LETTER

The distribution of deer biomass in North America supports the hypothesis of exploitation ecosystems

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Abstract

The hypothesis of exploitation ecosystems (EEH) predicts that, along a productivity gradient in terrestrial environments, predators will regulate herbivores at a relatively constant density whenever primary productivity exceeds $700 \ \text{g m}^{-2} \ \text{y}^{-1}$; under this threshold, or if predators are absent, forage production determines herbivore density. I tested EEH using the pattern of deer biomass distribution over North America, the dominant family of large herbivores. Deer biomass increased from the High Arctic to the north of the boreal forest and remained in the same range southward within the gray wolf range; for the same latitude, deer biomass increased by a factor of 5 in the absence of wolves. South of the wolf range, there existed a clear relationship between actual evapotranspiration, a proxy of primary productivity, and deer biomass. Highest deer densities occurred in the south-east of the continent where only white-tailed deer are present. The observed pattern lends support to EEH and suggests that the removal of large predators in southern North America may have imposed an unprecedented pressure on plants eaten by deer.

INTRODUCTION

The proposition (HSS) made by Hairston *et al.* (1960) that terrestrial ecosystems are green because predators keep herbivores in check, raised a controversy as to whether top–down or bottom–up forces have primacy (Power 1992). Fretwell (1977, 1987) refined HSS by suggesting that the length of food chains determined the nature of trophic interactions: with odd numbers of trophic level, predators would regulate grazers, whereas with even numbers, plants would regulate grazers. Fretwell also predicted that primary productivity would set the length of food chains. Oksanen and his coworkers have formalized and extended Fretwell's model (L. Oksanen 1988, 1992, 1999; T. Oksanen, 1990; L. Oksanen *et al.* 1981, 1992; T. Oksanen *et al.* 1992, 1995), exploring mathematically the role of such factors as connection between habitats, evolution, herbivore defences against predators, etc. These analyses suggested, in particular, that the hypothesis of exploitation ecosystems (EEH) should apply at the landscape level because movements of predators can eliminate local differences in trophic dynamics (Holt 1985). Rosenzweig's (1971) laissez-faire

approach to trophic exploitation represents the cornerstone of EEH (L. Oksanen 1983); it assumes that energy transfer from one trophic level to the other depends on absolute, instantaneous biomass of the lower. EEH does not distinguish species although the consequences of natural selection on the body size of carnivores and herbivores were evaluated (L. Oksanen 1992) and included in the most recent models. EEH predicts a stepwise accrual of plant and herbivore biomass along productivity gradients (Moen & Oksanen 1998; L. Oksanen 1999). In very unproductive areas, only plants grow whose biomass increases with primary productivity until viable herbivore species appear ($\approx 50 \ \text{g m}^{-2} \ \text{y}^{-1}$). Above this level, plant biomass remains relatively constant until resident carnivore species can subsist, i.e. at $\approx 700 \ \text{g m}^{-2} \ \text{y}^{-1}$, and then increases almost linearly. EEH predicts that herbivore biomass will increase linearly between an annual production varying from 50 to $700 \ \text{g m}^{-2}$, but will remain relatively constant in the presence of carnivores above this threshold, no matter what the primary productivity. The primary productivity reaches $\approx 700 \ \text{g m}^{-2} \ \text{y}^{-1}$ in the transition from the tundra to the boreal forest (L. Oksanen 1983; L. Oksanen

et al. 1992). In three-link systems, a trade-off between elusiveness and use of marginal forage, and coevolution allow some slow increase of herbivore biomass along with productivity even under predator regulation (L. Oksanen 1992). Finally, according to EEH, carnivore biomass increases asymptotically along with primary productivity in productive terrestrial ecosystems; there, the removal of carnivores would lead to a substantial increase of herbivore biomass and a corresponding decrease of plant biomass. Many recent studies on insects (e.g. Fraser 1998; Moran & Hurd 1998) gave support to EEH, showing experimentally top–down trophic cascades; the pattern of deer distribution on the Québec-Labrador peninsula also supported EEH (Crête & Manseau 1996). Competing hypotheses with EEH include bottom–up regulation of food webs and various possibilities of colimitation by predators and resources (Power 1992). The prediction of stepwise accrual of plant and herbivore biomass along productivity gradients and trophic cascades distinguish EEH for alternative hypotheses.

I used the distribution of deer biomass (family: cervidae) throughout North America in order to test the predictions derived from EEH. According to this hypothesis, deer biomass would increase from the High Arctic to the transition zone between the tundra and the forest (two trophic levels), would remain at the same level within the wolf range (three trophic levels), and would be a function of primary productivity south of the wolf range (two trophic levels). EEH predicts a major increase of deer biomass for the same latitude in the absence of wolves.

