

# Comparative Effects on Plants of Caribou/Reindeer, Moose and White-Tailed Deer Herbivory

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**ABSTRACT.** We reviewed the literature reporting negative or positive effects on vegetation of herbivory by caribou/reindeer, moose, and white-tailed deer in light of the hypothesis of exploitation ecosystems (EEH), which predicts that most of the negative impacts will occur in areas where wolves were extirpated. We were able to list 197 plant taxa negatively affected by the three cervid species, as opposed to 24 that benefited from their herbivory. The plant taxa negatively affected by caribou/reindeer (19), moose (37), and white-tailed deer (141) comprised 5%, 9%, and 11% of vascular plants present in their respective ranges. Each cervid affected mostly species eaten during the growing season: lichens and woody species for caribou/reindeer, woody species and aquatics for moose, and herbs and woody species for white-tailed deer. White-tailed deer were the only deer reported to feed on threatened or endangered plants. Studies related to damage caused by caribou/reindeer were scarce and often concerned lichens. Most reports for moose and white-tailed deer came from areas where wolves were absent or rare. Among the three cervids, white-tailed deer might damage the most vegetation because of its smaller size and preference for herbs.

**Key words:** caribou, forage, herbivory, moose, reindeer, vegetation, white-tailed deer, wolf

**RÉSUMÉ.** À la lumière de l'hypothèse de l'exploitation des écosystèmes (EEH), nous avons examiné les publications qui mentionnent les effets négatifs ou positifs, sur la végétation, du broutement du caribou/renne, de l'orignal et du cerf de Virginie. Cette hypothèse prédit que les impacts négatifs se concentrent dans des endroits où le loup a été éliminé. Nous avons pu énumérer 197 taxons végétaux affectés négativement par les trois cervidés, contre 24 qui profitaient du broutement. Le nombre de taxons végétaux affectés négativement par le broutement du caribou/renne (19), de l'orignal (37) et du cerf de Virginie (141) représentait respectivement 5, 9 et 11 p. cent des plantes vasculaires situées dans les aires de répartition spécifiques des animaux. Chaque cervidé affectait surtout les espèces consommées durant la saison de croissance végétale: lichens et plantes ligneuses pour le caribou/renne, plantes ligneuses et aquatiques pour l'orignal, et plantes herbacées et ligneuses pour le cerf de Virginie. Selon les rapports, ce dernier était le seul cerf qui broutait des plantes menacées ou en voie de disparition. Les études rapportant des dommages causés par le caribou/renne étaient rares et traitaient souvent des lichens. La plupart des rapports sur l'orignal et le cerf de Virginie couvraient des zones où le loup était rare ou absent. Des trois cervidés, celui qui causerait le plus de dommages à la végétation est le cerf de Virginie, en raison de sa taille plus petite et de sa préférence pour les plantes herbacées.

**Mots clés:** caribou, cerf de Virginie, herbivore, loup, nourriture, orignal, renne, végétation

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## INTRODUCTION

Ecologists and plant physiologists have devoted considerable attention to the impact on vegetation of large herbivores, particularly because they capture proportionally more energy than small herbivores do in terrestrial ecosystems (Silva and Downing, 1995). At the individual and species level, controlled studies have considered plant responses to herbivory in terms of biomass, components, and morphology. Tissue loss can stimulate plant production under some conditions (de Mazancourt et al., 1998), although repeated herbivory often reduces plant biomass. In woody

species, plant consumption during the growing season generally reduces production (Hjältén et al., 1993; Canham et al., 1994; Ouellet et al., 1994; Bergström and Danell, 1995; Manseau, 1996; Crête and Doucet, 1998), whereas most of these species can tolerate browsing during dormancy (Aldous, 1952; Krefting et al., 1966; Danell and Bergström, 1989; Hjältén et al., 1993; Canham et al., 1994). Herbivory can modify the chemical composition of plants: hypotheses suggest that some compounds, such as phenolics and terpenoids, represent one of the major mechanisms of woody plant defence against herbivores, although current hypotheses cannot adequately predict plant

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biochemical responses to tissue loss (Koricheva et al., 1998). Herbivory often induces change in the morphology of woody species that may facilitate or hinder future plant consumption (Krefting et al., 1966; Willard and McKell, 1978; Danell and Bergström, 1989; Edenius, 1993; Danell et al., 1994; McLaren, 1996).

