Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities?

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Abstract The concept of an alternate stable state (i.e., a stable condition in an ecological community at a different stage than that which would be predicted, based on the prevailing ecological and successional conditions) has been examined in recent reviews in the literature of rangeland vegetation communities. This concept also may be useful for understanding the impacts of white-tailed deer (*Odocoileus virginianus*) browsing on woody-plant communities. Our review of the literature revealed at least 3 mechanisms whereby deer can create such states. We present an example of an apparent alternate stable state created by deer, as well as several examples of suppressed forest regeneration that may be precursors to such a state. Evidence suggests that deer may create alternate stable states in woody plant communities of the eastern United States. The trend of increasing deer populations in many parts of the eastern United States suggests that the ecological effects of deer on plant communities may intensify in the future.

Key words alternate states, biodiversity, browsing, eastern United States, habitat fragmentation, *Odocoileus virginianus*, overabundance, plant communities, regeneration, tree seedlings, white-tailed deer, woody vegetation

Steadily increasing populations of white-tailed deer (*Odocoileus virginianus*) and their ecological impacts in the eastern United States have catalyzed a lively discussion on the management of biotic resources in ecosystems (Underwood and Porter 1991, Warren 1991, Porter et al. 1994). At the heart of the debate is whether current deer populations represent a normal fluctuation in a long-term dynamic equilibrium between herbivore and vegetation or a system out of synchrony with normal checks and balances (Caughley 1981). We examine some of the literature describing deer browsing impacts on woody vegetation in the eastern United States with the following questions in mind: Is there evidence that deer are causing alternate stable states in woody vegetation communities in this region? Are these deer-induced changes in vegetation communities no more than suppressed regeneration that can be reversed by reducing deer densities, or are they evidence of alternate stable states that may require more diverse, extensive, and costly management and restoration efforts?

The theory that an ecological system may have >1 domain of attraction where it can persist in a changed configuration was discussed by Holling (1973). May (1977) reviewed the substantial evidence that many natural communities and ecosystems have multiple stable states. Communities with >1 stable state have been examined primarily in marine (Sutherland 1974, Barkai and McQuaid 1988) and rangeland (Noy-Meir 1975, Hart and Norton 1988, Archer and Smeins 1991) ecosystems. Multiple stable states and thresholds or transitions between these states in the range management literature

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(Westoby et al. 1989, Friedel 1991, Laycock 1991) may be especially relevant to deer-vegetation relationships.

The range management definition of a stable lower successional state (Laycock 1991) or a more degraded successional state (Friedel 1991) implies that once a threshold has been crossed into a lower (more degraded) state, then a return to the former state cannot be accomplished without significant management effort, such as prescribed burning, plowing, or herbicide application (Friedel 1991). Merely reducing or suspending grazing normally will not be sufficient to return a system to the former state (Laycock 1991). The implications for wildlife habitat management and natural resource management in the eastern United States are clear. If the impacts of deer herbivory on eastern vegetation communities can be mitigated by herd reduction, which is analogous to grazing control in the range management context, then natural resource managers in the eastern United States have a simple management challenge. On the other hand, if deer are creating alternate stable states in eastern forest ecosystems, then this threat, coupled with increased habitat fragmentation (Wilcove et al. 1986) and the concomitant invasion of exotic plant species, poses a greater challenge for those attempting to maintain the natural diversity of species and community assemblages in the region.

