Direct and indirect effects of white-tailed deer in forest ecosystems

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Direct and indirect effects of white-tailed deer in forest ecosystems☆

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Abstract

Ungulates can profoundly alter the structure and composition of forest communities via both direct and indirect mechanisms. Individual plant species often respond in a unique way to the direct effect of herbivory as a function of their sensitivity to browse damage, ungulate food preferences, and the density of ungulates present. Sustained browsing pressure can limit the regeneration of favored and susceptible woody plants and eliminate populations of favored or susceptible herbaceous plants. These losses, in turn, give rise to indirect effects via trophic cascades or physical habitat modification. These indirect effects affect many other plant and animal populations. In the mixed conifer–hardwood forests around the Great Lakes in North America, widespread habitat modification and the extirpation of native predators and other ungulates have acted to boost populations of white-tailed deer (*Odocoileus virginianus*) to historically high densities. Such densities have curtailed regeneration of several important conifers (e.g. *Tsuga canadensis* and *Thuja occidentalis*) as evidenced by demographic analysis. Deer also appear to limit regeneration of *Quercus* and *Betula* in many areas. Impacts on understory herbs are harder to assess, but baseline data from 50 years ago indicate that these communities are changing in a pattern that implicates deer: grasses, sedges, and some ferns are increasing while overall herb diversity is declining. Thus, deer are playing a keystone role in these communities. We are currently assessing an additional set of questions, including: How best can we measure and represent ungulate impacts? At which densities do deer threaten forest diversity? How do impacts depend on initial plant and ungulate densities? Which species emerge as 'winners' or 'losers' in heavily-browsed landscapes? What characteristics or traits make a species susceptible to ungulate herbivory? How do ungulates affect patterns of diversity and relative abundance in ecological communities? What are the pathways by which ungulates exert indirect effects on species? and How significant are indirect effects?
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1. Introduction

Ungulates profoundly alter the structure and composition of ecological communities. Ungulate fora-

ging has both direct and indirect effects on the plant and animal communities they occupy. Because ungulates interact strongly with plants, greatly affecting their distribution or abundance, they act as keystone herbivores to restructure whole ecological communities (McShea and Rappole, 1992; Waller and Alverson, 1997; Paine, 2000; Rooney, 2001). As with all keystone species, the strength of these interactions varies spatially and temporally (Paine, 1996), with the strongest interactions occurring where ungulate

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densities are greatest. Ungulates also disperse parasites (Ostfeld et al., 1996) and seeds (Gill and Beardall, 2001), create concentrated patches of nutrients through urination and defecation (Hobbs, 1996; Persson et al., 2000), and mechanically damage vegetation by trampling and bedding (Persson et al., 2000). To keep things manageable, we ignore these other effects in this review.

Because white-tailed deer (*Odocoileus virginianus*) occupy a broad range of habitats and can reproduce rapidly under favorable conditions, their populations have increased sharply in recent decades throughout much of their range (Garrott et al., 1993). In the absence of native predators like gray wolf (*Canis lupus*) and cougar (*Puma concolor*), hunting acts as the primary factor limiting deer population sizes. Without hunting, deer populations can reach very high densities. An extreme example comes from Sharon Woods Metro Park, Ohio, where over 150 vascular plant species were extirpated when the unmanaged white-tailed deer population reached densities > 110 animals per square km (Peek and Stahl, 1997). Even in managed populations, deer densities routinely significantly exceed pre-settlement densities (Alverson et al., 1988; Crête, 1999). While deer population densities can be easily manipulated in small reserves, Brown et al. (2000) document a constellation of ecological, social and political factors that tend to limit the effectiveness of hunting in controlling deer populations in today's landscapes. If their analysis is correct, white-tailed deer populations will increase further in coming decades. Because white-tailed deer are a keystone species, we anticipate a major restructuring of forest communities with current and projected population densities. While some species clearly benefit from increased deer densities, we project an overall decline in biological diversity in forest communities based on our empirical investigations of forest–herb communities in Wisconsin.

In this paper, we first examine the direct effects of white-tailed deer browsing in the mixed coniferous–deciduous forests of northern Wisconsin. Drawing on our own research, we examine how the regeneration of four tree species responds to increasing numbers of deer. We also examine how forest–herb communities, representing the bulk of plant diversity in temperate forests, respond to high deer densities. We then examine indirect pathways by which ungulate browsing can influence community structure and composition. We extend our analysis to include other forest ungulates, and distinguish between indirect effects arising as a consequence of food web interactions from those arising from habitat modification. Finally, we propose some future avenues for research that should improve our understanding of how ungulate foraging affects biological diversity.