At the community level, Caughley (1976) proposed a simple model describing trophic interactions of plants and ungulates, which applies at an ecological time scale. This model predicts reduction and dampened oscillations of plant (and herbivore) biomass after the colonization of a virgin area by ungulates. More recently, the impact of white-tailed deer (*Odocoileus virginianus*) herbivory in predator-free areas has led some authors to suggest that herbivore/plant systems could have two stable steady-state equilibria, one at high and the other at low plant density (Schmitz and Sinclair, 1997; Stromayer and Warren, 1997; Augustine et al., 1998). Extending a hypothesis put forward by Hairston et al. (1960), Oksanen et al. (1981) proposed a model which predicts trophic interactions along gradients of productivity at an evolutionary time scale: the hypothesis of exploitation ecosystems (EEH; see also Oksanen and Oksanen, 2000). According to the EEH, food chains would be reduced to plants and herbivores in unproductive areas, i.e., those producing less than 700 g per m<sup>2</sup> per year, a level of productivity that corresponds to the transition between the boreal forest and the tundra along a latitudinal gradient (Oksanen et al., 1981). Vegetation would then have evolved under strong grazing pressure in unproductive areas. In more productive landscapes, the EEH predicts that predators would have regulated herbivores, relaxing in turn the grazing pressure on plants; thus plants would have been regulated by competition for light, nutrients, and water. In addition, a trade-off would exist for herbivores in productive ecosystems between predator elusion and forage quality, herbivores selecting nutrient-rich forage to minimize digestive tract weight and to maximize agility (Oksanen, 1992). According to the EEH, the removal of predators from productive areas would cause herbivores to be regulated by competition for forage. This would result in strong grazing pressure, particularly on nutrient-rich plants, i.e., community-wide trophic cascades. Although the existence of community-wide trophic cascades has not yet been shown in terrestrial ecosystems, a meta-analysis indicates that trophic cascades represent a common outcome of predator removal at the species level (Schmitz et al., 2000).

North America is an appropriate continent for testing the EEH because natural predators of large mammals have persisted with relatively limited human interference over its northern half. The current distribution of biomass of cervids, the dominant group of large herbivores in North America (Crête, 1999), supports the EEH. In the High Arctic (> 75°N), cervid biomass reaches only 0.7 kg per km<sup>2</sup>. This figure increases to 16 kg per km<sup>2</sup> on the southern islands of the Canadian Arctic Archipelago (between ≈ 70°N and 75°N), and to 106 kg per km<sup>2</sup> in the continental Northwest Territories

and northern Québec, where the large Canadian herds of migratory caribou are located. Farther south, in more productive systems, cervid biomass averages 62 kg per km<sup>2</sup> throughout the boreal and mixed forests of Canada where gray wolves (*Canis lupus*) and bears (*Ursus americanus*, *U. arctos*) have remained present, but 299 kg per km<sup>2</sup> at the same latitudes when wolves are absent or recolonizing (Crête, 1999). Similar or higher biomasses of free-ranging cervids occur in Fennoscandia with insignificant predator numbers (Pullianen, 1980; Skogland, 1986; Sagør et al., 1997; Angelstam et al., 2000). South of the wolf range in North America, cervid biomass shows a direct relationship with primary productivity: densities are highest in the southeast of the continent, where the only cervid present is white-tailed deer (Crête, 1999).

We compared the effects on vegetation from herbivory of three well-studied cervid species: reindeer/caribou (*Rangifer tarandus*), moose (*Alces alces*), and white-tailed deer. Under the assumption of the EEH, we predicted that the occurrence of negative effects of cervid herbivory would be concentrated in areas devoid of natural predators, particularly the gray wolf. Caribou coexist with gray wolves throughout their range except on the Island of Newfoundland and in a few other isolated populations. Moose live in the presence of wolves and bears almost everywhere in Canada west of the St. Lawrence River valley, but not in Newfoundland, the Maritimes, and New England. In the northwestern United States, where wolves are locally recolonizing, they have had a marginal impact on moose for many decades. The ranges of white-tailed deer and wolves overlap only slightly, in southern Canada west of the St. Lawrence River valley. Bears and wolves have been kept at very low density in Fennoscandia for many decades (Pullianen, 1980; Sagør et al., 1997).

## METHODS

We searched the literature for studies reporting effects of caribou (reindeer), moose, and white-tailed deer herbivory on vegetation found within their natural distribution, which excluded islands of the South Atlantic. We separated plant species into five groups: lichens and mosses, aquatics, other herbs, woody plants with terminal bud within reach of herbivores (≈ 1.5 to 3 m depending on cervid species and season), and woody plants with terminal bud out of reach. For each reference, we noted by species (or in some cases by genus) whether herbivory (a) had a positive or negative influence on plant attributes (i.e., coverage, height, biomass, density, and survival); (b) caused damage (topping, bark stripping, or death); or (c) threatened plant existence locally. When reports compared browsed and unbrowsed sites, we took only those species for which a significant difference existed; otherwise, we accepted the authors' opinion. We mapped the location of each study area, but considered separately each of multiple publications originating from the same site. To compare the three cervid species on the same basis, we divided the