STUDY AREA AND METHODS

In North America, caribou [*Rangifer tarandus* (Linné)] characterize the north of the boreal forest and the tundra, whereas moose [*Alces alces* (Linné)] dominate in coniferous and mixed forests growing further south. White-tailed deer [*Odocoileus virginianus* (Zimmermann)] are typical of the deciduous forests of the east, whereas mule deer [*O. hemionus* (Rafinesque)] replace them in the mountainous terrain of the west. Wapiti [*Cervus elaphus* (Linné)] possess the smallest range, mostly adjacent to the prairies in the west. The two large obligate carnivores preying on deer show a reduced distribution: wolves [*Canis lupus* (Linné)] are almost restricted to Canada and Alaska, whereas cougars [*Felis concolor* (Linné)] are mostly to the mule deer range. The combined predation of wolves and bears [black or brown: *Ursus americanus* (Pallas), *U. arctos* (Linné)] appears to regulate moose numbers at low density in North America; neither the gray wolf nor a bear species seems capable alone of regulating moose populations (Crête 1998). Large herds of migratory caribou living in the transition zone between the boreal forest and the tundra appear regulated by forage, whereas forest

dwelling caribou are regulated by predation (Crête & Manseau 1996). There exists no published indication that mountain lions can regulate their prey, which might depend on low densities caused by past human decimation; therefore, I assumed that lion predation did not regulate deer species that they preyed upon. This assumption does not dismiss the possibility for cougars to limit their prey (e.g. Ross *et al.* 1997).

I sent a questionnaire to the 60 jurisdictions (state, province, territory) responsible for deer management in the continental U.S.A. and in Canada, to which all responded (Crête & Daigle 1999). Respondents indicated the estimated population size of each species within their jurisdiction; no question concerned the methods used, but all deer species can be censused from the air (Crête & Daigle 1999). The answers to the questionnaire allowed me, in particular, to compute the average crude standing deer biomass per jurisdiction (Crête & Daigle 1999). In the case of the Northwest Territories, I divided it into three subunits: High Arctic ($>75°$N), southern Arctic archipelago (including Baffin Island: ~ 70–$75°$N), and continental Northwest Territories.

RESULTS

North America harbours currently $\sim 40 \times 10^6$ deer: 28.5×10^6 white-tailed deer, 5.0×10^6 mule deer, 3.6×10^6 caribou, 1.1×10^6 moose, and 1.1×10^6 wapiti (Crête & Daigle 1999). The testing of EEH necessitated that animal communities had reached an equilibrium, which can be disrupted in particular by climatic factors or human interference (Power 1992). Large herbivores exhibit relatively constant adult survival rates in various circumstances (Gaillard *et al.* 1998), which tends to stabilize their demography. However, human exploitation can keep them at low density where regulation may remain undetectable (Fowler 1981) and testing of models is impossible. Sport hunting represents currently the major mortality factor of North American deer; between 1992 and 1996, the mean harvest rate varied between 3% for caribou and 17% for white-tailed deer (Crête & Daigle 1999). Overall, deer exploitation has been conservative in North America in recent decades and most populations have likely been kept close to carrying capacity (Crête & Daigle 1999).

When combining all species in terms of standing deer biomass, a general pattern emerged. The lowest densities occurred in the tundra and the boreal forest, in the prairies and in south-western U.S.A. (Fig. 1). In comparison, the highest standing biomasses were concentrated in the south-east quarter of the continent. By jurisdiction, extremes varied between 28 kg km^{-2} in Nevada and 901 kg km^{-2} in Indiana. In the High Arctic ($>75°$N), the

Figure 1 Distribution of deer biomass density (kg km^{-2}) in North America when combining the five extant indigenous species (caribou, moose, white-tailed deer, mule deer, and wapiti). Densities represent winter estimates and were averaged for each of the 60 jurisdictions responsible for deer management in U.S.A. and Canada (Crête & Daigle 1999). Figures are not corrected for unsuitable habitats.

biomass of caribou averaged only 0.7 kg km^{-2}, whereas it increased to 16 kg km^{-2} on the southern islands of the Arctic archipelago (between $\sim 70°$N and $75°$N). The standing deer biomass averaged 106 kg km^{-2} in the continental Northwest Territories and northern Québec, which corresponds to the distribution of the large Canadian migratory herds of caribou. I excluded Alaska (123 kg km^{-2}) in this computation because this state may be less homogenous than the rest of the continent with respect to the distribution of the tundra and the boreal forest; I also excluded Yukon (39 kg km^{-2}) because migratory caribou are seasonal residents only. In the range that moose shared with established gray wolf populations in the centre of the continent (British Columbia to southern Québec; Yukon excluded), the combined deer biomass averaged 62 kg km^{-2}, which contrasts with 299 kg km^{-2} in the rest of the moose range where wolves were very rare or absent [Maritime Provinces (absent), northern New England (absent), and north-west U.S.A. (rare, recolonizing)].

South of the wolf range, I related deer biomass and primary productivity, using the actual evapotranspiration (AE: USSR National Committee for the International Hydrological Decade 1977) as a proxi for primary productivity; Rosenzweig (1967) showed that these two variables exhibit a closed linear relationship for a wide range of terrestrial ecosystems. I found a significant relationship between deer biomass km^{-2} (ln-transformed to normalize residues) and AE (Fig. 2); highest standing deer biomass and highest AE values coincided in the south-east portion of the continent. My results indicated a poor relationship between species richness and primary productivity; all five North American deer occurred in a few mountainous jurisdictions of the north-west where AE reaches intermediate values, whereas only white-tailed deer were present in the productive South-east.