2. Ungulate browsing and direct effects: tree regeneration and forest understory communities in northern Wisconsin

Prior to settlement by Europeans (circa 1800), white-tailed deer densities in northern Wisconsin forests were lower than four animals per square km (McCabe and McCabe, 1984). Unregulated hunting nearly eliminated Wisconsin's deer population, but the combination of bucks-only hunting laws and a system of game refuges allowed deer population densities to rise to 9–14 animals per square km in the 1930s and 1940s. High deer densities during this time resulted in heavy damage to agricultural crops and forests (Dahlberg and Guettinger, 1956). Following both-sex hunts, population densities dropped through the 1960s and 1970s, but rose again in the 1980s and 1990s (Wisconsin Department Natural Resources, unpublished data). Over the past decade, deer densities have averaged 10 animals per square km (Rooney et al., 2002). These densities exceed both pre-settlement densities (by 2.5–5 times) and the density goals established by the DNR-(at 50–70% of carrying capacity) across all deer management units in northern Wisconsin.

2.1. Tree regeneration

White-tailed deer impacts have been extensively studied in Wisconsin since the 1940s, although most studies concentrated on the regeneration of commercially-valuable tree species (Alverson et al., 1988). Exclosure studies (Graham, 1954) and deer-free island studies (Beals et al., 1960) reveal deer browsing can depress local regeneration of favored tree species. Deer browsing can undoubtedly limit the regeneration of favored tree species in some places and in some years. However, researchers should not assume browsing limits regeneration on a regional scale when

observations of browsing impacts are restricted to a few locations (Mladenoff and Stearns, 1993). Moreover, regeneration can be limited during any phase in the life cycle, and by different ecological factors operating on different phases. Robust generalizations about the role of deer browsing in limiting tree regeneration emerge only after researchers analyze multiple, potentially-limiting factors across broad geographic areas using several demographic size or age classes (Waller et al., 1996).

Over the past decade, we used a broad-scale, multi-factor approach to examine the role of deer in limiting the regeneration of eastern hemlock (*Tsuga canadensis*) and northern white-cedar (*Thuja occidentalis*). Both hemlock and white-cedar are evergreen and an important winter food for deer. For both species, we conducted regionally-extensive regeneration surveys in 1990–91 (142 hemlock sites, 77 white-cedar sites) and again in 1996 (100 hemlock sites, 49 white-cedar sites). At each site we collected data on light levels, stand composition, leaf litter composition and depth, and local deer browsing pressure (using the sugar maple browse index, or SMBI—Frelich and Lorimer, 1985). The SMBI uses sugar maple (*Acer saccharum*), a shade-tolerant, regionally ubiquitous species as a phytometer of deer browsing intensity. The index is based on the number of browsed and unbrowsed terminal sugar maple twigs located 30–200 cm above the ground on 12–20 maple saplings per site. We estimate browsing intensity on a scale from 0 (lowest) to 1 (highest) by taking the ratio of browsed terminal twigs to total number twigs sampled.

We created multiple hemlock and white-cedar seedling height classes, recognizing that limiting factors change as a function of seedling size. We used path analysis, a multivariate procedure, to examine the relative importance of each potentially-limiting factor on hemlock and white-cedar regeneration across all size classes. In both species, regeneration of seedlings > 30 cm tall declined linearly as local browsing pressure increased, and complete regeneration failure occurred where browsing pressure was greatest (Waller et al., 1996; Rooney et al., 2000, 2002). Because light levels and microtopography can limit the number of seedlings, reductions in deer browsing alone may not necessarily translate into greater regeneration.