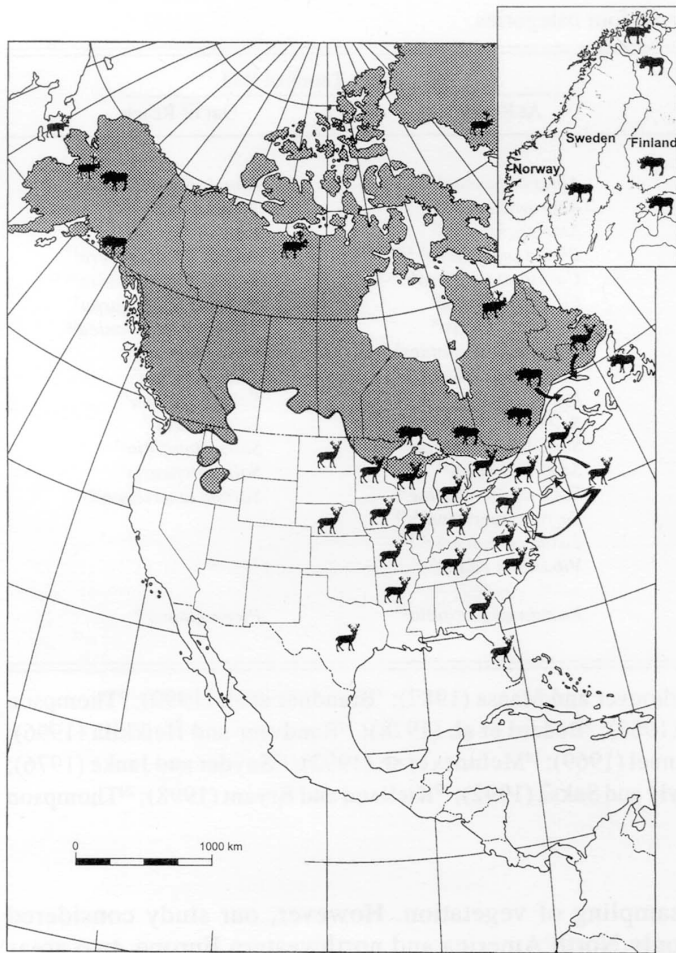


FIG. 1. Location of study areas in which effects of caribou/reindeer, moose and white-tailed deer herbivory on plants were reported. Symbols identify the species (moose facing left, caribou facing right, white-tailed deer facing forward). The shaded area represents the current distribution of the gray wolf in North America.

number of vascular plant species that each cervid negatively affected by the estimated number of plants growing in the centre of its range, taking these estimates from Barthlott et al.'s (1996) map. We selected values of 250 vascular plants within the central range for caribou/reindeer, 400 for moose, and 1250 for white-tailed deer.

RESULTS

We found nine records of caribou/reindeer affecting vegetation from five areas: Alaska, a small island in the Northwest Territories, northern Québec, Greenland, and northern Fennoscandia (Fig. 1). Within the range that moose share with established wolf populations (Fig. 1), we found two reports from Alaska, six from Isle Royale (Michigan), one from Ontario, and one from southern Québec. Outside the wolf range or in lightly populated areas, we found 10 reports, which came from southeastern Québec, Newfoundland, Sweden, Finland, and Estonia. The 25 reports concerning white-tailed deer came from 24

TABLE 1. Number of plant species negatively (or positively) affected by the browsing of three cervid species in North America and Fennoscandia and type of impact on those plant species, as reported in the literature. In some cases, only the genus was specified.

	Caribou/Reindeer	Moose	White-tailed Deer
<b>Trees and Shrubs</b>			
Out of reach	0	14(0)	1(0)
At reach	7(0)	16(2)	46(3)
<b>Herbs</b>			
Terrestrial	5(2)	1(2)	93(5)
Aquatic	0	6(0)	0
<b>Lichens/mosses</b>			
	7(5)	0	1(0)
<b>Type of Effect</b>			
Coverage	18(5)	0(2)	26(4)
Density	0	9(1)	11(3)
Height	0	14	13(3)
Biomass	7(2)	7(1)	6
Bark/top	0	10	1
Survival	0	7	0
Conservation	0	0	98

TABLE 2. Plants in three broad groups (non-vascular, herbaceous, and woody) negatively or positively affected by caribou/reindeer herbivory, as reported in the literature.

Non-vascular	Herbaceous	Woody
<b>Negative Effects</b>		
<i>Cetraria nivalis</i> <sup>1</sup>	<i>Eriophorum vaginatum</i> <sup>2</sup>	<i>Betula glandulosa</i> <sup>2,3,4</sup>
<i>Cladina arbuscula</i> <sup>7,8</sup>	<i>Oxytropis nigrescens</i> <sup>8</sup>	<i>Caluna vulgaris</i> <sup>2,6</sup>
<i>Cladina stellaris</i> <sup>1,3,5,6</sup>	<i>Pedicularis sudetica</i> <sup>8</sup>	<i>Empetrum nigrum</i> <sup>2,3,6</sup>
<i>Cladina mitis</i> <sup>1</sup>	<i>Rubus chamaemorus</i> <sup>3</sup>	<i>Salix herbacea</i> <sup>3</sup>
<i>Cladina rangiferina</i> <sup>1</sup>	<i>Solidago macrophylla</i> <sup>3</sup>	<i>Salix planifolia</i> <sup>3</sup>
<i>Stereocaulon paschale</i> <sup>1</sup>		<i>Vaccinium vitis-idaea</i> <sup>3,6</sup>
<i>Sphagnum</i> sp. <sup>3</sup>		<i>Vaccinium uliginosum</i> <sup>2</sup>
Lichens sp. <sup>2,3,9</sup>		
<b>Positive Effects</b>		
<i>Cladina arbuscula</i> <sup>5,6</sup>	<i>Carex bigelowii</i> <sup>1</sup>	
<i>Cladina rangiferina</i> <sup>5,6</sup>	<i>Festuca ovina</i> <sup>1</sup>	
<i>Dicranum</i> sp. <sup>5,6</sup>		
<i>Pleurozium schreberi</i> <sup>6</sup>		
Mosses sp. <sup>2,3</sup>		

<sup>1</sup> Oksanen (1978); <sup>2</sup>Henry and Gunn (1991); <sup>3</sup>Manseau et al. (1996); <sup>4</sup>Crête and Doucet (1998); <sup>5</sup>Väre et al. (1995); <sup>6</sup>Väre et al. (1996); <sup>7</sup>Pegau (1975); <sup>8</sup>Klein (1987); <sup>9</sup>Thing (1984).

jurisdictions where long-established wolf populations were absent.

