

1 **Large Predators Limit Herbivore Densities in Northern Forest Ecosystems**

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7 Running Head: Large Predators Limit Herbivore Densities

8

9 **Abstract**

10 There is a lack of scientific consensus about how top-down and bottom-up forces
11 interact to structure terrestrial ecosystems. This is especially true for systems with large
12 carnivore and herbivore species where the effects of predation versus food limitation on
13 herbivores are controversial. Uncertainty exists whether top-down forces driven by large
14 carnivores are common, and if so, how their influences vary with predator guild composition
15 and primary productivity. Based on data and information in 42 published studies from over a
16 50-year time span, we analyzed the composition of large predator guilds and prey densities
17 across a productivity gradient in boreal and temperate forests of North America and Eurasia.
18 We found that predation by large mammalian carnivores, especially sympatric gray wolves
19 (*Canis lupus*) and bears (*Ursus* spp.), apparently limits densities of large mammalian
20 herbivores. We found that cervid densities, measured in deer equivalents, averaged nearly six
21 times greater in areas without wolves compared to areas with wolves. In areas with wolves,
22 herbivore density increased only slightly with increasing productivity. These predator effects
23 are consistent with the exploitation ecosystems hypothesis and appear to occur across a broad
24 range of net primary productivities. Results are also consistent with theory on trophic
25 cascades suggesting widespread and top-down forcing by large carnivores on large herbivores
26 in forest biomes across the northern hemisphere. These findings have important conservation
27 implications involving not only the management of large carnivores, but also that of large
28 herbivores and plant communities.

29

30 **Key Words:** large carnivores, wolves, bears, cervids, productivity, trophic cascades,
31 herbivory

32 **Introduction**

33 Over a half century ago Hairston et al. (1960) introduced the green world hypothesis
34 (GWH), suggesting that predators maintain global plant biomass at high levels by limiting
35 herbivore densities. This view of “top-down” controls upon food-web interactions
36 contradicted the prevailing bottom-up view that food-webs are nutrient-driven, as reflected in
37 the classic food-web theory. Subsequently Fretwell (1977) and Oksanen et al. (1981) refined
38 and extended the GWH to what is known as the exploitation ecosystems hypothesis (EEH).
39 The EEH predicts stepwise trophic relationships among plants, herbivores, and predators
40 along an increasing net primary productivity (NPP) gradient. The EEH also suggests that
41 herbivore biomass increases linearly with increasing NPP in unproductive ecosystems
42 ($<0.7\text{kg/m}^2/\text{yr}$), but remains somewhat constant in the presence of predators in productive
43 ecosystems ($>0.7\text{kg/m}^2/\text{yr}$). According to the EEH, plants and carnivores in forests and other
44 relatively productive ecosystems are resource limited, whereas herbivores are regulated by
45 predation. Thus, with increasing primary productivity, the EEH predicts significant increases
46 in plant and carnivore biomass, but little increase in herbivore biomass. Conversely, where
47 apex predators have been functionally extirpated, herbivore irruptions (sharp increases in
48 densities) and impacts to plant communities would be likely.

49 Because these seminal top-down theories were advanced, questions have been raised
50 and the importance of trophic cascades in ecosystem processes and functions remains
51 controversial (Polis 1999; Terborgh et al. 1999; Schmitz et al. 2000). Trophic cascades have
52 been criticized as simplistic, only rarely relevant at the community level, and far less
53 significant within terrestrial ecosystems than aquatic ecosystems (Halaj and Wise, 2001).
54 Additionally, the vast majority of studies concerning trophic cascades in terrestrial ecosystems

55 involve invertebrate communities (Borer et al. 2005). Thus, uncertainty persists about
56 whether terrestrial trophic cascades are common in the presence of large carnivores (Crête and
57 Manseau 1996; Ray et al. 2005).

58 Large mammalian carnivore species have experienced substantial range contractions
59 throughout the world during the last two centuries (Ceballos and Ehrlich 2002; Laliberte and
60 Ripple 2004). Nevertheless, there have been a significant number of case studies performed in
61 an attempt to understand the effects of wolves and other predators on prey populations in
62 northern North America (Orians et al. 1997; Mech and Peterson 2003; citations in Appendix
63 1). In general, these reviews suggest that wolf predation can be a limiting factor for prey
64 populations, especially when wolves coexist with bears, holding prey to levels well below
65 what could be supported by the forage base. However, Mech and Peterson (2003) state that
66 there is “still no scientific consensus on the significance of wolf predation in prey population
67 dynamics” because each case study has a combination of ecological factors that make it
68 unique from the others.