Studies documenting deer-induced changes to plant species composition (Ross et al. 1970, Mitchell 1975, Marquis 1981, Tilghman 1989), community structure (Hough 1965, Whitney 1984, Michael 1992), and regeneration (Harlow and Downing 1970, Bratton and Kramer 1990, Anderson 1994) cover many forest types (Anderson and Loucks 1979, Bratton 1979, Storm et al. 1989). They arise from different management situations, including national parks (Wright 1992), national forests (Mitchell 1975), and private lands (Bennett 1957) in the eastern United States. In the abundance of literature on this subject, there are regions and forest types where deer-vegetation interactions, particularly the effects of deer browsing on seedling advance regeneration of economically valuable, locally abundant, or otherwise important tree species, have been studied most intensively. Two of these regions are the Allegheny Plateau of northwestern Pennsylvania and the northern forests of the Great Lakes States. Factors contributing to knowledge about deer-vegetation relationships in these regions include: the importance of hardwood silviculture, the large number of national parks and forests, and the steady increases in deer populations since the 1920s. We begin this paper with a review of the literature on both of these intensively studied regions, followed by several particularly relevant studies on other areas of the eastern United States.

A review of the evidence

Evidence from the Allegheny Plateau

The Allegheny hardwood forest type occupies 1.4 million ha of the Allegheny Plateau in northwestern Pennsylvania and produces high-value hardwood timber species such as white ash (*Fraxinus americana*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and black cherry (*Prunus serotina*; McClenahen and Hutnik 1979). These forests are mainly even-aged as a result of widespread clearcutting between 1890 and 1920 (Mitchell 1975). Deer populations in the area grew rapidly between 1915 and 1935 after game laws were adopted to protect deer from overhunting (Marquis and Brenneman 1981). The widespread clearcutting prevalent at this time provided abundant browse and created ideal conditions for the growth of deer populations (Marquis and Brenneman 1981). Bennett (1957) indicated that silvicultural practices in the region exacerbated the deer overpopulation problem. He cited factors favoring understory deer-browse production and creating extremely large amounts of edge (e.g., pulpwood cuts starting at 35–40 years, thinnings each 15–20 years thereafter, and a dense logging road network).

In the last 20 years, deer browsing has been shown to have profound effects on the establishment of regeneration, species composition, and density of hardwood seedlings on the Allegheny Plateau (Marquis 1974, 1981). Some areas have failed to regenerate to tree species following clearcutting even when they were protected from deer browsing by exclosures (Marquis 1974). These regeneration failures have been attributed to inadequate advance regeneration of seedlings due to excessive browsing of the understory by deer, followed by invasion of forest weeds, ferns, and grasses, which further inhibited the growth of tree seedlings (Horsely 1977*a*,*b*; Horsely and Marquis 1983).

Horsely and Marquis (1983) distinguished between the relative contributions of heavy deer browsing and forest weeds to the failure of hardwood regeneration during 2 critical stages of shelterwood cutting. During the first stage of this regeneration method (the seed cut), the understory of the mature stand was thinned to allow vigorous seedling establishment. During the second stage (the removal cut), the overstory was removed to allow the seedlings to grow as quickly as possible out of reach of browsing deer. Deer browsing reduced the density and vigor of hardwood seedlings before and after each cutting. Deleterious effects of forest weeds included prevention of seedling buildup after the seedling cut and reduction of seedling growth after the removal cut.

Marquis and Grisez (1978) noted that once regeneration fails, ecological changes make it increasingly difficult to establish hardwood seedlings. The seed bank usually becomes exhausted 3 or 4 years after clearcutting (Marquis and Grisez 1978), and deer contribute indirectly to the herbaceous-ground-cover stable state by heavily browsing blackberry (*Rubus* spp.) regeneration. Blackberry regeneration interferes with ferns and grasses, thereby facilitating establishment of hardwood seedlings (Horsely and Marquis 1983, Tilghman 1987). Horsely and Marquis (1983) concluded that under the current situation of high deer densities, browsing by deer often results in an alternate stable state of self-perpetuating ferns and grasses. In the absence of deer browsing, hardwood regeneration suppressed by grasses was expected to recover, but that suppressed by ferns was not. Horsely and Marquis (1983) predicted this kind of lower stable state as likely to occur when 70% of sample plots are stocked with >30% ground surface cover of ferns and grasses before the removal cut.