Caribou/reindeer, moose, and white-tailed deer negatively affected 19, 37, and 141 plant taxa respectively, as compared to 7, 4, and 8 taxa that took advantage of browsing by the respective cervids (Table 1). Caribou impacted shrubs and lichens/mosses similarly and, to a lesser extent, terrestrial herbs, whereas the majority of plants affected by moose and white-tailed deer were trees/shrubs and herbs, respectively. Caribou and white-tailed deer mostly reduced plant coverage, as opposed to moose, which often reduced plant height and density. With one exception, only moose were reported to be killing some stems and topping and bark stripping trees. White-tailed

TABLE 3. Plants negatively or positively affected by moose herbivory, in four categories.

Herbaceous		Woody with Terminal Bud	
Aquatic	Terrestrial	At Reach	Out of Reach
<b>Negative Effects</b>			
<i>Chara vulgaris</i> <sup>1</sup>	<i>Aralia nudicaulis</i> <sup>2</sup>	<i>Abies balsamea</i> <sup>3, 4, 5, 6</sup>	<i>Alnus sinuata</i> <sup>7</sup>
<i>Characae</i> sp. <sup>8</sup>		<i>Acer spicatum</i> <sup>4, 9</sup>	<i>Picea abies</i> <sup>10</sup>
<i>Nitella flexilis</i> <sup>1</sup>		<i>Amelanchier</i> sp. <sup>9</sup>	<i>Pinus sylvestris</i> <sup>11, 12</sup>
<i>Potamogeton alpinus</i> <sup>1, 8</sup>		<i>Betula papyrifera</i> <sup>3, 4, 6, 13</sup>	<i>Populus balsamifera</i> <sup>17</sup>
<i>Potamogeton epihydrus</i> <sup>8</sup>		<i>Cornus stolonifera</i> <sup>4, 14, 15</sup>	<i>Populus tremuloides</i> <sup>16, 17</sup>
<i>Potamogeton foliosus</i> <sup>8</sup>		<i>Corylus cornuta</i> <sup>9</sup>	<i>Populus trichocarpa</i> <sup>7</sup>
		<i>Pinus sylvestris</i> <sup>18</sup>	<i>Prunus pensylvanica</i> <sup>16</sup>
		<i>Populus tremuloides</i> <sup>3, 4</sup>	<i>Salix alaxensis</i> <sup>7</sup>
		<i>Prunus pensylvanica</i> <sup>6</sup>	<i>Salix barclayi</i> <sup>7</sup>
		<i>Prunus</i> sp. <sup>14</sup>	<i>Salix bebbiana</i> <sup>17</sup>
		<i>Salix alaxensis</i> <sup>19</sup>	<i>Salix lanata</i> <sup>17</sup>
		<i>Salix branchycarpa</i> <sup>19</sup>	<i>Salix planifolia</i> <sup>17</sup>
		<i>Salix lasiandra</i> <sup>19</sup>	<i>Salix sitchensis</i> <sup>7</sup>
		<i>Salix novae-angliae</i> <sup>19</sup>	<i>Sorbus americana</i> <sup>16</sup>
		<i>Sorbus americana</i> <sup>14, 15</sup>	
		<i>Taxus canadensis</i> <sup>4, 15</sup>	
		<i>Viburnum edule</i> <sup>15</sup>	
<b>Positive Effects</b>			
	<i>Melampyrum lineare</i> <sup>15</sup>	<i>Kalmia angustifolia</i> <sup>20</sup>	<i>Picea glauca</i> <sup>15</sup>
	<i>Rubus parviflorus</i> <sup>14</sup>		

<sup>1</sup> Aho and Jordan (1979); <sup>2</sup>Edwards (1985); <sup>3</sup>Pimlott (1963); <sup>4</sup>Risenhoover and Maass (1987); <sup>5</sup>Brandner et al. (1990); <sup>6</sup>Thompson et al. (1992); <sup>7</sup>MacCracken et al. (1997); <sup>8</sup>Fraser and Hristienko (1983); <sup>9</sup>Bédard et al. (1978); <sup>10</sup>Randveer and Heikkilä (1996); <sup>11</sup>Heikkilä (1991); <sup>12</sup>Faber and Thorson (1996); <sup>13</sup>Bergerud and Manuel (1969); <sup>14</sup>McInnes et al. (1992); <sup>15</sup>Snyder and Janke (1976); <sup>16</sup>Desmeules (1968); <sup>17</sup>Miquelle and Van Ballenberghe (1989); <sup>18</sup>Lyly and Saksala (1992); <sup>19</sup>Kielland and Bryant (1998); <sup>20</sup>Thompson and Mallik (1989).

deer were unique in threatening some species, but most cases reported came from a single study based on an interview of state botanists (Miller et al., 1992).