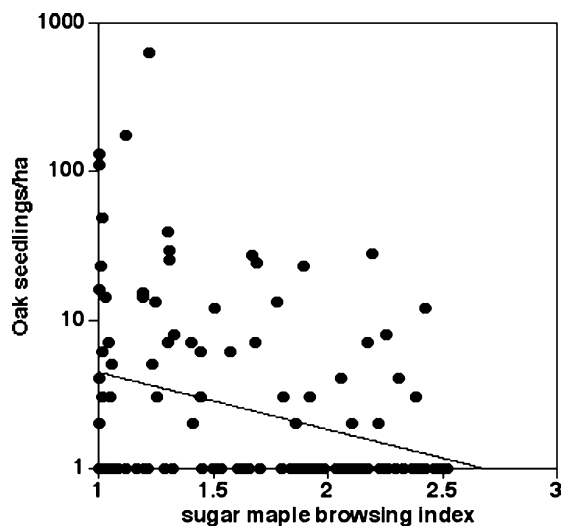We recently examined the effects of deer browsing on two deciduous species, red oak (*Quercus rubra*) and

Fig. 1. The relationship between the density of red oak seedlings per hectare (*y*) and the local deer browsing pressure (*x*). $\ln y = 2.38 - e^{0.89x}$ ($n = 119$; $r^2 = 0.10$; $P < 0.001$).

yellow birch (*Betula alleghaniensis*). Unlike evergreens, these species are browsed in the spring and summer. We tallied the number of seedlings 4–300 cm tall present in two 49 m² plots at 119 stands containing red oak, and 88 stands containing yellow birch. Red oak seedling density varies in response to local deer browse (estimated via the SMBI, Fig. 1). Seedling densities drop precipitously as browsing pressure increases from low to intermediate, indicating that red oak regeneration is strongly limited by deer. In contrast, yellow birch seedling density did not show a consistent relationship with the SMBI. However, when we substituted 1991 deer density estimates from the Wisconsin Department Natural Resources (unpublished data, based on the sex-age-kill model) for the SMBI as an alternate measure of browsing intensity, an interesting pattern emerged. Seedling densities were highest at intermediate deer densities, and lowest for very low or very high deer densities (Fig. 2). Given that the seedling size classes span almost two orders of magnitude, it is not surprising that the relationships we report are weak. More detailed work on the regeneration ecology of these species, perhaps following the methods we used for hemlock and white-cedar, would allow us to better understand how important deer browsing is. Because results from exclosure and deer-free island studies indicated deer browsing suppressed regeneration of red oak and
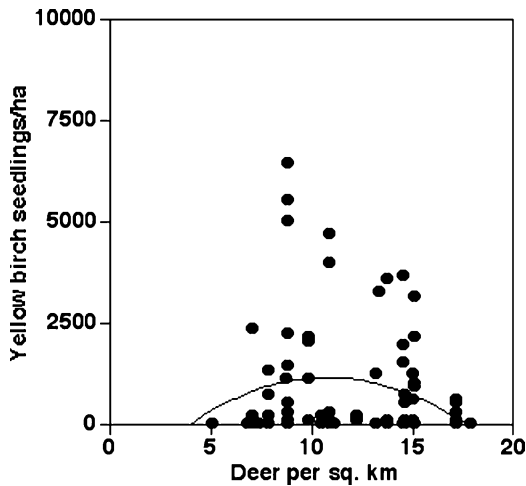
Fig. 2. The relationship between the density of yellow birch seedlings per hectare (y) and the density of deer per km^2 (x) within Wisconsin deer management units. $\ln y = -0.68x^2 + 1.48x - 3.27$ ($n = 88$; $r^2 = 0.07$; $P = 0.045$).

yellow birch (Graham, 1954; Beals et al., 1960), ecologists and foresters have overlooked the potential for non-linear relationships. We suspect that non-linear relationships between seedling densities and browsing intensity are common but remain undetected in geographically-restricted studies.

2.2. Forest herb communities

While most published research on deer impacts focuses on trees, understory herbs comprise most of the vascular plant diversity in temperate and boreal forests. For example, the northern mesic forests in our study area have 27 native tree species, and at least 254 vascular herbaceous plants (Curtis, 1959). Herbs may also be more vulnerable to ungulate browsing as they never grow large enough to escape browsing impacts. Browsing can reduce both growth and reproduction of individual herbs like *Trillium* (Rooney and Waller, 2001). Studies using natural exclosures (Rooney, 1997) or deer-free islands (Balgooyen and Waller, 1995) reveal that deer directly reduce the abundance of browse-sensitive herbs. In addition, plant responses may be density or frequency dependent. Augustine et al. (1998), for example, found that *Laportea* (Urticaceae) plants in stands with low initial densities are more likely to decline and be extirpated than plants occurring in stands with high initial densities.