69 Since little work has been done comparing predator/prey dynamics across productivity
70 gradients (Crête 1999), there has been a lack of literature addressing trophic level dynamics in
71 endotherm food webs across boreal and temperate forests of the Northern hemisphere
72 (Aunapuu et al. 2008). Little is known, for example, about the range in cervid densities
73 normally occurring for partial versus complete large predator guilds and how cervid densities
74 vary with productivity (Crête and Manseau 1996).

75 Herein we address relationships among predator guilds and cervid densities in boreal
76 and temperate forest biomes of the northern hemisphere. In retrospect, the extirpation of large
77 carnivores by the 20th century in portions of the mid- and northern latitudes provided a series

78 of natural experiments (Diamond 1983). Thus, previously published studies allowed us to
79 compare results from areas where carnivores remain and where they had been extirpated.

80 Consistent with the GWH (Hairston et al. 1960) and the EEH (Oksanen 1992), we
81 hypothesize a set of trophic interactions across a gradient of primary productivity for boreal
82 and temperate ecosystems that are productive enough to support carnivores. In systems with
83 intact and ecologically effective large carnivore guilds (i.e., tri-trophic cascades, left side of
84 Figure 1), we expect 1) carnivore densities to be resource limited and positively correlated
85 with primary productivity and 2) herbivores mainly predator limited, such that, herbivore
86 density increases only slightly with increasing productivity. In this system, herbivore damage
87 to palatable plants would be relatively low regardless of productivity. Although not rigorously
88 tested herein, EEH predicts that when the removal of large predators occurs (i.e., truncated
89 trophic cascades, right side of Figure 1), herbivore density would be positively correlated with
90 productivity and damage to palatable plants relatively high regardless of primary productivity.

91 Understanding the effects of large predator and herbivore populations upon native
92 plant communities has potentially important conservation implications. If large predators
93 reduce plant damage by altering cervid behavior and limiting their densities, the maintenance
94 of large predators across landscapes could be a crucial option for sustaining the ecological
95 integrity of ecosystems (Miller et al. 2001; Soulé et al. 2003; Terborgh and Estes 2010; Estes
96 et al. 2011). Furthermore, in areas where large predators have been displaced or locally
97 extirpated, their reintroduction may represent a particularly effective approach for passively
98 restoring those ecosystems.

99

100 **Methods**

101 Expanding on previous work by Peterson et al. (2003), we conducted a literature
102 search to find articles that reported cervid densities [white-tail deer (*Odocoileus virginianus*),
103 caribou (*Rangifer tarandus*), elk (*Cervus elaphus*), and moose (*Alces alces*)]. We searched the
104 literature using electronic databases as well as reference lists from Peterson et al. (2003) and
105 other publications. In selecting articles, we avoided using case studies with migrating cervids,
106 non-native cervids, and islands (e.g., Isle Royale). Some cervids are hypothesized to migrate
107 to avoid their predators, which can reduce the impacts of predation on their numbers. We did
108 not attempt to examine migratory cervids because their densities exhibit high spatial and
109 temporal variability and are thus difficult to characterize for comparative purposes. This
110 criterion resulted in the exclusion of elk in the northern Rocky Mountains of North America,
111 because elk densities in this region are highly variable as animals migrate between summer
112 and winter ranges across an elevation gradient. We also excluded vicinities of major human
113 impacts such as built-up areas, agriculture, or livestock. We excluded areas with high levels
114 of large carnivore harvesting by humans. For example, wolf/cervid data from Poland's
115 primeval forest were not included due to wolf harvesting, limited habitat, and other human
116 disruptions there (Jędrzejewska and Jędrzejewski 1998). We inspected each study area with
117 remote sensing imagery and all selected study areas were composed of >90% forest/grass
118 cover. We did not exclude sites that contained forest harvesting. Finally, we examined
119 historical range maps to determine the original range of wolves and bears to determine sites
120 where they have been extirpated. Due to a lack of consistent information on felids, we were
121 unable to include felid species in our analysis.

122 For each case study, we recorded 1) an estimate of net primary productivity (*NPP*)
123 from MC1, a dynamic global vegetation model, 2) the presence or absence of predators

124 including wolves, bears, and human hunters, and 3) the density ($\#/km^2$) of the primary cervid
125 species present. We recorded wolf density ($\#/1000 km^2$) when available and normalized
126 cervid densities to deer equivalent (*DE*) densities (DE/km^2 , deer = 1 *DE*, caribou = 2 *DE*, elk
127 = 3 *DE*, moose = 6 *DE*) for comparative purposes (Peterson et al. 2003). We also recorded if
128 the authors described cervid impacts to plants.

