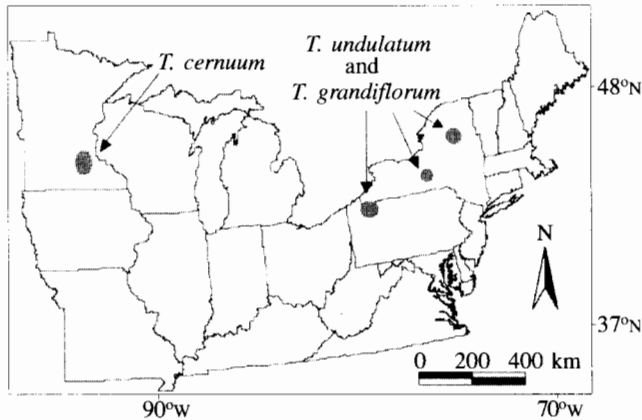


FIGURE 2. Map of the eastern United States showing locations of sites where *Trillium* spp. populations were sampled.

adjacent 190-y-old unmanaged second-growth forest dominated by sugar maple, yellow birch (*Betula alleghaniensis*), beech, black cherry (*Prunus serotina*), and hemlock (Runkle, 2000). ANF-1 was located in the Tionesta Natural and Scenic Area, which contains the largest tract of old-growth forest between ASP in New York and the Great Smoky Mountains National Park in Tennessee and North Carolina. The second site (ANF-2) was an 80- to 100-y-old second-growth forest dominated by northern hardwoods and hemlock. ANF-2 was fragmented by roads constructed in 1998 and 1999 and bordered on the east and south by recent (1998-1999) logging operations, such that no part of ANF-2 was > 250 m from edge habitat. The third site (ANF-3) was a 50- to 110-y-old second-growth forest dominated by northern hardwoods, black cherry, hemlock, and red maple (*Acer rubrum*). This site was less fragmented than ANF-1, but 3% of the landscape within a 1.5-km radius of the study area consisted of grassy forest openings and road edges and another 3% was affected by recent logging activity. The fourth site (ANF-4) was a mosaic of oak-hickory, mixed hardwood, and northern hardwood forests. ANF-4 was centred in a contiguous second-growth landscape with no forest openings or recent logging activity other than a grassy opening on a steep hillside to the south. The ground layer of all ANF sites was dominated by beech and ferns. Hobblebush (*Viburnum lantanoides*) was formerly a widespread component of the forest understory in this region, but has declined significantly in the last half-century (Hough, 1965).

In New York, the site at Hoxie Gorge (HG) was a 5-ha forest corridor dominated by mature sugar maple, beech, hemlock, yellow birch, and black cherry and bordered on the north and south by grass-dominated fields. The site was adjacent to the Hoxie Gorge State Forest, which experiences heavy annual hunting pressure. In the Adirondack State Park, New York, the first site (ASP-1) was an old-growth forest dominated by northern hardwoods, hemlock, and red spruce (*Picea rubens*). No large-scale canopy disturbance has occurred in the past 250 y. The second site (ASP-2) was a mature second-growth stand dominated by northern hardwoods that regenerated after a fire in 1903. The third site (ASP-3) was a mature second-growth stand dominated by northern

hardwoods, hemlock, and occasional red spruce. The stand was logged in 1953, when most hardwoods > 36 cm dbh were removed. The understory of all ASP study sites was dominated by hobblebush, beech, and ferns.

TRILLIUM SAMPLING

At the Minnesota sites, we sampled populations of *T. cernuum* using systematically distributed transects (HD-1 and MD-2) or extensive understory searches (HD-2, where *Trillium* was extremely rare; Augustine & Frelich, 1998). We also sampled *T. cernuum* at a fourth site using 100 1-m² plots inside a 7-y deer enclosure (E) and 200 1-m² plots outside the enclosure (MD-1). All surveys were conducted during the first 2 weeks of June in 1995 or 1996. For each individual *Trillium* occurring in the plots, we recorded stem height, length, and width of one randomly-selected leaf, number of leaves, and flowering status. Any *Trillium* stems browsed by deer were also counted. At MD-1 and HD-1 and HD-2, we also recorded the presence or absence of summer browse (foliage < 1 m tall recorded by species) and the presence or absence of any deer browse on those species in 49 systematically distributed 6-m² circular plots. From these surveys, we calculated 1) the proportion of plots containing woody sapling foliage < 1 m tall (*Acer saccharum*, *Ulmus* spp., *Fraxinus* spp., and *Tilia americana*) that contained evidence of summer browsing on those species (woody sapling browse index) and 2) the proportion of plots with any herbs or woody species < 1 m high that contained evidence of summer deer browsing (overall browse index). All Minnesota sites were dominated by sugar maple in both the canopy and understory.

In Pennsylvania and New York, we sampled *T. undulatum* at seven sites and *T. grandiflorum* at two sites. All sites were sampled during the first 2 weeks of June, 2002, using systematically distributed 2-m radius (12.6 m²) plots. Plot number per site varied inversely with *Trillium* abundance. We sampled 60 plots within a 5-ha area at HG, where *Trillium* was common, 120-160 plots within a 50-ha area at ANF-2, ANF-4, ASP-2, and ASP-3, where *Trillium* was moderately abundant, and 200-260 plots within an 80- to 100-ha area at ANF-1, ANF-3, and ASP-1, where *Trillium* was less abundant. *Trillium* individuals in each plot were measured in the same manner as for *T. cernuum* in Minnesota. We also recorded 1) the proportion of plots containing foliage of beech < 1 m tall with evidence of summer browsing on this species (woody sapling browse index) and 2) the proportion of plots with any foliage (herbs and woody species) < 1 m high that contained evidence of summer deer browsing (overall browse index).