Studies like those just mentioned are sometimes criticized on the grounds that the deer effects they document could be local. We therefore conducted a spatially extensive analysis of deer impacts on understory herbs. Rather than survey sites randomly, we revisited (in 2000–2001) 51 dispersed forest stands that had been surveyed by John Curtis and colleagues in the 1940s and 1950s as part of their research on the plant communities of Wisconsin (Curtis, 1959). Our study was designed to analyze current patterns of community structure, and use the historic data to provide a baseline for charting subsequent change. Curtis sampled understory herbs present in $20 \times 1\,m^2$ quadrats. Because we considered this inadequate for rarer species, we surveyed herbs over $120 \times 1\,m^2$ quadrats at each site. We further characterized sites

Table 1
Documented impacts of ungulate feeding on vascular forest plants that have been observed

Ungulate activity	Citation	Organisms potentially affected
Leaves and stems		
Consumption of leaves	Alverson and Waller (1997)	Herbivorous insects, slugs, plant pathogens
Consumption of stems	Augustine et al. (1998)	Stem-galling insects, sucking insects
Suppress future plant size	Rooney and Waller (2001)	Same as above
Flowers, fruits, and seeds		
Consumption of flowers	Balgooyen and Waller (1995)	Nectar- and pollen-feeding animals
Consumption of dry fruits	McShea and Rappole (1992)	Granivorous animals, seed pathogens, ants
Consumption of fleshy fruits	Sargent (1990)	Frugivorous animals, fruit pathogens
Suppress future reproduction	Rooney (1997)	Same as above
Roots		
Suppress fine root biomass production	Kielland et al. (1997)	Mycorrhizal fungi, nematodes, insects

The citations and the list of organisms potentially affected (modified from Crawley, 1983) are not exhaustive.

based on soil nitrogen, successional stage, and local deer browse intensity (SMBI). We used Simpson's Dominance Index (D) as our measure of diversity (Magurran, 1988): $D = \sum p_i^2$, where p_i is the proportion of the ith species, based on the relative number of quadrats occupied by each species. As D increases, the diversity within a community declines, reflecting dominance by a few species. We used stepwise multiple regression with backward elimination to examine relationships between D and soil nitrogen, successional stage, and deer browsing (measured using the SMBI). By analyzing multiple factors across a broad geographic area, we hoped to draw robust conclusions about how abundant deer affect understory herb communities.

Stepwise multiple regression indicated that D was not related to either successional stage ($P = 0.74$) or soil nitrogen ($P = 0.37$). However, D increases linearly with local browsing intensity ($r = 0.285$; $P = 0.043$), suggesting that abundant deer directly reduce forest understory herb diversity. We also expected that graminoids and ferns might increase with local deer browsing intensity (Coughenour, 1985; Gill, 1992; Rooney, 2001). Regression analysis indicates that this is indeed the case: the proportion of graminoids and ferns increases with estimated browsing intensity ($n = 51$; $r = 0.293$; $P = 0.037$). Thus, as local deer browsing increases in mixed coniferous–deciduous forest stands, understory herb community diversity declines, while ferns, grasses, sedges, and rushes become increasingly dominant.

We gained further insight into deer browsing impacts by examining long-term changes in diversity and the pattern of species abundance in two stands. These stands are both located in different state parks (Brunet Island State Park and Gogebic State Park), where deer hunting is prohibited. Consequently, deer are more abundant in both parks than in the surrounding landscape. Between 1950 and 2000, Simpson's Dominance Index increased from 0.061 to 0.245 in Brunet Island State Park, and from 0.078 to 0.256 in Gogebic State Park. At both sites, the number of species present in at least 5% of sampled quadrats declined from 24 to 6 between the two time periods. Rank-abundance plots indicate both communities have shifted over the past 50 years towards a simpler community structure (Fig. 3). The proportion of graminoids and ferns also increased from 22 to 91%
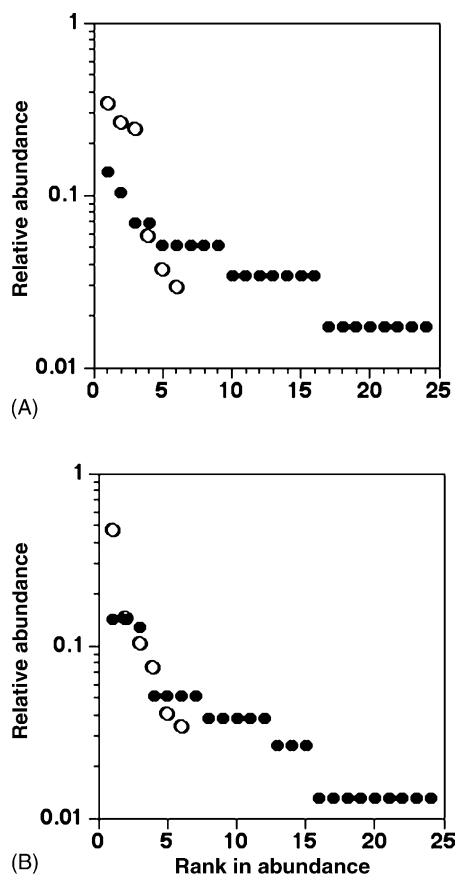