On the Allegheny Plateau, the combined effects of timber harvesting, heavy deer browsing, and competition from forest weeds appear to have produced an alternate stable state in a temperate-zone, hardwood-forest community. This continued hardwood regeneration failure, even after the exclusion of deer, fits the conceptual model for an alternate stable state (Friedel 1991, Laycock 1991). It also agrees with a key prediction of the state-and-transition model of Westoby et al. (1989), that for transitions between 2 states to occur, a combination of climatic or management actions is usually necessary.

Vigorous regrowth of Chinese privet in 1995 at Chickamauga Battlefield Park, Georgia, 3 growing seasons after cutting to ground level despite intense winter deer browsing pressure (≥60% of current year's growth the first year postcutting).

Evidence from the Great Lakes States

Interest in deer-vegetation interactions in the northern Great Lakes States forest regions of Wisconsin, Minnesota, and Michigan first developed out of concerns about regeneration of valuable timber species (DeBoer 1947, Graham 1954, Switzenberg et al. 1955, Stoeckeler et al. 1957). Of the trees found in large areas of the mixed, conifer-hardwood forests characteristic of this region (Blouch 1986), hemlock (*Tsuga canadensis*), white cedar (*Thuja occidentalis*), and yellow birch (*Betula lutea*) are generally considered preferred or second-choice deer browse species that decrease in abundance when subjected to light-to-moderate deer browsing (Stoeckeler et al. 1957). Sugar maple also is a preferred browse species, but it can withstand severe browsing for many years without mortality (Switzenberg et al. 1955, Stoeckeler et al. 1957). Balsam fir (*Abies balsamea*) is seldom browsed and thus is favored by heavy deer browsing on other species (Graham 1954).

Perhaps the best documentation of impacts of deer browsing in this region are studies indicating a displacement of conifers (e.g., hemlock, white cedar, and Canada yew [*Taxus canadensis*]) by hardwoods as a result of selective browsing (Alverson et al. 1988). For example, Beals et al. (1960) studied deer-vegetation interactions on the Apostle Islands in northern Wisconsin and reported that the typical mature understory vegetation of the islands was composed largely of Canada yew, but the yew rapidly disappeared under light-to-moderate browsing pressure.

Studies of deer browsing impacts on regeneration have focused on hemlock, which has declined from being a regional dominant in presettlement times to covering only 0.5% of the landscape today (Mladenoff and Stearns 1993). There was a strong tendency for sugar maple to replace hemlock in areas of high deer density (Anderson and Loucks 1979, Frelich and Lorimer 1985, Alverson et al. 1988). This apparent shift from a mixed hemlock–deciduous forest to a deciduous forest (Graham 1954) was attributed to differential responses of hemlock and sugar maple seedlings to deer browsing (Anderson and Loucks 1979). When terminal shoots of hemlock were browsed, the hemlock's potential for regrowth was greatly reduced (Anderson and Loucks 1979), whereas sugar maple resprouted readily and usually grew out of reach of deer even under yearly browsing pressure (Switzenberg et al. 1955). When deer were abundant, the impact of deer on hemlock regeneration was intensified by deer yarding in hemlock stands during the winter (Blouch 1986). Under these conditions, hemlock seedlings visible above the snow line were browsed heavily and seldom survived to produce a sapling (Mladenoff and Stearns 1993).

Mladenoff and Stearns (1993) examined the trend in declining hemlock regeneration in the Great Lakes States and concluded that many factors were involved in the decline of hemlock as a regional dominant. They suggested that site-specific browsing could have been an important factor limiting hemlock regeneration in some stands but that hemlock life-history characteristics and ecosystem interactions, in addition to climate change, were more significant factors at the regional level. They argued that exclosure studies (frequently cited as evidence of major deer impacts on hemlock regeneration) typically were conducted in locations where dramatic results were anticipated and thus did not provide an unbiased sample of regional trends.