129 T-tests (unequal variances) were used to test for significant ($p \leq 0.05$) differences in
130 cervid densities for areas with versus without wolves. Linear regression was used to
131 determine if wolf densities or cervid densities were significantly related to *NPP*. Multiple
132 regression was used to test for significant slope differences in cervid densities in relation to
133 *NPP* between sites with wolves present versus those without wolves (i.e., extirpated or rare).

134 The dynamic global vegetation model (0.5° lat. x 0.5° long. grid cells), MC1, includes
135 a biogeochemical module that simulates monthly carbon (C) and nutrient dynamics for a
136 combined tree and grass ecosystem. MC1 is a whole ecosystem model which accounts for
137 both overstory and understory processes in detail, including plant production, soil organic
138 matter decomposition, and water and nutrient cycling where *NPP* in kg of dry mass/ m^2/yr is a
139 function of a maximum potential rate of plant production constrained by the effects of soil
140 moisture, soil temperature, soil nutrients, atmospheric CO_2 concentration, shading, and leaf
141 area index (Daly et al. 2000; Bachelet et al. 2001). Temperature, precipitation, humidity, and
142 soil properties are basic drivers for the biogeochemical module. See Bachelet et al. (2001), for
143 technical documentation of the MC1 model including the biogeochemical module.

144

145 **Results**

146 We obtained estimates of cervid densities for 42 sites in North America and Eurasia
147 meeting our criteria (Figure 2, Appendix 1). Wolf densities were available for 19 of the 42
148 sites. Human hunting occurred at 24 of the 42 sites. Both wolves and bears historically
149 existed at all 42 sites, with wolves being extirpated from 16 sites and bears extirpated from 7
150 of these 16 sites. We found that bears were sympatric with wolves in 26 of 42 studies, while
151 bears occurred alone in 9 of 42 studies, all of which were areas where wolves had been
152 extirpated. None of our 42 sites had wolves without bears.

153 Sites without wolves ($n = 16$) had significantly higher average cervid densities relative
154 to sites with wolves ($n=26$) (15.5 vs. 2.6 DE/km^2 , respectively, $p < 0.001$, Figure 3A). Also at
155 sites without wolves, 11 of 16 studies reported impacts to plants (See Appendix 1). Cervid
156 densities without wolves ranged from 2.8 to 32.4 DE/km^2 and with wolves ranged from 0.03
157 to 8.4 DE/km^2 . While cervid densities were significantly related to productivity when wolves
158 were absent ($p = 0.035$) and present ($p = 0.036$), densities increased with productivity at a
159 significantly greater rate in the absence of wolves compared to when wolves were present
160 (regression slope over 5 times steeper, $p = 0.02$, Figure 3B).

161 Variance of cervid density was not constant and increased with increasing NPP , but a
162 natural log transformation of density resolved this issue, and allowed a more direct evaluation
163 of the effect of wolves on the relationship. The log of cervid density was significantly related
164 to productivity ($p = 0.002$), but the R^2 was low, 0.22 . The addition of a categorical variable
165 for wolf presence or absence resulted in a highly significant relationship ($p < 0.001$) that
166 explained 70% of the variation in density (adjusted $R^2 = 0.70$). In fact, wolf presence alone,
167 without accounting for productivity, explained 60% ($R^2 = 0.60$) of the variation in log of
168 cervid density.

169 On average, we found wolf densities to be 17.8 /1000 km² (range 2.3-40.2). Wolf
170 densities were positively related to increases in productivity ($p = 0.008$, Figure 4).

171 **Discussion**

172 Results from our analyses suggest that top down forcing may be relatively strong in
173 systems with wolves, in that cervid densities are significantly lower than in predator guilds
174 where wolves are absent. These findings support research findings by others that the
175 combined predation pressure from wolf and bear populations may limit cervid densities
176 (Gasaway et al. 1992; Messier 1994; Orians et al. 1997; Mech and Peterson 2003). Our results
177 are also consistent with predictions made by Oksanen et al. (1981) for 1) the predator trophic
178 level, because wolf density increased with increasing productivity and 2) the herbivore trophic
179 level, because cervid densities in ecosystems with wolves remained relatively low regardless
180 of productivity.