Fig. 3. Rank abundance plots indicating the change in species abundance between 1950 (dark circles) and 2000 (open circles) in Brunet Island State Park (A) and Gogebic State Park (B).

(Brunet Island) and from 23 to 61% (Gogebic). While such evidence is circumstantial, these changes are entirely consistent with the types of changes that we expect when understories face high deer densities (Gill, 1992; Rooney, 2001).

3. Ungulate browsing and indirect effects

Indirect effects arise in ecosystems when the influence of one species is transmitted through a second species or biotic habitat feature to a third "receiver species" (Morin, 1999). By feeding on plants, ungulates can exert indirect effects on receiver species through food web interactions, or by modifying the structure of habitats. There have been relatively few

studies of these indirect effects, but they illustrate the far-reaching and sometimes counterintuitive effects ungulates have in ecosystems. For example, changes in plant diversity affect insect species diversity, because plant and insect diversity are often positively correlated (Murdoch et al., 1972; Haddad et al., 2001). Thus, losses in forest–herb diversity are likely to cause declines in insect species diversity, particularly among monophagous herbivores or specialist pollinators (Blakley and Dingle, 1978). Because insects and vascular plants represent two of the most diverse taxonomic groups known and 70% of all described species (Wilson, 1988), high deer densities appear to represent a clear and present threat to biological diversity.

3.1. Food web interactions

3.1.1. Mediation of plant–herbivore interactions

Ungulates potentially interact with many other organisms that feed on plant tissues (Table 1). These interactions can range from competition and to amensalism and commensalism. However, interactions between ungulates and other herbivores remain poorly documented, and the significance of ungulates as a determinant of herbivore community composition and structure is unknown.

Competition occurs when ungulates and other herbivores share a common food resource. In the Scottish Highlands, Baines et al. (1994) observed in an exclosure study that red deer (*Cervus elaphus*) reduce the average height of bilberry (*Vaccinium myrillus*) plants. The abundance of Geometrid moth larvae was four times greater inside exclosures, suggesting competition between deer and larvae for a shared food resource. In England, preferred browse species of trees (*Quercus*, *Salix*, *Populus*) also support high diversities of insect herbivores (Stewart, 2001), but the impacts of deer on these insect herbivores have not been examined.

Herbivores can alter resource quality for other herbivores via sequential herbivory. Herbivory can induce the production of secondary metabolites (Vourc'h et al., 2001), but these induced responses often exhibit low specificity against other herbivores, making it difficult to make generalizations about how induction affects plant quality (Karban and Myers, 1989). In a Minnesota old field, white-tailed deer avoided browsing on smooth sumac (*Rhus glabra*) ramets that were damaged in the

previous season by chrysomelid or cerambycid beetles (Strauss, 1991). However, these beetles attacked ramets independent of deer browsing on those ramets in the previous season. This result indicates an amensalism with the ungulate being adversely affected. Commensalism has also been observed. Moose browsing increased the proportion of juvenile shoots of the willow, *Salix novae-angliae*. These young shoots supported higher densities of two species of sawflies than older shoots (Roininen et al., 1997). At high densities, ungulates can reduce willow abundance (Singer et al., 1994, 1998), and potentially offset this benefit.

3.1.2. Mediation of plant–plant interactions

Because they feed preferentially on some plants and avoid others, and because some plants compensate for herbivory whereas others do not, ungulates alter the relative competitive ability of plants within a community. Plants avoided by deer and/or able to compensate in response to herbivory have a competitive advantage over those plants preferred by deer and/or unable to compensate in response to herbivory (Augustine and McNaughton, 1998). Over time, we expect the relative abundance of browse-tolerant species to increase in the community, and browse-intolerant species to decline.