DEER DENSITY ESTIMATES

For sites in Minnesota, the measure of deer density (deer·km⁻²) was obtained by counting the number of deer during winter aerial surveys within a 3-km radius of the forest fragment and dividing by the area of winter habitat within the survey (Augustine & Jordan, 1998). Counts were conducted by experienced observers during periods of complete snow cover and were not corrected for observability bias. Reported densities are the average and

range of all winter counts conducted during 1991-1995 (MD-1) or 1991-1996 (all other sites).

For sites in Pennsylvania and Hoxie Gorge, New York, deer density was calculated from spring pellet-group counts. Estimates for the Pennsylvania sites are based on 250 4.67-m² plots counted within a 256-ha area centred over the 50-ha *Trillium* sampling grids or 500 4.67-m² plots within a 512-ha area centred over the 100-ha *Trillium* sampling grids. For Hoxie Gorge, pellet groups were sampled with 50 28.27-m² plots distributed over the same 5-ha area where *Trillium* was sampled. Deer density was estimated based on the length of the pellet deposition period in the winter of sampling and 25 pellet groups · deer⁻¹ · day⁻¹. The pellet-group production rate estimate was taken from the literature (Sawyer, Marchinton & Lentz, 1990) and confirmed by D. deCalesta based on comparisons of deer density estimated by deer drives versus pellet-group counts for a fenced deer population in northwest Pennsylvania (D. deCalesta, unpubl. data). Pellet counts were conducted at ANF-1 for 3 y in the mid-1990s (1994-96) and again in 2002. ANF sites 2, 3, and 4 were measured only in 2001 and 2002.

Sites in ASP were located within the Huntington Wildlife Forest. On ASP-1 and ASP-2, hunting occurred during 1966-1970 and 1978-1984; no hunting occurred on ASP-3. Based on annual road counts conducted in June each year (Adirondack Ecological Center, unpubl. data) calibrated to actual densities following Underwood (1990), the long-term mean deer densities (± SE) for 1966-2001 were 5.7 ± 0.4 · km⁻² for ASP-1 and 2 (range, 1.6-13.3 · km⁻²) and 6.9 ± 0.4 · km⁻² for ASP-3 (range, 1.7-11.8 · km⁻²).

EVALUATING FORB POPULATION STRUCTURE

For each *Trillium* population, we analyzed four characteristics: 1) proportion browsed stems (browsed stems / total stems), 2) proportion flowering stems (unbrowsed stems flowering / unbrowsed stems), 3) mean stem height, and 4) a histogram of stage-class distributions. We divided *Trillium* populations into stage classes based on total leaf area following Kawano, Ohara, and Utech (1986). For *T. cernuum* populations in Minnesota, we grouped stage classes 1-3 (small non-flowering plants; 0-6.3 cm² leaf area), classes 4-7 (mid-size non-flowering plants; 6.3-39.8 cm²), classes 5-10 (large non-flowering plants; 39.8-158.5 cm²), and classes 11-14 (primarily flowering plants; 158.5-1,000 cm²) (Ohara & Utech, 1988). For *T. undulatum*, which typically exhibits a stage-class distribution skewed more toward smaller, single-leaved plants (Kawano, Ohara & Utech, 1986), we grouped stage classes 1-2 (small, one-leaved plants; 0-4.0 cm² leaf area), 3-4 (intermediate, one-leaved plants; 4.0-10.0 cm²), 5-6 (large, one-leaved plants; 10.0-25.1 cm²), 7-8 (non-flowering, three-leaved plants; 25.1-63.1 cm²), and 9-11 (mostly flowering, three-leaved plants; 63.1-250 cm²). χ^2 analyses were used to test for differences between populations in the distribution of individuals within the stage-class groups (Agresti, 1996). For each chi-square test, the standardized residuals for the smallest and largest stage-class groups were calculated to test whether differences in population structure are consistent with the hypothesized

effects of deer on the largest stage classes due to consumption and the small stage classes due to suppressed reproduction. Standardized residuals > 2 were considered significant (Agresti, 1996).

Results

In fragmented forests in Minnesota, *Trillium cernuum* populations at the two high deer-density sites (overwinter densities > 20 · km⁻²) consisted primarily of individuals in size classes 4-10 (mid-sized, non-reproductive plants) while seedlings and large reproductive individuals were rare (Figure 3). At one site with moderate deer densities, flowering plants were largely eliminated by deer (29.4% browsed in the year of sampling versus 6.5% flowering). At a second site with moderate deer densities, 16.4% of plants were grazed and significantly more large, flowering plants remained in the population relative to one high deer-density site (Tables II and III). Populations at both moderate deer-density sites contained a proportion of small juveniles similar to that of the population protected from deer for 8 y (Figure 3; Table III). The enclosure population contained the highest proportion of both small juveniles and large, reproductive plants compared to all other populations (Figure 3; Table III). Thus, the distribution of size classes in populations at high deer-density sites reflected previously documented severe effects of deer on *Trillium* reproduction (Augustine & Frelich, 1998). High browsing intensity at MD-1 may reflect a recent increase in deer density at that site (Table II).