181 Other than humans, which occupy an ecological niche as top predator in many
182 ecosystems, gray wolves, by virtue of their widespread geographic distribution, group-
183 hunting, and year-round activity, represent the most significant cervid predator in the northern
184 hemisphere (Peterson et al. 2003). Thus predation pressure from wolves, in combination with
185 bears, can apparently maintain cervid populations at low densities. An exception, perhaps, is
186 that some migrating cervids, such as barren ground caribou herds, may not be limited by
187 predation and often cycle over wide ranges of abundance.

188 With both wolves and bears present, we found cervid densities to increase only slightly
189 with increasing net primary productivity, possibly because of an evolutionary response to
190 intense predation pressure involving anti-predator adaptations and selection for more elusive
191 prey (Oksanen 1992). Because predators may not completely counter anti-predator

192 adaptations of their prey, increasing primary productivity should lead to slight increases in
193 herbivore density (Oksanen 1992). Costs related to antipredator behavior could be partially
194 offset by any positive effects of increasing productivity. In systems with high primary
195 productivity, traits that affect prey fitness through their ability to avoid predation are prone to
196 be under strong selection (Abrams 2000). Like Crête (1999), we found that cervid densities
197 increased steeply with increasing productivity for ecosystems without wolves. The high
198 variance in cervid densities associated with an absence of wolves may be due to unevenness in
199 the effectiveness of partial predator guilds and human hunting as well as various bottom-up
200 factors such as climate variability or forest conditions.

201 Our results are consistent with a relatively extensive body of literature in that bears
202 alone appear insufficient to preclude cervid irruptions whereas the combination of wolf and
203 bear predation, with or without human hunting, maintains cervid densities lower than without
204 wolves and bears (Bergerud et al. 1983; Gasaway et al. 1983; Bergerud and Elliot 1985;
205 Ballard et al. 1987; Van Ballenberghe 1987; Fuller 1989; Messier 1994; Hayes and Harestad
206 2000). Because bears are opportunistic omnivores, have access to a variety of foods, and their
207 effects appear to be secondary to wolves, an understanding of their role in trophic cascades
208 has been elusive. Both black (*Ursus americanus*) and brown (*Ursus arctos*) bears commonly
209 prey on neonatal cervids, taking a large percentage of the annual offspring less than one month
210 old (Zager and Beecham 2006). Their role as predator appears to vary with the density of
211 cervids and has the greatest impact when cervid densities are low rather than high (Gasaway et
212 al. 1992). At low cervid densities, bear predation on neonates is mostly additive rather than
213 compensatory, thus removing young animals before they have an opportunity to reproduce
214 (Zager and Beecham 2006). This leads us to hypothesize that bears may provide multiple and

215 linked positive feedback loops in their sympatric predation effects with wolves such that: 1) as
216 wolves provide subsidies to bears through scavenging opportunities on wolf-killed carrion,
217 higher bear densities are supported, causing more predation on neonatal cervids and lower
218 cervid densities; and 2) when cervid densities become lower, bear predation tends to be more
219 effective as an additive predation force further limiting cervid densities. In the case of Isle
220 Royale National Park where wolves exist on an island, wolves alone have been unable to
221 consistently limit cervid densities over time possibly due to inbreeding, disease, and/or a lack
222 of bears (Peterson et al. 2003; Peterson 2007; Wilmers et al. 2006).

223 Hypercarnivorous felids may also have important roles in affecting cervid densities
224 and trophic cascades. In western North America, cougars (*Puma concolor*) were found to limit
225 mule deer (*Odocoileus hemionus*) densities releasing woody plants from browsing
226 suppression, thus maintaining biodiversity (Ripple and Beschta 2006; 2008). Furthermore,
227 our two-predator results for wolves and bears in this study are similar to the findings of Melis
228 et al. (2009) involving combined wolf and lynx (*Lynx lynx*) predation on roe deer (*Capreolus*
229 *capreolus*) in Europe. They found that roe deer densities were significantly lower in areas
230 with sympatric wolves and lynx compared to areas with wolves alone or areas without either
231 predator (Figure 5). Their results indicate that top-down influences were stronger than
232 bottom-up influences because there were no significant differences in productivity as
233 measured by the fraction of absorbed photosynthetically active radiation (FPAR) in their areas
234 with both wolves and lynx ($\bar{x} = 56.2$, 95% C.I. 4.4), wolves without lynx ($\bar{x} = 54.4$, 95% C.I.
235 5.3), and neither predator present ($\bar{x} = 56.2$, 95% C.I.=3.5).