Caribou/reindeer could affect lichens of the genus *Cladina* positively or negatively, depending on browsing pressure (Table 2). Mosses and graminoids often took advantage of caribou herbivory because caribou browsing and trampling can almost completely destroy terrestrial lichens (Thing, 1984; Klein, 1987; Manseau et al., 1996). Two genera were particularly affected by moose, *Potamogeton* among aquatics, and *Salix* among shrubs (Table 3). Moose had very little influence on terrestrial herbs, and very few species benefited from their herbivory. White-tailed deer had a detrimental effect on forest herbs in particular (Table 4), but the importance of their impact might be overestimated, because 80% of the taxa listed came from a single study (Miller et al., 1992). Similarly, 44% of taxa listed for woody plants, the other group impacted by white-tailed deer, were tallied by Miller et al. (1992).

The proportion of vascular plants negatively affected reached 5% for caribou/reindeer, 9% for moose, and 11% for white-tailed deer. However, if we exclude the Miller (1992) study, this last percentage decreases to 3%.

## DISCUSSION

Our evaluation of deer herbivory is likely biased because it relied on the literature rather than on a systematic

sampling of vegetation. However, our study considered only North America and northwestern Europe, two areas where cervids have received much attention for many decades. We believe that the numerous field ecologists working in North America and Fennoscandia have probably detected most cases of severe impacts of deer herbivory. We argue that our literature review describes at least qualitatively the impact of caribou/reindeer, moose, and white-tailed deer on the ecosystems in which they live.

Overall, caribou/reindeer, moose, and white-tailed deer herbivory caused mostly negative impacts on the vegetation, affecting in particular lichens, shrubs, and terrestrial herbs, respectively (Table 1). The results give some support to our prediction that detrimental effects of cervid herbivory would show up mostly in areas devoid of gray wolves. Reports of vegetation damage caused by caribou/reindeer were limited to a few locations. In Alaska, one report referred to introduced reindeer on St. Matthew Island (Klein, 1987) and the other to Nelchina caribou in the early 1970s (Pegau, 1975). The only report from the Northwest Territories (Henry and Gunn, 1991) concerned an unusual situation: a large group of caribou that remained trapped on a small island after spring breakup of the ice was reduced to starvation. The vegetation recovered soon after this browsing episode. Severe impacts of summer herbivory in northern Québec might also represent a special case because of area geography. On the Québec/Labrador peninsula, the preferred summer habitat of caribou, tundra, covers a much smaller area than their

TABLE 4. Herbaceous and woody plants negatively or positively affected by white-tailed deer herbivory.