Population structure of *T. undulatum* was similar at all four study sites with low deer density (Figure 4; Table IV) despite wide among-site variation in disturbance history. In contrast to the all-aged *Trillium* population structure at these low deer-density sites, *Trillium* populations

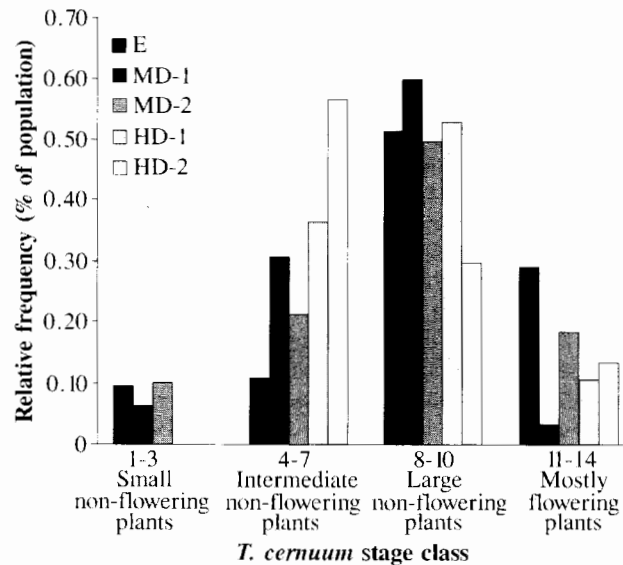


FIGURE 3. Histogram of stage-class distributions for five *Trillium cernuum* populations from maple-basswood forests in south-central Minnesota. Deer density and other *Trillium* population characteristics for each site are given in Table II. E: enclosure; MD-1, MD-2: moderate deer density, sites 1 and 2; HD1, HD2: high deer density, sites 1 and 2.

TABLE II. Population characteristics of *T. cernuum* at four maple-basswood forests in south-central Minnesota. Exclosure studies at the two high deer-density sites demonstrated deer were eliminating > 50% of reproductive individuals annually and causing reduced plant size in subsequent years.

Site ³	Deer density (ind. · km ⁻²)			<i>Trillium</i> population characteristics				Sapling browsing index (%) ¹	Overall browsing index (%) ²
	Year of sampling	Mean of past 6 y	Range (min - max)	Mean stem height (cm)	% flowering	% browsed	% flowering plants browsed		
HD-1	36.3	23.5	13.6 - 36.4	16.0	8.2	45.6	64.7	8.8	64.0
HD-2	25.3	22.5	19.5 - 25.3	11.9	2.6	19.1	76.9	9.5	47.9
MD-1	16.4	10.5	3.4 - 16.4	19.2	6.5	29.4	-	-	-
MD-2	11.4	12.0	2.8 - 21.6	17.8	17.7	16.5	35.7	7.7	28.9
E	0	0	0	26.4	34.2	0.0	-	-	-

¹ Proportion of plots containing woody plant foliage < 1 m in height that also contained evidence of summer browsing by deer.

² Proportion of plots containing any foliage < 1 m in height (herbs and/or woody plants) that also contained evidence of summer deer browsing.

³ Abbreviations as in Figure 3.

TABLE III. Results of chi-square comparisons of *Trillium cernuum* population structure among study sites. Chi-square comparisons evaluated differences in the distribution of individuals among the four groups of stage classes shown in Figure 3: stages 1-3, 4-7, 8-10, and 11-13 (Kawano, Ohara & Utech, 1986). The reported standardized residuals are for population 1 in each comparison and are presented for stage classes 1-3 (small juveniles) and stage classes 11-13 (mostly flowering plants). If a Bonferroni correction is applied for multiple tests, differences among populations should only be considered significant for *P* < 0.0085.

Population 1 ²	Population 2	χ^2	df	<i>P</i>	Standardized χ^2 residuals ¹ Stage classes	
					1-3	11-13
MD-1	E	21.9	3	< 0.001	-0.73	-4.41
MD-2	E	6.1	3	0.105	0.11	-1.24
MD-2	MD-1	11.1	3	0.011	0.57	1.91
HD-2	HD-1	5.3	2	0.070	-	0.59
HD-1	E	22.4	3	< 0.001	-2.71	-2.90
HD-2	E	29.2	3	< 0.001	-2.73	-2.59
HD-1	MD-2	12.4	3	0.006	-4.15	-2.30
HD-2	MD-2	20.0	3	< 0.001	-4.17	-1.51
HD-1	MD-1	7.4	3	0.062	-2.03	1.69
HD-2	MD-1	14.4	3	0.002	-2.04	2.66

¹ A residual > 2, shown in boldface, indicates a significant difference between the two populations in that particular group of stage classes (Agresti, 1996).

² Abbreviations as in Figure 3.

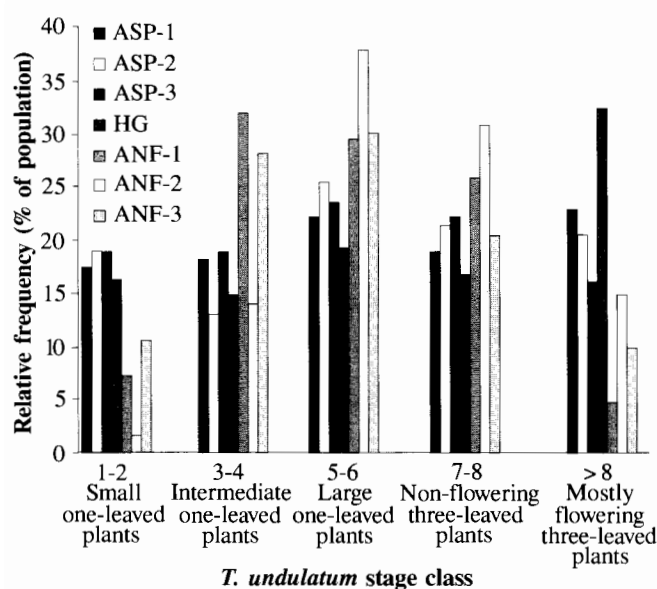


FIGURE 4. Histogram of stage-class distributions for seven *Trillium undulatum* populations from forests in Pennsylvania and New York. Deer densities and other *Trillium* population characteristics for each site are given in Table V. ASP-1, ASP-2, ASP-3: Adirondack State Park sites 1, 2, and 3; HG: Hoxie Gorge; ANF-1, ANF-2, ANF-3: Allegheny National Forest sites 1, 2, and 3.