236 While the occurrence of human hunting and winter weather events in the presence of
237 wolves can influence cervid populations through additive mortality (Gasaway et al. 1983;

238 Gasaway et al. 1992; Orians et al. 1997; Mech and Peterson 2003), evidence from our
239 analysis shows that in many cases, humans, using contemporary hunting laws and strategies,
240 are ineffective in the absence of wolves in preventing hyper-abundant cervid densities.
241 Similarly, Melis et al. (2009) found that human hunting in Europe had little influence on roe
242 deer abundance. This situation likely occurs because the interest of hunting managers is to
243 generally maximize game meat production, not to limit cervid densities. In addition, hunting
244 by humans is often not functionally equivalent to predation by large, wide ranging carnivores
245 such as wolves. Differences include factors such as killing distance, seasonal and diurnal
246 timing, age and sex of selected prey, as well as effects on mesopredators, intra-guild
247 predation, and carrion-scavenger relationships (Berger 2005). Non-lethal effects such as
248 predation risk and the “ecology of fear” triggered by large mammalian carnivores can also
249 influence ecosystem structure and function, but these effects may be different than any risk
250 effects caused by human hunters (Laundré et al. 2001; Ripple and Beschta 2004; Berger
251 2005).

252 Although we were unable to rigorously test for trophic cascades in our dataset, below
253 we tentatively address the plant damage portion of EEH. In reviewing our case studies, at
254 sites without wolves ($n = 16$) we found that most authors ($n = 11$) reported impacts to plants.
255 In the presence of a functional large predator guild that can exert significant influence via
256 lethal and nonlethal effects, cervids are normally unable to impact the general recruitment
257 (i.e., growth of seedlings and sprouts into tall saplings and larger growth forms) of palatable
258 woody species (Ripple et al. 2010). However, where reduced lethal/nonlethal effects of large
259 predators and higher cervid densities occur, deforestation can develop gradually as herbivory
260 prevents tree recruitment over time (Beschta and Ripple 2009) as well as the closure of forest

261 gaps. Thus, over ecological time the exclusion of large carnivores from forest landscapes may
262 lead to simplified plant communities, alternative stable states, and altered biodiversity
263 (Terborgh et al. 2001; Côté et al. 2004; Beschta and Ripple 2009; Estes et al. 2011).
264 Examples from the case studies we reviewed include a lack of tree regeneration for fir (*Abies*
265 spp.), pine (*Pinus* spp.), hemlock (*Tsuga* spp.), and deciduous species, sometimes resulting in
266 a conversion to less palatable spruce (*Picea* spp.) forests or increases in grasses (Angelstam et
267 al. 2000; Palmer and Truscott 2003; Heuze et al. 2005). Declines in palatable understory
268 shrub species (Trumbull et al. 1989; Schreiner et al. 1996), as well as changes in invertebrate
269 communities (Suominen 1999), were also identified.

270 Cervid irruptions following wolf extirpation have been documented in diverse
271 ecosystems of western North America (Leopold et al. 1947; Ripple and Beschta 2005). Plant
272 damage following cervid irruptions has also been found in regions with relatively low
273 productivity as well as those with very high productivity (Beschta and Ripple 2009). Changes
274 in forest plant communities, such as a reduction in the abundance of woody browse species
275 after wolf extirpation, can cause accelerated streambank erosion, thus leading to changes to
276 stream morphology and fish habitat (Beschta and Ripple 2011). Loss of large carnivores may
277 have potential implications for climate change by reducing long-term sequestration of carbon
278 due to a lack of recruiting woody plants as well as creating simplified and novel ecosystems
279 that may be less resilient to a changing climate. Any reductions in intense herbivory that slow
280 deforestation and increase forest regeneration could conserve and sequester carbon, especially
281 in the mid- and high-latitudes where most of the world's forest carbon is stored (Dixon et al.
282 1994; Luysaert et al. 2008).

283 The analysis of published studies may contain various biases (e.g., non-randomization
284 of study sites, continental bias, biome bias, species bias). Our reliance on published articles
285 resulted in the data herein being biased toward North America ($n = 29$) over Eurasia ($n = 13$),
286 and for moose ($n = 26$) over the other cervid ($n = 16$) species. There are also more study sites
287 in the boreal than in the temperate biomes. This is likely due to more human development and
288 predator extirpations in temperate regions. We were also unable to assess the potential
289 importance of bottom-up variables, other than productivity, that could affect cervid abundance
290 in northern latitudes (e.g., winter severity). Results may be affected by the influence of
291 humans upon wolves, since wolf density in southern areas may be reduced due to greater
292 abundance of people. However, southern sites also have less severe winters which may
293 partially account for any increases in ungulate abundance, so results could be confounded.
294 We also note that our estimates of potential *NPP* were derived from a global model with grid
295 cells typically larger than the cervid study areas.