In deciduous forest understories, graminoids and ferns benefit from heavy browsing pressure (Gill, 1992; Cooke and Farrell, 2001; Kirby, 2001; Rooney, 2001). Many (though not all) ferns are avoided, possibly because of leaf tissue chemistry (Rooney and Dress, 1997). Most graminoids have basal meristems and silica in their leaves, making them relatively tolerant of herbivory (Coughenour, 1985). However, some woodland graminoids decline in response to ungulate grazing (Kirby, 2001) indicating variation in susceptibility within this group. Because ferns and graminoids have relatively few insect herbivores and provide no nectar or pollen resources, their increase could cause invertebrate species richness to decline (Stewart, 2001).

Sustained browsing pressure on tree seedlings and saplings will affect forest canopy structure and composition. Frelich and Lorimer (1985) modeled the long-term effects of deer browsing on forest canopy composition in Porcupine Mountains State Park, Michigan. They predict that continued regeneration failure in eastern hemlock will cause it to decline as a major canopy dominant within the next 100–150 years. Moose browsing can similarly shift boreal

forests, causing balsam fir (*Abies balsamea*) to decline and white spruce (*Picea glauca*) to increase (McInnes et al., 1992). A forest succession model of white pine (*Pinus strobus*) stands in northwestern Minnesota revealed that white-tailed deer browsing represents a major impediment to restoration (Tester et al., 1997). White-tailed deer browsing can also reduce the time required for browse-tolerant, late-successional species to dominate the forest canopy (Seagle and Liang, 1997). Sustained browsing, however, can also contribute to more widespread failures in tree regeneration and thus a shift to sparser stands both directly by reducing the density of tree seedlings and indirectly by favoring grasses, sedges, and ferns that inhibit tree seedling success (Stromayer and Warren, 1997).

3.1.3. Ungulates as predators and scavengers

Ungulates are occasionally predatory, thereby creating direct predator–prey linkages with some species. Incidental predation occurs when ungulates consume other herbivores while foraging on plants. Deer and moose both consume lepidopteran eggs (Eliasson, 1991; Dempster, 1997). Egg-laying behavior in the white admiral (*Ladoga camilla*) appears subject to selection, and where browsing pressure is sufficiently high, females are laying eggs above browse lines (Pollard and Cooke, 1994). Other insect herbivores, such as leaf miners, are probably incidentally consumed by ungulates regularly. White-tailed deer occasionally prey on songbirds and songbird eggs (Sealy, 1994; Pietz and Granfors, 2000), although the relative importance of deer compared to other nest predators is unknown.

There have been accounts of deer scavenging on fish. Many of these incidents appear isolated and opportunistic, like an account of three white-tailed deer eating salmon (Shea, 1973). During the late-spring alewife (*Alosa pseudoharengus*) die-off in Lake Michigan, numerous deer feed on the fish as they wash ashore on Manitou Island (Case and McCullough, 1987). Here, deer potentially compete with other scavengers for these protein rich resources.

3.2. Habitat modification

3.2.1. Altered vegetation structure

When ungulate browsing reduces vegetative cover in the forest understory layer, the forest floor microclimate is altered. Soil moisture and humidity decline, while temperature and light increase. Gastropods appear adversely affected by the microclimatic changes created by ungulate browsing (Suominen, 1999), but ground-dwelling beetles benefit (Suominen et al., 1999). The loss of cover may increase avian predation on small mammals (as well as mammal predation on bird nests), driving population declines (Flowerdew and Ellwood, 2001; Suda et al., this volume). Other species may benefit from the decrease in vegetative cover. Solitary bees and wasps require patches of bare ground for nesting sites, and the southern wood ant (*Formica rufa*) show a positive numerical response to such bare patches (Stewart, 2001).

By reducing the density of the shrubs and saplings, browsing can also reduce vertical complexity in forest stands (deCalesta, 1994; McShea and Rappole, 2000; Fuller, 2001). In North America, such reduced vertical complexity reduces the abundance and diversity of shrub-nesting birds (deCalesta, 1994) and the densities of migrant birds (McShea and Rappole, 2000). Shrub-nesters also declined over a 30 year period in Wytham Woods, England, as deer populations increased (Perrins and Overall, 2001). Fuller (2001) notes that because >60% of woodland passerines in Britain nest and/or feed in the shrub and ground layer, ungulates may play a key role in structuring avian communities.