Herbaceous	Woody
<b>Negative Effects<sup>a</sup></b>	
<i>Abronia macrocarpa</i> <sup>1</sup>	<i>Abies balsamea</i> <sup>1, 3, 4, 5, 6, 25</sup>
<i>Aconitum noveboracense</i> <sup>1</sup>	<i>Acer rubrum</i> <sup>8, 9</sup> <i>saccharum</i> <sup>5, 9, 10</sup> <i>spicatum</i> <sup>3, 11</sup>
<i>Actaea pachypoda</i>	<i>Arctostaphylos uva-ursi</i> <sup>1</sup>
<i>Anemone quinquefolia</i> <sup>7</sup>	<i>Betula alleghaniensis</i> <sup>5, 9, 11</sup> <i>lenta</i> <sup>9</sup> <i>papyrifera</i> <sup>4</sup> <i>uber</i> <sup>1</sup>
<i>Angelica atropurpurea</i> <sup>7</sup>	<i>Chamaecyparis thyoides</i> <sup>23</sup>
<i>Arabis serotina</i> <sup>1</sup>	<i>Cornus rugosa</i> <sup>1</sup>
<i>Aralia nudicaulis</i> <sup>11</sup>	<i>Corylus cornuta</i> <sup>3</sup>
<i>Arisaema triphyllum</i> <sup>1, 7, 24</sup>	<i>Diervilla lonicera</i> <sup>4</sup>
<i>Asclepias meadii</i> <sup>1</sup> <i>ovalifolia</i> <sup>1</sup> <i>verticillata</i> <sup>1</sup>	<i>Dirca palustris</i> <sup>1</sup>
<i>Astragalus robbinsii</i> <sup>1</sup>	<i>Evonymus americanus</i> <sup>1</sup> <i>atropurpureus</i> <sup>1</sup> <i>obovatus</i> <sup>1</sup>
<i>Chamaelirium luteum</i> <sup>1</sup>	<i>Fraxinus americana</i> <sup>1</sup>
<i>Cirsium pitcheri</i> <sup>12, 13</sup>	<i>Iliamna remota</i> <sup>1</sup>
<i>Cladrastis lutea</i> <sup>1</sup>	<i>Larix laricina</i> <sup>6</sup>
<i>Claytonia virginica</i> <sup>10</sup>	<i>Lindera melissifolia</i> <sup>1</sup>
<i>Clematis socialis</i> <sup>1</sup>	<i>Litsea aestivalis</i> <sup>1</sup>
<i>Clintonia borealis</i> <sup>11</sup>	<i>Lonicera polypetala</i> <sup>1</sup>
<i>Coelogyne viride</i> <sup>1</sup>	<i>Mitchella repens</i> <sup>14</sup>
<i>Corallorrhiza trifida</i> <sup>1</sup>	<i>Neviusia alabamensis</i> <sup>1</sup>
<i>Corydalis sempervirens</i> <sup>1</sup>	<i>Populus grandidentata</i> <sup>15</sup>
<i>Croonia pauciflora</i> <sup>1</sup>	<i>Prunus pennsylvanica</i> <sup>3</sup> <i>pumila</i> <sup>1</sup> <i>serotina</i> <sup>8</sup>
<i>Cypripedium acaule</i> <sup>1</sup> <i>candidum</i> <sup>1</sup> <i>reginae</i> <sup>1</sup>	<i>Quercus buckleyi</i> <sup>22</sup> <i>ellipsoidalis</i> <sup>16</sup>
<i>Dalea foliosa</i> <sup>1</sup>	<i>fusiformis</i> <sup>22</sup> <i>macrocarpa</i> <sup>16</sup>
<i>Delphinium exaltatum</i> <sup>1</sup>	<i>Rhododendron prunifolium</i> <sup>1</sup>
<i>Dicentra cucullaria</i> <sup>7, 10</sup>	<i>Ribes hirtellum</i> <sup>1</sup>
<i>Erythronium americanum</i> <sup>10</sup>	<i>Rosa acicularis</i> <sup>1</sup>
<i>Eupatorium purpureum</i> <sup>1</sup>	<i>Sorbus americana</i> <sup>3, 11</sup>
<i>Filipendula rubra</i> <sup>1</sup>	<i>Styrax texanus</i> <sup>1</sup>
<i>Gaura neomexicana</i> <sup>1</sup>	<i>Taxus canadensis</i> <sup>1, 11</sup>
<i>Helianthus microcephalus</i> <sup>1</sup>	<i>Thuja occidentalis</i> <sup>6</sup>
<i>Helonias bullata</i> <sup>1</sup>	<i>Tilia americana</i> <sup>5</sup>
<i>Hymenocallis</i> sp. <sup>1</sup>	<i>Torreya taxifolia</i> <sup>1</sup>
<i>Isotria medeoloides</i> <sup>1</sup> <i>verticillata</i> <sup>1</sup>	<i>Tsuga canadensis</i> <sup>5, 6, 17, 18, 19</sup>
<i>Lathyrus venosus</i> <sup>16, 26</sup>	<i>Ulmus rubra</i> <sup>2</sup>
<i>Lesquerella filiformis</i> <sup>1</sup>	<i>Virbunum lantanoides</i> <sup>14</sup>
<i>Liatis scariosa</i> <sup>1</sup>	<i>Woodwardia virginica</i> <sup>1</sup>
<i>Lilium canadense</i> <sup>1</sup> <i>grayi</i> <sup>1</sup> <i>iridollae</i> <sup>1</sup> <i>philadelphicum</i> <sup>1</sup>	
<i>Liparis loeselii</i> <sup>1</sup>	
<i>Listera smallii</i> <sup>1</sup>	
<i>Lithospermum caroliniense</i> <sup>1, 20</sup>	
<i>Lobelia kalmii</i> <sup>1</sup>	
<i>Lupinus perennis</i> <sup>1</sup>	
<i>Lysimachia quadriflora</i> <sup>1</sup>	
<i>Maianthemum canadense</i> <sup>7, 11</sup>	
<i>Melanthium latifolium</i> <sup>1</sup> <i>virginicum</i> <sup>1</sup>	
<i>Osmorhiza claytonii</i> <sup>24</sup>	
<i>Oxypolis canbyi</i> <sup>1</sup>	
<i>Panax quinquefolius</i> <sup>1</sup>	
<i>Pedicularis furbishiae</i> <sup>1</sup>	
<i>Penstemon haydenii</i> <sup>1</sup> <i>lemhiensis</i> <sup>1</sup>	
<i>Plantago cordata</i> <sup>1</sup>	
<i>Platanthera blephariglottis</i> <sup>1</sup> <i>ciliaris</i> <sup>1</sup> <i>crystata</i> <sup>1</sup>	
<i>flava</i> <sup>1</sup> <i>grandiflora</i> <sup>1</sup> <i>integrilabia</i> <sup>1</sup> <i>leucophaea</i> <sup>1</sup>	
<i>peramoena</i> <sup>1</sup> <i>praeclara</i> <sup>1</sup> <i>psycodes</i> <sup>1</sup>	
<i>Pycnanthemum torrei</i> <sup>1</sup>	
<i>Sanguinaria canadensis</i> <sup>1</sup>	
<i>Sarracenia oreophila</i> <sup>1</sup> <i>purpurea</i> <sup>1</sup>	
<i>Saxifraga micranthidifolia</i> <sup>1</sup>	
<i>Schwalbea americana</i> <sup>1</sup>	
<i>Silene polypetala</i> <sup>1</sup>	
<i>Spiranthes diluvialis</i> <sup>1</sup> <i>ochroleuca</i> <sup>1</sup>	
<i>Thalictrum cooleyi</i> <sup>1</sup>	
<i>Trifolium reflexum</i> <sup>1</sup> <i>stoloniferum</i> <sup>1</sup>	
<i>Trillium cernuum</i> <sup>1</sup> <i>cuneatum</i> <sup>1</sup> <i>decumbens</i> <sup>1</sup>	
<i>grandiflorum</i> <sup>1, 7</sup> <i>persistens</i> <sup>1</sup> <i>pusillum</i> <sup>1</sup> <i>reliquum</i> <sup>1</sup> <i>rugelii</i> <sup>1</sup> sp. <sup>21</sup>	
<i>Uvularia perfoliata</i> <sup>7</sup>	
<i>Viola macloskeyi</i> <sup>14</sup> sp. <sup>7, 10</sup>	