296 There are other factors that can contribute to high herbivore densities in the absence of
297 wolves, such as the creation of early seral forests by humans, which may make it difficult for
298 predators to serve as restorative agents (Ray et al. 2005; Ritchie et al. 2012). However, in our
299 analysis, we consistently found relatively low cervid densities in regions that have both
300 wolves and extensive logging, including southern Canada and northern Minnesota. Moreover,
301 due to the limits of human tolerance, it may not be possible for predators to achieve
302 ecologically functional population sizes in many of the areas where cervids have become
303 highly abundant (Beschta and Ripple 2010).

304

305 **Conclusions**

306 On average, we found cervid densities in systems without wolves to be approximately
307 six times greater than that of systems with wolves (2.6 vs. 15.5 DE/km^2). Cervid densities in
308 systems with wolves and bears ranged from 0.03 to 8.4 DE/km^2 with density increasing
309 slightly with net primary productivity. These results could serve as benchmarks, based on the
310 productivity of a particular region, for designing and evaluating the management of non-
311 migratory cervid populations where the goal is to emulate the range of densities typically
312 found when wolves and bears are present in northern forests. Additionally, the wolf densities
313 presented herein ($\bar{x} = 17.8 /1000 km^2$, range 2.3-40.2) could also be used as benchmarks for
314 assessing wolf management goals across a range of productivities. In general, regions with
315 higher productivity and intact habitat have the capability to support higher wolf densities than
316 areas with lower productivity (Fig. 4).

317 Recent research suggests that conservation programs based on the presence of apex
318 predators may lead to broader biodiversity benefits (Sergio et al. 2008). Thus, sites containing
319 intact carnivore guilds and which retain ecological processes should be considered as priority
320 areas for both research and conservation planning (Woodroffe and Ginsberg 2005).
321 Additionally, repatriating large carnivores to portions of their former range may still be
322 possible and could have positive ecological effects. For example, the reintroduction or
323 recolonization of wolves, decades after extirpation, has shown to positively affect tree and
324 shrub recruitment at some sites on ungulate winter ranges where cervids seasonally migrate
325 (Beschta and Ripple 2007; Ripple and Beschta 2012). More research is needed to determine
326 to what extent large predators structure ecosystems in areas with both migrating and
327 nonmigrating large herbivores. The preservation or recovery of large predators may thus

328 represent an important conservation need for helping to maintain the resiliency of northern
329 forest ecosystems, especially in the face of a rapidly changing climate.

330

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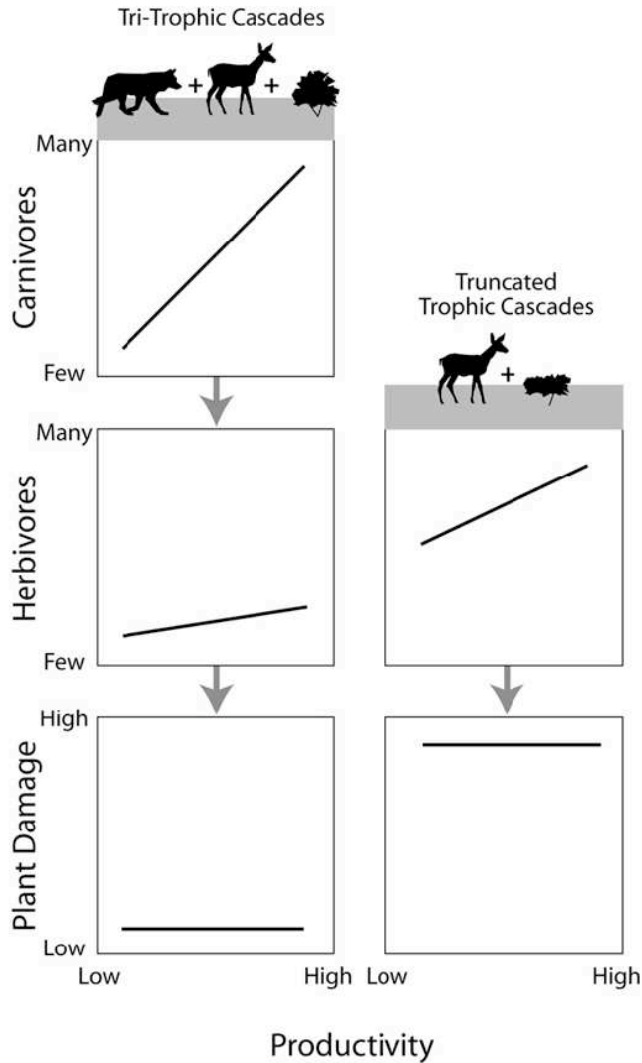
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495 **List of Figures**