at the high deer-density sites in the Allegheny National Forest contained a lower frequency of both large and small individuals (Figure 4). Population structure differed significantly in all pairwise comparisons of low-deer to high-deer sites (Table IV). In most low versus high deer-density comparisons, high deer-density sites contained significantly less *Trillium* recruitment (Table IV). This difference was most pronounced for the contiguous old-growth forest study area in Tionesta Scenic and Natural Area (ANF-1), where no flowering individuals of *T. undulatum* were recorded and deer browsing pressure on both beech saplings and the overall understory community was high (Table V). ANF-2 contained an intermediate level of large, flowering plants (Figure 4), but also experienced high browsing pressure on *Trillium* and the overall understory community (Table V). This site was highly fragmented, and mature forest was within 250 m of road or logging edges. ANF-3 contained an intermediate level of flowering plants and some recent *Trillium* recruitment (Figure 4), consistent with the low levels of browsing (Table V). ANF-3 was less fragmented, but still contained road edges and forest clearings in the immediate vicinity.

Trillium grandiflorum is less common in New York and northwestern Pennsylvania than *T. undulatum* and *T. erectum* (Case & Case, 1997), but we surveyed two

TABLE IV. Results of chi-square comparisons of *Trillium undulatum* population structure among study sites. Chi-square comparisons evaluated differences in the distribution of individuals among the five groups of stage classes shown in Figure 4: stages 1-2, 3-4, 5-6, 7-8, and 9-11 (Kawano, Ohara & Utech, 1986). The reported standardized residuals are for population 1 in each comparison and are presented for stage classes 1-3 (small juveniles) and stage classes 11-13 (mostly flowering plants). If a Bonferroni correction is applied for multiple tests, differences among populations should only be considered significant for $P < 0.0043$.

Population 1 ²	Population 2	χ^2	df	P	Standardized χ^2 residuals ¹	
					Stage classes 1-3 P1	Stage classes 11-13 P1
LOW DEER- VERSUS LOW DEER-DENSITY POPULATIONS						
ASP-1	ASP-2	1.8	4	0.775	-0.29	0.43
ASP-2	ASP-3	2.4	4	0.663	0.01	1.01
ASP-2	HG	6.1	4	0.189	0.61	-2.22
ASP-1	ASP-3	2.6	4	0.622	-0.34	1.57
ASP-1	HG	3.5	4	0.479	0.29	-1.84
ASP-3	HG	12.7	4	0.013	0.65	-3.54
HIGH DEER- VERSUS LOW DEER-DENSITY POPULATIONS						
ANF-3	ASP-1	16.1	4	0.003	-1.74	-3.12
ANF-3	ASP-2	16.9	4	0.002	-2.01	-2.53
ANF-3	ASP-3	11.1	4	0.025	-2.16	-1.65
ANF-3	HG	33.4	4	< 0.001	-1.51	-5.03
ANF-2	ASP-1	26.6	4	< 0.001	-4.06	-1.61
ANF-2	ASP-2	22.2	4	< 0.001	-4.27	-1.12
ANF-2	ASP-3	24.4	4	< 0.001	-4.35	-0.24
ANF-2	HG	36.4	4	< 0.001	-3.89	-3.29
ANF-1	ASP-1	20.7	4	< 0.001	-2.10	-3.51
ANF-1	ASP-2	21.9	4	< 0.001	-2.30	-3.12
ANF-1	ASP-3	15.5	4	0.004	-2.39	-2.50
ANF-1	HG	33.3	4	< 0.001	-1.92	-4.80

¹ A residual > 2, shown in boldface, indicates a significant difference between the two populations in that particular group of stage classes (Agresti, 1996).

² Abbreviations as in Figure 4.

TABLE V. Characteristics of *Trillium undulatum* populations in late-successional and old-growth forests in the Adirondack State Park of New York, in Hoxie Gorge of central New York, and in the Allegheny National Forest of Pennsylvania.

Site ³	Deer density (ind. · km ⁻²)		<i>Trillium</i> population characteristics			Beech browsing index (%) ¹	Overall browsing index (%) ²
	Year of sampling	Longer-term mean (range)	<i>Trillium</i> % flowering	<i>Trillium</i> % browsed	<i>Trillium</i> mean stem height (cm)		
ASP-1	4.5	5.7 (1.6 - 13.3)	7.7	0.7	9.3	1.7	4.6
ASP-2	4.5	5.7 (1.6 - 13.3)	7.4	0.8	9.1	0.0	3.3
ASP-3	3.1	6.9 (1.7 - 11.8)	6.3	0.6	8.2	1.1	8.3
HG	3.0	NA	11.8	2.4	11.6	4.8	21.7
ANF-1	10.9	14.5 (10.9 - 17.4)	0.0	2.4	7.4	22.0	24.3
ANF-2	22.8	20.4 (18.0 - 22.8)	5.3	16.8	9.2	13.0	19.0
ANF-3	15.1	15.1 (14.8 - 15.5)	4.7	0.6	7.3	9.6	8.4

¹ Proportion of plots containing beech foliage < 1 m in height that also contained evidence of summer browsing by deer on beech.