3.2.2. Altered nutrient cycling

Plant community composition and the decomposition of soil organic matter are linked through plant tissue chemistry (Pastor and Naiman, 1992). By allowing browse-tolerant species to increase in abundance, ungulate browsing can favor browse-tolerant species whose leaves often have high lignin concentrations and/or high C:N ratios (Hobbs, 1996; Augustine and McNaughton, 1998). Such leaves are mineralized more slowly (Pastor and Naiman, 1992) causing litter to accumulate. Alternatively, we can infer that ungulates increase mineralization rates in forests where they shift canopy composition from conifers to hardwoods (Frelich and Lorimer, 1985). Nitrogen mineralization rates are lower beneath forest canopies dominated by eastern hemlock than those dominated by sugar maple (Mladenoff, 1987), probably because the lignin/N ratios of hemlock leaf litter relative to hardwood leaf litter (Ferrari, 1999). By altering the mineralization rate, ungulates affect site fertility, creating positive or negative feedbacks favoring or

undermining the persistence of other understory and canopy species.

4. Future directions

We think answers to the following questions will improve our understanding of direct and indirect ungulate impacts. While space limitations prevent us from exploring all of these questions in detail, we hope that other researchers follow these lines of inquiry.

4.1. How can we best measure and represent ungulate impacts?

We have numerous examples of how ungulates affect particular species, but fewer attempts to develop indicators of browsing intensity that land managers can use to assess local browsing damage. Many managers recognize "browse lines" as an indicator of ungulate impacts, but by the time browse lines appear, impacts are well underway. In other words, the browse line is a 'lagging' indicator. Several potential "early warning" or 'leading' indicators have been developed, such as the sugar maple browse index (Frelich and Lorimer, 1985), flower scape height in *Clintonia borealis* (Balgooyen and Waller, 1995), and average stem height in *Trillium grandiflorum* (Anderson, 1994). An increase in the relative abundance of graminoids (relative to all other species) might also serve to indicate increasing ungulate impacts. We also advocate using experimental plantings of plants sensitive to browsing (e.g. lillies or orchids) as 'phytometers' of continuing deer impacts. Such phytometers could be useful for sites that have already lost their native indicator species and to 'test the water' before attemtpting any more comprehensive ecological restoration. Ultimately, we would like to see managers using a comprehensive suite of reliable indicators to monitor browsing impacts (Waller and Alverson, 1997).

4.2. How dependent are ungulate impacts on initial plant and initial ungulate densities?

Ungulate impacts can be a function of both ungulate densities and the initial densities of impacted species. Noy-Meir (1975) and Augustine et al. (1998) demon-strate that plant densities can exhibit two stable states in response to browsing pressure, with that state determined by both initial herbivore and plant densities. For example, browse-sensitive plant populations are most likely to be extirpated when initial plant densities are low, even if ungulate densities are not very great (Augustine et al., 1998). At high ungulate densities, some plants may be browsed to extinction, regardless of their initial densities (Noy-Meir, 1975). At this point, it is not known if the phenomenon of alternate stable states in plant–ungulate interactions is widespread.

4.3. Which species emerge as "winners" or "losers" in heavily-browsed landscapes? what characteristics or traits make species susceptible to ungulate herbivory?

There is a rich and growing literature on species that increase or decline in response to ungulate browsing and grazing (winners and losers, respectively, in the lexicon of McKinney and Lockwood, 1999). The species-by-species approach to identifying winners and losers is inefficient and offers little predictive power. We think grouping plants by shared characteristics (i.e. guilds or functional groups) or traits will increase our ability to anticipate the response of unstudied organisms to increases in ungulate densities. Plant characters showing promise include: taxonomic grouping (Morecroft et al., 2001; Miller et al., 1992), herb stature (Kirby, 2001) and foliage lignin:N ratios (Augustine and McNaughton, 1998). Bird guilds based on vegetation strata-based feeding and nesting guilds also show promise (deCalesta, 1994; Fuller, 2001).

4.4. How do ungulates affect patterns of diversity and relative abundance in forest communities? at what densities do deer and other ungulates threaten diversity in forest ecosystems?