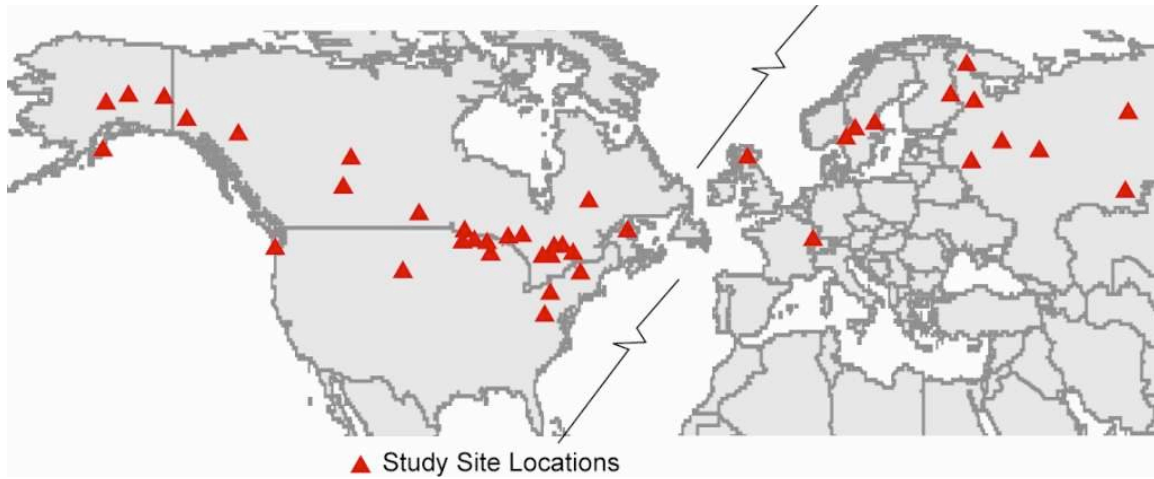
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497 Figure 1. Conceptual diagram of trophic cascades showing hypothesized predator densities,
498 herbivore densities, and plant damage for populations across a productivity gradient in the
499 presence (left column) and absence (right column) of large predators in productive ecosystems
500 with NPP > 0.7 kg/m²/yr (based on Oksanen *et al.* 1981, Oksanen 1992).