² Proportion of plots containing any foliage < 1 m in height (herbs and/or woody plants) that also contained evidence of summer deer browsing.

³ Abbreviations as in Figure 4.

populations of *T. grandiflorum* because of its wide distribution in the mid-western U.S.A. and the frequent reports of negative deer impacts (Anderson, 1994; Augustine & Frelich, 1998; Fletcher *et al.*, 2001; Rooney & Gross, 2003; S. Kalisz, pers. comm.). The *T. grandiflorum* population in central New York was skewed toward large, flowering individuals (Figure 5). Although ~10% of the population was browsed by deer, particularly in large patches of flowering plants 25-50 m from forest edges, browsing rates were lower than flowering rates. In contrast, the population at ANF-4 lacked large, flowering plants and deer browsing pressure on beech was much greater than at Hoxie Gorge (Table VI). Browsing pressure was greater for beech foliage than for the overall understory at ANF-4 (Table VI) because most of the understory was dominated by unpalatable ferns. In con-

trast, the Hoxie Gorge understory was dominated by a diverse herbaceous layer.

Discussion

INDIVIDUAL PLANTS

Studies over the past decade indicate white-tailed deer are affecting native plant species across many forest communities in eastern North America. However, deer have likely influenced plant communities throughout their evolutionary history. From the perspective of conserving native plant communities in parks and preserves, how can we tell when deer abundance and related impacts are too high? We suggest an approach of monitoring long-lived, understory forb species that are selected by deer and possess growth forms intolerant to herbivory. We advocate

TABLE VI. Characteristics of *Trillium grandiflorum* populations in central New York (Hoxie Gorge) and the Allegheny National Forest in Pennsylvania.

Site ³	Deer density estimates (ind. · km ²)	<i>Trillium</i> population characteristics				Overall browsing index (%) ²
		<i>Trillium</i> % flowering	<i>Trillium</i> % browsed	<i>Trillium</i> mean stem height (cm)	Beech browsing index (%) ¹	
HG	3.0	22.0	14.5	14.2	4.8	21.7
ANF-4	14.4	1.7	2.5	8.7	27.3	24.3

¹ Proportion of plots containing beech foliage < 1 m in height that also contained evidence of summer browsing by deer on beech.

² Proportion of plots containing any foliage < 1 m in height (herbs and/or woody plants) that also contained evidence of summer deer browsing.

³ HG: Hoxie Gorge site; ANF-4: Allegheny National Forest site 4.

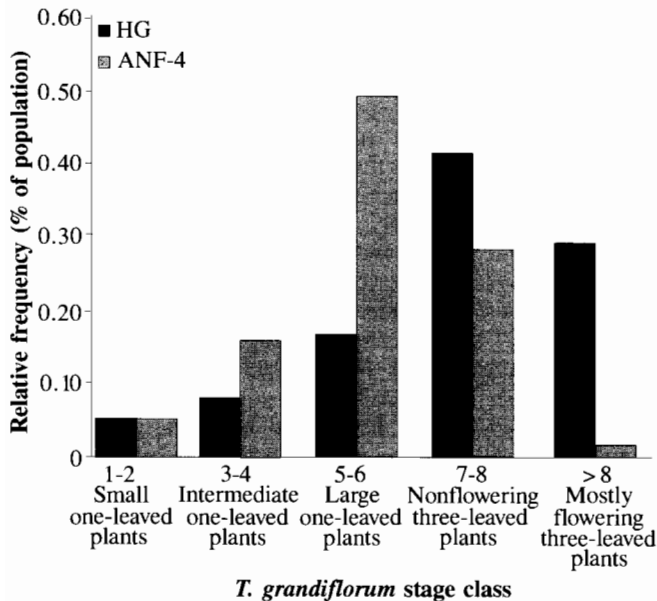


FIGURE 5. Histogram of stage-class distributions for two *Trillium grandiflorum* populations from forests in Pennsylvania and New York. Deer densities and other *Trillium* population characteristics for each site are given in Table VI. Abbreviations as in Table VI.

an analysis that combines measures of browsing pressure, mean plant size, plant flowering rates, and plant population size structure to identify situations where deer herbivory could be an important factor driving populations to local extinction. All of these measures can be calculated from data collected in a single field survey. Although a single index such as stem height has proven useful in some studies (Anderson, 1994), we found that stem height did not discriminate between two forests with drastically different effects of deer on *Trillium* populations in Minnesota (HD-1 versus MD-2 in Table II). Similarly, mean stem height was not associated with indices of browsing pressure in Pennsylvania and New York (Table V). Size-class histograms provided a better indicator of potential deer impact. Populations in forests supporting high deer densities showed a low frequency of both large (reproductive) and juvenile plants in the agricultural landscape of Minnesota (Figure 3) and the forested landscapes of Pennsylvania and New York (Figure 4), consistent with the expectation that heavy browsing on flowering plants limits reproduction and recruitment. The high frequency of non-flowering individuals in mid-size classes is also consistent with the expectation that persistent browsing of large individuals reduces leaf area in subsequent years.