DISCUSSION

I restricted my analysis to cervids because I used a database collected to summarize the current status of North American deer (Crête & Daigle 1999). The distribution pattern of deer biomass that I measured over North America supports EEH, although this hypothesis refers to the guild of herbivorous and carnivorous endotherms; EEH assumes though that the size bracket represented by deer should comprise a constant fraction of herbivores across a productivity gradient (Oksanen *et al.* 1981). This fit of deer biomass with EEH might also depend on the fact that large herbivores capture much more than their share in terrestrial ecosystems (Silva & Downing 1995), and that deer make up the dominant family of large herbivores in North America. The inclusion of mountain bovids [i.e. mountain goat (*Oreamnos americanus:* de Blainville); bighorn sheep (*Ovis canadensis:* Shaw); Dall's sheep (*Ovis dallis*: Nelson)], which currently number $\sim 86\,000$, 59 000, and 114 000, respectively (Shackleton and the IUCN/SSC Caprinae Specialist Group 1997), would not
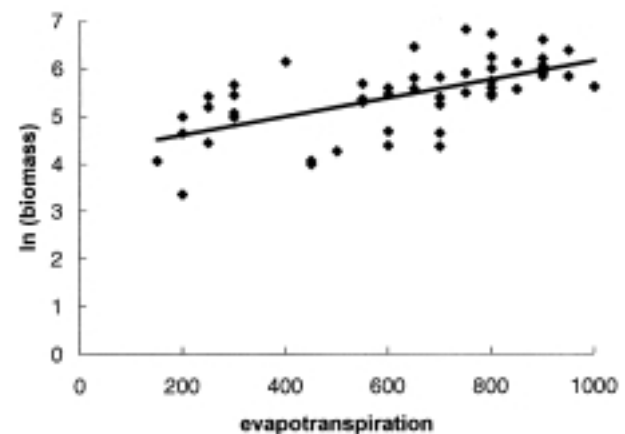

Figure 2 Relationship between deer biomass density (kg km^{-2}) (ln-transformed to normalize the residues) and actual evapotranspiration (AE; mm), a proxi of primary productivity, for the 51 jurisdictions of North America where grey wolf is absent or very rare. [ln (biomass) = 0.002 AE + 4.150; adjusted r^2 = 0.39; $P < 0.0001$.]

change the general pattern in western North America much because the combined biomass of sympatric mule deer and wapiti is 32.4 times greater than that of bovids. In the High Arctic, the addition of muskoxen [*Ovibos moschatus* (Zimmermann)] would not affect the general pattern either, their standing biomass averaging 12.3, 26.3, and 3.0 kg km^{-2} in the High Arctic, southern Arctic archipelago, and mainland Northwest Territories, respectively (Banfield 1974; Ferguson & Gauthier 1992). Finally, the major negative impact of agriculture on the habitat of American bisons [*Bison bison* (Linné)] and pronghorn [Antilocapra americana (Ord)] precludes any meaningful interpretation of their current numbers.

It is surprising that I found a good relationship between deer density and AE south of the wolf range, considering that I did not correct for factors such as areas of urbanization, agricultural lands, and nature of farm crops, which all influence deer abundance. It is also worth noting that deer behave like the rest of North American mammals, their diversity being unrelated to primary productivity (Currie 1991).

The pattern of deer distribution that I observed on the continent allows me to predict that deer abundance will significantly decrease in north-western U.S.A., where introduced and recolonizing gray wolves have been rapidly expanding in recent years (Bangs & Fritts 1996), if managers allow a natural equilibrium to establish between wolves and their prey in the presence of a bear species. The equilibrium biomass of deer should exceed that observed in the moose range (62 kg km^{-2}), because there are many deer species in this part of the continent, and equilibrium density appears higher in multispecies assemblages than when wolves prey on only one deer species (Crête & Manseau 1996).

The increased monopolization of ecosystem energy by deer in the absence of large predators may pose a problem of conservation for plant species consumed by deer and of competition with smaller herbivores and their predators. Botanists reported that white-tailed deer threaten many vascular plants in the U.S.A. (Miller *et al.* 1992). This situation might be particularly serious if food chains of large mammals counted three levels before the European colonization of the continent, with herbivores regulated by predators. In such a case, the extirpation of predators has imposed an unprecedented high browsing pressure on indigenous plant species consumed by deer everywhere on the continent where wolves disappeared.

My analysis indicated that the current pattern of deer distribution in North America matched with predictions made by EEH, but other hypotheses could also predict similar patterns (Power 1992). Measurements of plant biomass eaten by deer at a continental scale (Crête & Manseau 1996) would provide a powerful test for EEH.

According to this hypothesis, white-tailed deer biomass in the forests of eastern North America should increase along with primary productivity (Fig. 2), whereas that of plant species consumed by deer should remain almost constant.

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