The relationship between diversity and increased ungulate density can be complex as responses can be non-linear and some species invariably decline whereas others increase. There may also be confusion in interpreting results from exclosure studies. Because exclosures eliminate ungulates from a study plot, they create conditions that exist largely outside of the

natural range of variation of ungulate densities. While exclosures clearly and graphically demonstrate how ungulates can affect vegetation structure and composition, they can also be misleading when the relationship between ungulate density and the dependent variable is non-linear. For example, taxon richness or some other idealized response variable may change in various ways along an ungulate density gradient (Fig. 4). Curves A and C represent obvious losers and winners, respectively. Curve B, however, shows a negative quadratic response along the same gradient. Ungulate effects may be obscured if overall taxon richness or evenness within exclosures resemble those at intermediate or high ungulate densities.

A second source of confusion occurs when researchers assume that exclosures create the conditions that would occur without browsing. In fact, exclosures illustrate recovery of plots from browsing. Because the browsing history of the plot is not eliminated, changes in the plot will be strongly influenced by local species pools and seed banks (which may have already been depleted from chronic browsing). Finally, exclosure studies tend to treat ungulate browsing as binary (control plot versus exclosure) when in fact, browsing should be treated as a continuous
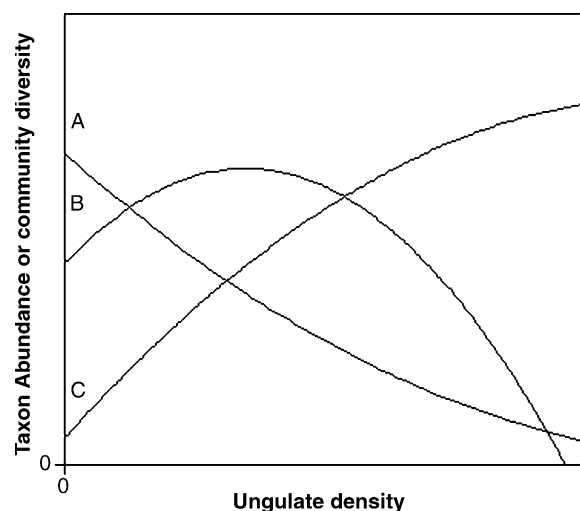

Fig. 4. The change in taxa abundance or community diversity along an ungulate density gradient. Curve A is an idealized representation of taxa or communities that are adversely affected by browsing, and Curve C represents taxa or communities that benefit. Curve B represents taxa or communities that benefit from intermediate ungulate densities.

variable. Exclosure studies should therefore be combined with knowledge regarding how gradients in ungulate density affect various elements of diversity. For example, Alverson and Waller (1997) combine data from replicated exclosures distributed across a gradient of deer densities to infer how variable deer densities (estimated from pellet counts) affect the growth and survival of eastern hemlock seedlings. As expected, the difference in seedling heights between exclosures and paired control plots increased with increased deer density.

4.5. What are the pathways by which ungulates exert indirect effects on species, and how significant are these indirect effects?

While ecologists have been quick to detect the direct ungulate impacts on forest communities, we are just beginning to appreciate the magnitude and extent of the various indirect effects they have. These indirect effects might account for significant changes in community structure and composition. Reviewing studies in rocky intertidal communities, Menge (1995) examined how direct (i.e. predation, grazing, competition, facilitation) and indirect (i.e. keystone predation, indirect mutualism or commensalism, apparent competition) species interactions affected food web structure. Because the data analyzed were not from a single region, organisms (whelks, mussels, algae) were grouped by trophic level. He found that regardless of the type of experimental manipulation, both direct and indirect effects made roughly equal contributions to observed changes in community structure. The relative importance of indirect effects in terrestrial systems is not well understood, but we would be foolish to assume that they are insignificant. We know that ungulates can give rise to indirect effects through food webs or habitat modification, but we do not know how important these indirect effects are in structuring ecological communities.

5. Parting remarks

Paine (2000) noted many similarities between the role of predators in structuring littoral communities and the role of large mammals structuring terrestrial systems. Littoral predators and large mammals are

both "strong interactors" in the sense that they can generate indirect effects, trophic cascades, and alternate stable states in their respective communities. If Paine is correct, and the same general processes play a role in structuring kelp forest, rocky intertidal, and temperate forest communities, we should consider two points carefully. First, we should heed Paine's (2000) call to look for similarities between ungulate–herbivore systems and littoral predator–consumer–producer systems. By doing so, we might make some critical advances. Second, if we ignore the keystone effects of ungulates in temperate and boreal forest communities, we risk losing the suite of species and processes needed to maintain ecosystem function.

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