TABLE 4. Herbaceous and woody plants negatively or positively affected by white-tailed deer herbivory – *continued*:

Herbaceous	Woody
<b>Positive Effects</b> <i>Berberis thunbergii</i> <sup>7</sup> <i>Dennstaedtia punctilobula</i> <sup>14</sup> <i>Dryopteris intermedia</i> <sup>14</sup> <i>Stellaria media</i> <sup>7</sup>	<i>Acer pensylvanicum</i> <sup>9</sup> <i>Fagus grandifolia</i> <sup>8,9</sup> <i>Prunus serotina</i> <sup>9</sup>

<sup>a</sup> also one moss species: *Hyperzia lucidula*<sup>14</sup>.

<sup>1</sup> Miller et al. (1992); <sup>2</sup>bark stripping: Fuller and Michael (1993); <sup>3</sup>Pimlott (1963); <sup>4</sup>Potvin and Breton (1992); <sup>5</sup>Anderson and Katz (1993); <sup>6</sup>van Deelen et al. (1996); <sup>7</sup>Koh et al. (1996); <sup>8</sup>Marquis (1981); <sup>9</sup>Tilghman (1989); <sup>10</sup>Riemenschneider et al. (1995); <sup>11</sup>Balگوoyen and Waller (1995); <sup>12</sup>Phillips and Maun (1995); <sup>13</sup>Phillips and Maun (1996); <sup>14</sup>Rooney and Dress (1997); <sup>15</sup>Prachar and Samuel (1988); <sup>16</sup>Ritchie et al. (1998); <sup>17</sup>Long et al. (1998); <sup>18</sup>Anderson and Loucks (1979); <sup>19</sup>Frelich and Lorimer (1985); <sup>20</sup>Cambell (1993); <sup>21</sup>Augustine and Frelich (1998); <sup>22</sup>Russel and Fowler (1999); <sup>23</sup>Zampella and Lathrop (1997); <sup>24</sup>Webster and Parker (2000); <sup>25</sup>Cornett et al. (2000); <sup>26</sup>Knops et al. (2000).

winter habitat, forest-tundra and boreal forest (Crête and Huot, 1993). Finally, supplementary feeding in winter may have imposed an artificially high browsing pressure on the vegetation used by reindeer in Fennoscandia (Kumpula et al., 1998). It is noteworthy that we found no mention of herbivory effects on vegetation in the range of the large migratory herds in northwestern Canada and Alaska, where caribou density has been high in recent years (Ferguson and Gauthier, 1992). The crucial impact of caribou on lichens and the slow recovery of this vegetation (e.g., Klein, 1987) make plausible the hypothesis of a long-term, cyclic/fluctuating dynamic (Messier et al., 1988). Cyclic dynamics also characterize populations of small mammals (Turchin and Hanski, 1997) and snowshoe hares (*Lepus americanus*: Boutin et al., 1995) at the same latitudes.

Our results generally support our prediction for moose and white-tailed deer (Fig. 1). Within the wolf range, the two cases involving moose in Alaska (Miquelle and Van Ballenberghe, 1989; MacCracken et al., 1997) and the one in southern Québec (DesMeules, 1968) concerned bark stripping, a feeding behaviour with limited effects on plants (Faber and Edenius, 1998) that can be observed at low population density (DesMeules, 1968). Reports of negative effects of moose herbivory on Isle Royale, where gray wolves occur, would depend on moose being regulated by forage competition, in the absence of black bears. The combined action of wolf and bear species is needed to regulate moose by predation (Crête, 1987; Messier, 1994; Crête, 1999). The last study reporting negative effects of moose herbivory in the wolf range dealt with aquatic feeding in Ontario (Fraser and Hristienko, 1983). Many studies reported negative effects of moose and white-tailed deer herbivory from areas with few (Fennoscandia) or no wolves. However, agriculture might act as a confounding factor in the case of white-tailed deer because some crops help to sustain deer populations (e.g., Nixon et al., 1991), and crop browsing increases the browsing pressure on native plants growing in adjacent woodlots (Augustine and Frelich, 1998).

### *Deer Impact What They Eat During the Growing Season*

During summer, caribou/reindeer consume mostly leaves of shrubs, graminoids, and some herbs, although they continue to eat lichens (Skogland, 1984; Thing, 1984; Gauthier et al., 1989; Crête et al., 1989). Graminoids are very resilient to grazing (e.g., Manseau, 1996). This resilience, as well as their low palatability (Crête et al., 1989), explains the absence of reports on detrimental effects of caribou herbivory for this group. During the snow-free period, trampling by caribou, as well as consumption, might contribute to extirpation of lichens. During the rest of the year, snow cover offers some protection from trampling, though caribou do form craters in the snow to search for food. Moose include mostly leaves of woody plants and some aquatics in their summer diet, but eat very few herbs (Cushwa and Coady, 1976; Morow, 1976; Belovsly, 1981; Crête and Jordan, 1981; Irwin, 1985; Butler, 1986). White-tailed deer consume a broad variety of food items during the growing season according to availability, but in forested areas, they concentrate their browsing on leaves of woody plants, herbs, and grass (Healy, 1971; McCaffery et al., 1974; Skinner and Telfer, 1974; McCullough, 1985; Rose and Harder, 1985; Johnson et al., 1995).