Collectively, studies of *Trillium* populations in different regions suggest two different types of deer-affected forb populations. The combination of low mean plant size, high grazing rates, intermediate flowering rates, and a size-class distribution lacking large, reproductive plants suggests a recent increase in deer browsing pressure is affecting the plant population. In contrast, sites affected by long-term high deer densities exhibit low browsing rates on *Trillium* but also low *Trillium* flowering rates; these populations contained relatively fewer individuals in both large and small stage classes. In these cases, mean plant size may not be indicative of deer impacts on the population; due to a lack of both large size classes and small juveniles, most plants will be in intermediate, non-reproductive size classes. However, indices of plant size that exclude juvenile plants (Webster & Parker, 2000; Fletcher *et al.*, 2001) might still serve as reliable indicators of deer impact. Measurable browsing pressure on species such as *Trillium* is low in these forests because few flowering plants occur in the population. However, the severely compressed population structure suggests browsing could lead to long-term loss of the species. In this situation, reduction in deer density or manipulation of the landscape to increase preferred deer forage will likely be needed if conservation of presettlement plant communities is a management objective. We also note that deer-induced reductions in understory plant density and diversity have been linked to reductions in native forest bird populations (deCalesta, 1994; McShea & Rappole, 2000), such that plant-based indicators of overabundance could also identify situations where deer are negatively affecting vertebrate communities.

Although our results show that *Trillium* population structure varies in accordance with our expectations based on deer density and landscape structure, these findings do not prove that deer are the responsible factor, or even that deer will eventually drive *Trillium* to extinction at some sites. Only in the case of the two high deer-density sites in Minnesota have experiments demonstrated that the skewed population structure is due to deer impact (Augustine & Frelich, 1998). If population structure of forbs is to serve as a useful index of deer overabundance, two avenues of research and monitoring could be used to link population structure, deer impact, and the long-term probability of plant extinction. First, stage-based models of plant population dynamics relating population demographics to the long-term probability of plant extirpation are needed. Rooney and Gross (2003) have developed the first such model for *T. grandiflorum* populations in

Wisconsin hardwood forests. Their model projects a slow, long-term population decline even in the absence of deer browsing, likely due to low rainfall in the year of growth-rate measurements. However, deer browsing even at a low level of 8% (compared to a 7% flowering rate for unbrowsed plants) can accelerate the rate of population decline 2-3 fold (Rooney & Gross, 2003). More detailed and longer-term studies are expanding upon this modeling approach for *T. grandiflorum* populations affected by deer in southwestern Pennsylvania (S. Kalisz & T. Knight, pers. comm.). Model predictions may be complicated by uncertainties concerning the effects of canopy disturbance on forb population dynamics, in particular the importance of forb growth and reproduction following large-scale canopy removal (e.g., windthrow, clearcuts) versus small but more frequent canopy gaps. At the same time, these plant population models can begin to provide predictions about the viability of forb populations with varying stage-class structures and flowering rates. A second approach is simply to monitor forb stage-class structure over a series of years. Increasing compression of the population into intermediate size classes over time (combined with evidence that deer are the responsible factor) would indicate the population cannot be sustained under current conditions.

THE ROLE OF LANDSCAPE STRUCTURE VERSUS DEER DENSITY

Disruption of the historical relationship between deer populations and forest communities could occur due to reduced hunting and predation (top-down regulation hypothesis), changes in the disturbance regime that produce more or less forage, especially interspersed of forest with agriculture or other forms of canopy disturbance (edge effect hypothesis), or both. In agricultural landscapes with small forest fragments, reduced predation and increased forage availability could both be important factors leading to deer overabundance, and the only management recourse may be to significantly reduce deer numbers. However, landscape effects can still influence deer management goals. For example, deer densities may need to be reduced to a greater degree in parks surrounded by low-quality forage types and to a lesser degree in parks surrounded by high-quality forage such as alfalfa and hay fields (deCalesta & Stout, 1997; Augustine & Jordan, 1998). In primarily forested landscapes, distinguishing between edge effects and top-down regulation is important because solutions could include both landscape-level forage management (increased production through the distribution of timber harvest or food plots) and deer population control (hunting or otherwise).

Careful consideration of the research already conducted on the scale at which deer perceive and use landscapes can provide significant insight into the likely effects of landscape structure and edges on deer browsing pressure. One of the most widely reported conclusions from telemetry studies of deer in eastern North America is the high degree of life-time fidelity to seasonal home ranges (Nelson & Mech, 1981; Tierson *et al.*, 1985; Beier & McCullough, 1990; Nixon *et al.*, 1991 and references therein). These studies report summer deer home ranges of 40-220 ha for adult females and 100-320 ha for

adult males. More recent work has shown that locally targeted deer removals can reduce deer density at scales of 1-2 km² for several years (Porter *et al.*, 1991; McNulty *et al.*, 1997). As a result, we suggest that landscape structure at the scale of seasonal deer home ranges influences the level of impact the local deer population exerts on forest plant communities (deCalesta & Stout, 1997; Augustine & Jordan, 1998; Van Deelen, 1999) and dictates the degree and spatial extent of removals necessary to mitigate deer impact.

In highly fragmented landscapes (Figure 6a; all Minnesota sites, Hoxie Gorge, and ANF-2), deer can have a pervasive effect on forest vegetation because forest patches comprise only a small proportion of an individual deer's home range, and patch interiors are immediately accessible to deer. At these study sites, the maximum distance of any plot to a forest edge was 0.25 km, and browsing was observed throughout the 5- to 16-ha forest fragments. Although deer have access to abundant forage from agricultural crops, fields, residential neighborhoods, roadside edges, and clearcuts, they continually use forests for cover, travel, foraging, and fawning during the growing season (Nixon *et al.*, 1991; Rouleau, Crête & Ouellet, 2002) and selectively forage on the most palatable forbs (Augustine & Jordan, 1998; Rouleau, Crête & Ouellet, 2002). Low-density deer populations (1·km⁻²) in agricultural landscapes have even been shown to avoid agricultural fields and concentrate foraging in forest patches (Lesage *et al.*, 2002). Selective foraging on forest plants in fragmented, agricultural landscapes is analogous to the increased degree of selective foraging on natural vegetation exhibited by white-tailed deer receiving supplemental feed (Murden & Risenhoover, 1993).