A constellation of factors may have contributed to the regional decline in hemlock abundance, but stand level is the appropriate scale at which to measure the role of deer in creating alternate stable states in hemlock and other habitat types. Extensive browse surveys conducted in northern and central Wisconsin (DeBoer 1947), as well as more recent browse surveys (Frelich and Lorimer 1985) and exclosure studies by Anderson and Loucks (1979) documented severe local suppression of hemlock regeneration. For example, DeBoer (1947) reported successful regeneration of an average 580 hemlock reproductive stems per acre on the Lac du Flambeau Indian Reservation, Wisconsin, where deer were kept to a low density by year-round, either-sex hunting. This situation contrasted with that on the adjacent Northern Highland State Forest where no hemlock regeneration was evident in the talliable height class (>0.3m in height) and where deer densities were greater due to restrictive hunting regulations.

Because of the long lifespan of hemlock and evidence that reproduction may occur periodically at intervals of several decades (Frelich and Lorimer 1985), unequivocal evidence for a deer-induced alternate stable state in this system would require a long-term exclosure study. Suppression of all advance regeneration for even decades is not adequate evidence of an alternate stable state in tree communities where dominant species have life cycles that span centuries. In an experiment by Anderson and Loucks (1979), 12 years of exclosure fencing produced densities of hemlock seedlings several hundred times more abundant than in an adjacent browsed plot. The implication of this study is that elimination of deer herbivory could result in restoration of hemlock regeneration. Thus, in some sites, deer browsing on hemlock may not have resulted in an alternate stable state, but simply a suppression of hemlock advance regeneration.

Evidence from other areas in the United States

Studies from other areas of the eastern United States suggest that if deer are creating alternate stable states, then the likely mechanism is the suppression of regeneration for long periods of time, leading to local extirpation of populations. These cases of blocked regeneration may be interpreted as the necessary precursors to alternate stable states. For example, Little and Somes (1965) reported that a 1954 wildfire that covered 19,500 acres and killed 500 acres of white cedar stands in New Jersey was followed by intensive deer browsing that almost entirely suppressed white cedar regeneration, which had averaged about 150,000 seedlings per acre in 1955. Apparently, the impact of heavy deer browsing was exacerbated by the moss and soupy peat of the swamps in which many browsed seedlings were uprooted (Little and Somes 1965:3). They concluded, "The evidence is incontrovertible that excessive deer browsing is now eliminating Atlantic white cedar from many swamps in the New Jersey Pine Region where the species had maintained itself fairly successfully through three centuries of the white man's cuttings and fires."

Michael (1992) studied the composition of balsam fir stands in the Canaan Valley, West Virginia, and reported that in all but 1 site, sampled deer had browsed the main leaders and side branches of surveyed seedlings. Whereas all stands surveyed had an adequate number of intermediate-sized trees to eventually replace the existing mature trees, Michael (1992) predicted that if balsam fir regeneration in the area continued to be suppressed and in-

A winter browse survey being conducted in 1994 at Chickamauga Battlefield Park, Georgia, to assess the relative use of winter browse species by deer and long-term changes in browse availability. Note the relatively open understory in this well-drained woodland.

termediate-sized trees grew old and died, there would be few small trees to replace them. In this event, balsam fir probably would be replaced by red spruce (*Picea rubens*) because it is one of few tree species in the area not commonly browsed by deer.

Evidence from forest fragments and islands

Forest fragments and islands may be at the greatest risk for loss of tree species from deer browsing. Strole and Anderson (1992) suggested that deer impacts on isolated Illinois forest preserves might favor low-use, shade-tolerant, and browse-tolerant species at the expense of high-use, shade-intolerant species. Based on browse surveys at their study site, they concluded, "The fact that deer have a high preference for white oak (*Quercus alba*) and a low preference for sugar maple (*Acer saccharum*), along with fire exclusion and competition from other low-use, browse-tolerant species, may add to the degradation of a reproducing oak forest," (Strole and Anderson 1992:143).