On the basis of the crude list of plant taxa that we present, we should conclude that white-tailed deer have a greater detrimental impact on the vegetation than do caribou/reindeer or moose. In addition, only white-tailed deer pose a risk for rare plant species. White-tailed deer prefer many herb species, in particular lilies and orchids (Miller et al., 1992), and herbs might be less resistant to repeated defoliation than woody species, being more exposed to complete defoliation. White-tailed deer herbivory could also cause the greatest negative impact by reason of relative body size. Given equal forage quality, the smallest cervid should be capable of positive foraging at the lowest plant biomass per surface area (Illius and Gordon, 1987), which means that white-tailed deer (male = 66 kg; Crête and Daigle, 1999) could extirpate a plant species from an area more easily than could moose (442 kg) or caribou/reindeer (159 kg).

### Can Deer Herbivory Change the Structure of Plant Communities?

In the absence of predators, moose and white-tailed deer herbivory could convert forests into scrubland or chaparral after perturbation if they browsed down all tree and shrub species. Two case studies illustrate the mechanisms that prevent such an outcome: Potvin and Breton (1992) for white-tailed deer and McInnes et al. (1992) for moose.

White-tailed deer on Anticosti Island in the Gulf of St. Lawrence have controlled all palatable herbs, deciduous woody plants (Potvin and Breton, 1992), and balsam fir regeneration even in large clear-cut areas (> 1 km<sup>2</sup>: F. Potvin, pers. comm. 1999). However, white and black spruce (*Picea glauca*; *P. mariana*) receive very little browsing (Huot, 1982). Balsam fir has dominated the forests growing on this island until recently, but white spruce is likely replacing it; in the future, the island should remain treed, but forest composition should change drastically unless deer density declines significantly. Moose on Isle Royale in Lake Superior affect the vegetation in a similar manner, although their summer browsing concentrates on woody species. Moose reduce the leaf biomass of deciduous trees and shrubs, reduce their height, slow down canopy closure by deciduous trees, and favour herbs by letting more light reach the ground (McInnes et al., 1992). In addition, winter browsing on balsam fir postpones canopy closure by this species (McLaren and Peterson, 1994). However, moose rarely browse spruce, and Isle Royale should remain forested under the worst-case scenario; until recently, moose had not impeded paper birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) from growing out of their reach (McInnes et al., 1992).

At high caribou/reindeer population density, tundra plants could be at risk of extirpation since they all remain within the reach of herbivores. However, such plant communities appear to tolerate browsing well. Manseau et al. (1996) illustrate this point. Caribou in northern Québec have almost extirpated lichens, but their effect on vascular plants has remained more limited, only reducing the leaf biomass of some shrub species. For instance, their browsing has not destroyed stands of dwarf birch (*Betula glandulosa*), their preferred forage (Crête et al., 1989), although it has affected the health of stems (Crête and Doucet, 1998). The relative resilience of the tundra vegetation to caribou/reindeer browsing could result from coevolution at relatively high herbivore density, as suggested by the EEH.

Although deer herbivory cannot change the structure of ecosystems in an ecological time frame, it can substantially modify their plant composition and biomass. Browsing could threaten or eliminate some species: in particular, herbs could be threatened by white-tailed deer (Miller et al., 1992). This possibility exists (Crête, 1999), but local or total elimination should generally be improbable for at least two reasons. Woody species and herbs react to

defoliation in various ways that often reduce the efficiency of future herbivory because of size reduction (e.g., Balgooyen and Waller, 1995; Crête and Doucet, 1998). This reaction can produce a feedback in the herbivore by lowering its physical condition, fecundity, and population density, relaxing pressure on the vegetation. In addition, refugia exist for plants to escape herbivory, i.e., cliffs, inaccessible plateaux (Manseau et al., 1996), boulders (Rooney, 1997), and treefall mounds (Long et al., 1998). We conclude that the standing biomass of preferred forage species can be drastically reduced by deer herbivory, but that most taxa should persist during periods of high herbivory and should recolonize vacant areas when deer density decreases, a plausible possibility after severe forage reduction or reintroduction of natural predators (Crête, 1999). On an evolutionary time scale, the permanent exclusion of predators could allow the appearance (particularly in forests) of herbivores adapted to exploit nutrient-poor forage (e.g., spruce; Oksanen, 1992). In such a case, one should expect major changes in the structure and the composition of plant communities. Areas where large carnivores have been extirpated in recent times may currently represent coevolutionary hot spots (sensu Thompson, 1999).

We cannot conclude firmly whether the body of data collected to date on plant/herbivore interactions for these three cervid species supports the EEH. However, measuring cervid biomass and annual forage production along a productivity gradient would provide a powerful test of the hypothesis. Indeed, the EEH predicts that, in the absence of functional predators, the standing biomass of herbivores would increase along with primary productivity, whereas that of forage would remain constant or show a very modest increase (Oksanen and Oksanen, 2000). This test could be carried out in eastern North America, from the tip of the Gaspé Peninsula to Florida. It would involve measuring cervid biomass and standing forage biomass at the end of a normal growing season in natural areas where moose and white-tailed deer have not been strongly limited by hunting during previous decades.

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