As the amount of forest within a deer's home range increases (Figure 6b), we hypothesize that the per-deer browsing pressure on understory communities also declines (Figure 7) as foraging is concentrated in the few forest openings within the home range, while selective foraging on understory communities is distributed over a larger area. Again, the degree to which deer concentrate summer foraging in open patches (e.g., fields, recent clearcuts, food plots) will depend on the condition of the understory community in the adjacent closed-canopy forest, and is likely to be most important where deer densities exceed 10·km⁻² (Rouleau, Crête & Ouellet, 2002). A forested landscape with 6% canopy openings occurred at our site in Pennsylvania (ANF-3; Figure 6b) with the lowest measured browsing pressure (Table III) and the least degree of compression in the *T. undulatum* population's structure (Figure 4). Similarly, in a southern Appalachian forest landscape with ~4% clearcuts, summer deer browsing pressure (% of available stem-tips browsed) was significantly greater in clearcuts and clearcut edges relative to closed-canopy forest (Ford *et al.*, 1993), even though forage biomass was 77 times greater in clearcuts than in closed canopy forest (Johnson *et al.*, 1995). In this southern Appalachian landscape, deer densities of ~5-10·km⁻² have no negative effects on forest regeneration (Johnson *et al.*, 1995; Castleberry *et al.*, 2000), while in this type of landscape at ANF, deer densities of 8-15·km⁻² alter the species composition of forest

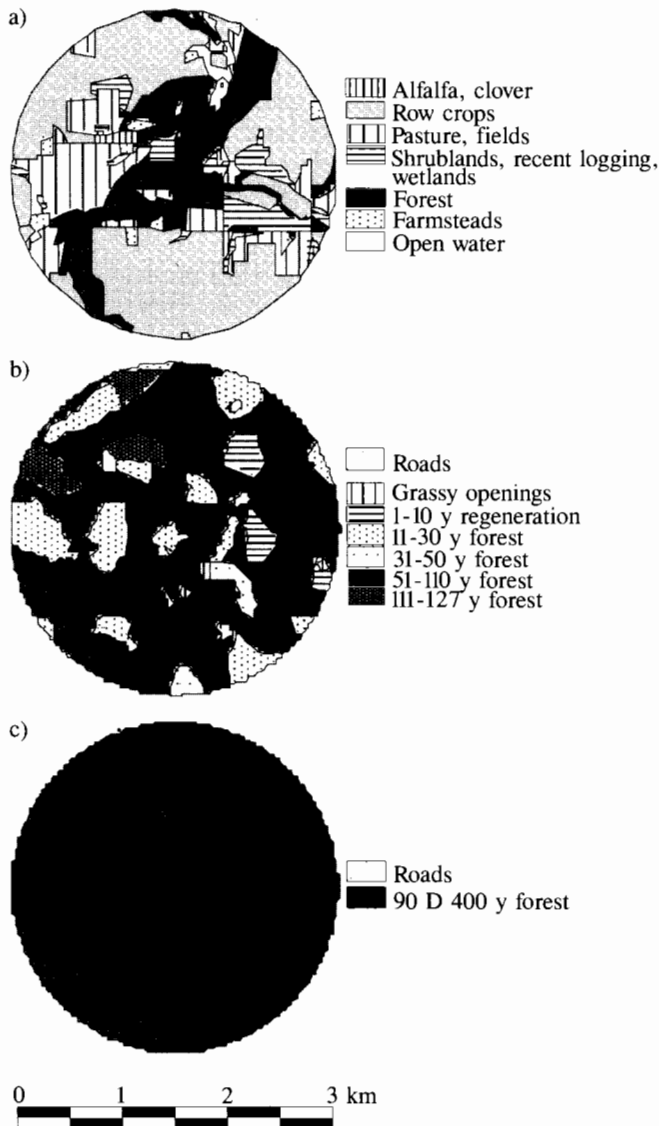


FIGURE 6. Examples of landscapes where *Trillium* populations were surveyed in this study. Each landscape is a 1.5-km radius area centred on the study site. This radius corresponds to an area 2-3 times larger than seasonal deer home ranges in forested and agricultural regions of the eastern U.S.A. Sites vary from the predominantly agricultural landscape surrounding MD-2 from south-central Minnesota (a: Landscape 1, 24% late-successional forest), to the managed second-growth forest landscape of ANF-3 (b: landscape 2, 76% late-successional forest), to the old-growth forest of the Tionesta Scenic and Natural Area (c: ANF-1, landscape 3, 99% late-successional forest). We hypothesize that for a given deer density, browsing impacts will vary from selective foraging on highly preferred understory species in Landscape 1, to lower browsing pressure on understory species in Landscape 2, where foraging will be concentrated in canopy openings, to high and more uniformly distributed browsing pressure on all understory species in Landscape 3. Abbreviations as are Figures 3 and 4.

regeneration (Horsley & Marquis, 1983; Tilghman, 1989). As deer densities increase, impacts may be focused both on the few forest openings within the area and on the most palatable species within closed-canopy forest.