Deer population ecology studies, including evaluation of deer browsing impacts, have been conducted on the Atlantic Coast barrier islands. Bratton and Kramer (1990) studied tree regeneration on Cumberland Island National Seashore, Georgia, and reported browsing so intense that tree sprouts seldom reached heights >10–12 cm unless protected from herbivores. They concluded that deer browsing was the primary reason for suppression of seedlings, sprouts, and saplings in the live-oak (*Quercus virginiana*) forest on the island. Construction of exclosures produced a dramatic sprout recovery after 1 year. This study was a classic case in which suppression of regeneration by overbrowsing could have produced an alternate stable state.

Conclusions

Our examination of the evidence describing deer-browsing impacts on woody vegetation communities in the eastern United States revealed 3 possible mechanisms (fire followed by deer browsing; clearcutting followed by deer browsing; and sustained, long-term suppression of regeneration approaching local extirpation) for the creation of deer-induced alternate stable states in northern temperate forests. There are other situations in which browsing by deer might combine with effects of climate change or disturbance factors on woody vegetation to create alternate stable states. These would include factors such as bark stripping (Michael 1987, Girard et al. 1993) and seed predation. Such factors might function alone or, more likely, in combination with other perturbations such as herbicide use, timber harvesting, fire, storms, and droughts.

Without careful experimental studies designed to differentiate the impact of deer browsing from other factors such as succession, disease, or climate change, deer-induced changes to vegetation (including the creation of alternate stable states) may go unrecognized. Experimental manipulations of forest habitats followed by monitoring of vegetation response under different deer densities, such as Tilghman's (1989), may be the best approach to determining the role of deer in creating alternate stable states. Hough (1965:373) observed that deer-induced changes to the species composition of forests with long-lived trees might take place so slowly that "many people might deny that the white-tailed deer had any part in this process."

The critical role of deer in the creation of alternate stable states in forest ecosystems may be to suppress advance regeneration that normally would restock a site following release of the overstory. Diverse scientific, economic, aesthetic, and conservation interests call for continued experimental and long-term descriptive research on the role of deer in shaping woody vegetation communities. At the same time, deer impacts may have a profound effect on animal communities (Casey and Hein 1983, deCalesta 1994) and a wide range of herbaceous plants in the forest understory (Miller et al. 1992). These in turn may have indirect effects on species composition, abundance, and structure of forests. Although interactions between deer and woody vegetation have been studied in North America since the beginning of wildlife management (Aldous 1944, Leopold et al. 1947), we have much to learn.

An empirical test?

Is it possible to conduct a test of the deer-induced alternate stable state hypothesis in forest plant communities of the eastern United States? The hypothesis for such an experiment might be stated: Deer have altered the vegetation community so profoundly that a mere reduction or cessation of browsing will not permit a return to the original (previous) state. To properly test this hypothesis might take ≥300 years, given the rate of succession in forest plant communities. The researcher would need to distinguish the role of deer from other environmental variables and their interactions and to consider questions of appropriate scale, methodology, and test design. Wu and Loucks (1995) have argued that ecosystems are hierarchical systems of patches that differ in size, shape, and successional stage; at what size, shape, and successional stage would a test of the deer-induced alternate stable state hypothesis be conducted? Considering such questions, experiments of this type would be complex and only narrow inferences could be drawn from any single experiment.

Because of the complexities inherent in examining the problem of deer creating alternate stable states in forest communities of the eastern United States, we do not suggest detailed experimental designs or research protocols for investigating this issue. Also, we acknowledge that the alternate stable state paradigm may be easier to apply in the context of range communities where browsing and grazing impacts create drastic changes during the course of a decade than in the context of forest communities, where the creation of deer-induced alternate stable states may take centuries. For these reasons, we challenge readers to think critically about the issues we have raised and to consider what actions should be taken, if any, as increasing deer populations continue to impact our fragmented system of forests, refuges, nature reserves, and national parks in the eastern United States.

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