In landscapes dominated by late-successional, all-aged forests (Figure 6c), the per-deer browsing pressure may

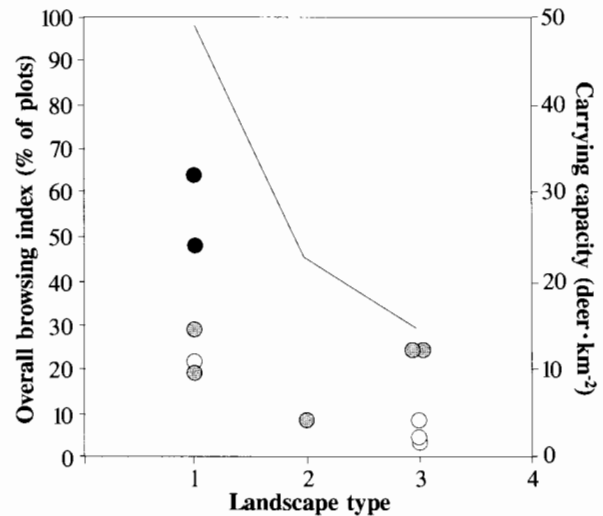


FIGURE 7. Deer browsing pressure on understory plant communities in relation to landscape structure (Landscape 1 = highly fragmented by agriculture and/or logging, Landscape 2 = forested landscape with ~5% canopy openings, Landscape 3 = contiguous forest landscape; see Figure 6) and deer density (open circles < 10 deer·km², grey circles = 10-24 deer·km², black circles ≥ 25 deer·km²). Carrying capacity (solid line) was estimated as 38-60 deer·km² in fragmented landscapes (McCullough, 1979; Underwood & Porter, 1997), 20-25·km² in forested landscapes with canopy openings (Tilghman, 1989; Healy, 1997), and 15·km² in contiguous, late-successional forest landscapes (this study). Note that all estimates of deer carrying capacity are derived from sites where severe winters are not a major source of deer mortality.

be even more severe than in landscapes with managed forest openings (Figure 7) because there is less alternate forage. Winter deer densities in the old-growth landscape of the Tionesta Scenic and Natural Area (ANF-1) were 14-17·km² in the mid-1990s and 11·km² in 2002. Summer browsing pressure in this landscape is high (Table V), and both reproduction and recruitment of *T. undulatum* are low (Figure 4). These results indicate deer can persist at high densities in late-successional forest landscapes where hunter access is low, wolves are absent, and winters are mild. Because deer subsist entirely on understory vegetation in this landscape, persistent high densities can lead to long-term losses of native plant species (Hough, 1965; Rooney & Dress, 1997).

Our predictions concerning the role of landscape structure in deer-plant interactions differ from the predictions of Alverson, Waller, and Solheim's (1988) edge-effect hypothesis, which suggested that creation of large, contiguous blocks of unmanaged, closed-canopy forest could effectively regulate deer at low densities (on the order of 4-6·km²) and eliminate negative deer effects on forest communities. In northern hardwood-conifer forests of New York, severe winter weather combined with black bear and coyote predation is sufficient to regulate deer densities below 10·km² (Underwood, 1990). However, in more southern regions, landscape management to increase contiguous forest cover may be insufficient to prevent severe deer overabundance (Crête, 1999). Large blocks of contiguous late-successional forest in regions that lack wolves and experience mild winters may be especially susceptible to severe deer browsing since hunter access to these areas is also limited. Combinations of deer manage-

ment via predator restoration, landscape management, and increased hunting pressure may be needed to retain sensitive understory species in such regions.

Clearly, deer density is also an extremely important determinant of deer browsing pressure. Widespread reports of severe deer impacts on understory herbaceous communities are all associated with deer densities exceeding $\sim 20 \cdot \text{km}^{-2}$ (Anderson, 1994; Augustine & Frelich, 1998; Fletcher *et al.*, 2001; Webster, Jenkins & Parker, 2001). A recent review of deer effects on forest communities concluded that significant negative deer impacts on regeneration of tree species are all associated with densities $> 8.5 \cdot \text{km}^{-2}$ (Russell, Zippin & Fowler, 2001), which exceeds presettlement estimates of 3-4 deer $\cdot \text{km}^{-2}$ (McCabe & McCabe, 1997). Studies reporting no significant deer effect are associated with deer densities of 4-10 $\cdot \text{km}^{-2}$ (Tilghman, 1989; Anderson, 1994; Castleberry *et al.*, 2000). It is worth cautioning that for a fixed deer density, impact will decrease with increasing site productivity. Since deer density also increases with increasing productivity south of the wolf range in North America (Crête, 1999), this may not be a critical factor, but should be taken into account when assessing the meaning of any specific deer density. We also emphasize that deer impact will depend on landscape features, and defining overabundance based on deer density is often confounded by variation in landscape structure and difficulties in measuring deer densities at appropriate seasonal and spatial scales. Precisely for these reasons, plant-based evaluations of forest communities can be particularly useful to deer managers. Results from this study suggest that evaluations of overabundance using combined measures of perennial forb population structure and deer browsing pressure on the understory, which elaborates on the indices originally developed by Anderson (1994), Webster and Parker (2000), and Fletcher *et al.* (2001), could provide a useful measure of the potential for deer-induced plant extirpations. Further development of forb population models (Rooney & Gross, 2003) and long-term monitoring programs that examine changes in forb population structure over time are needed to improve the interpretation of forb-based indices in terms of the probability and temporal scale of local plant extirpations.

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