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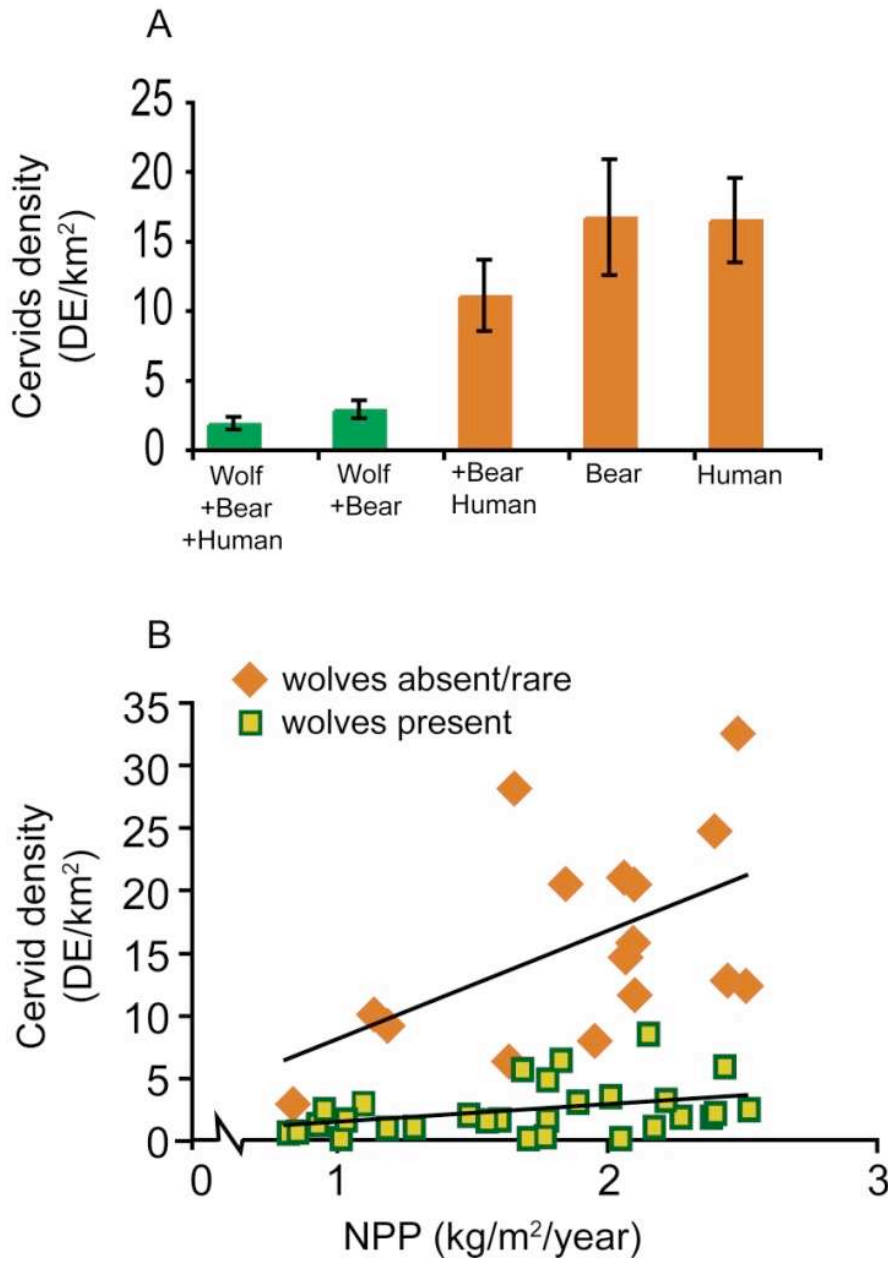
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505 Figure 2. Locations of study sites in North America and Eurasia.

506



507

508 Figure 3. (A) Mean cervid densities with standard errors by predator guild [wolf + bear +

509 human ($n = 14$), wolf + bear ($n = 12$), bear + human ($n = 3$), bear ($n = 6$), human ($n = 7$)] and

510 (B) cervid densities (y) as a function of net primary productivity (x) for study sites with

511 wolves present ($y = 1.54x - 0.06$; $SEE = 1.9$, $R^2 = 0.17$, $p = 0.036$, $n = 26$) and study sites

512 where wolves are absent/rare ($y = 8.64x - 0.99$; $SEE = 7.0$, $R^2 = 0.28$, $p = 0.035$, $n = 16$). SEE

513 represents standard error of the estimate.

514



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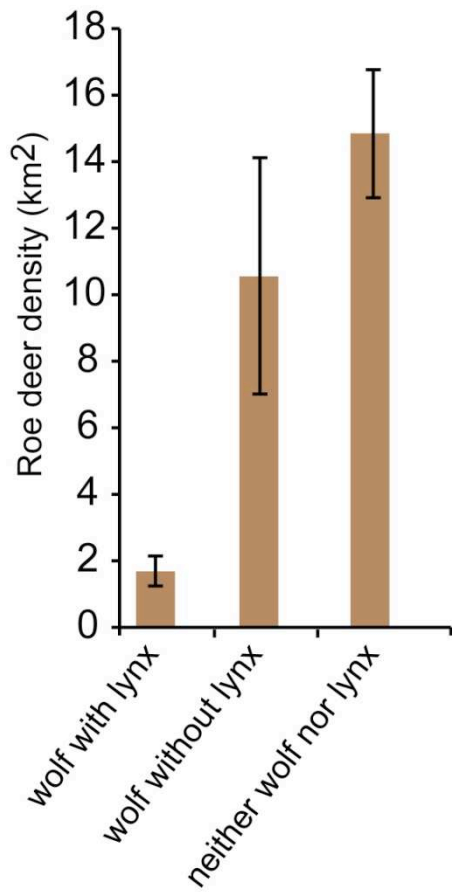
516 Figure 4. Wolf densities (y) as a function of net primary productivity (x) ($y = 13.08x - 3.49$;

517 $SEE = 10.0, R^2 = 0.35, p = 0.008, n = 19$). SEE represents standard error of the estimate.

518

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521

522 Figure 5. Mean roe deer densities in Europe with standard errors by predator guild [wolf with
523 lynx (n = 15), wolf without lynx (n = 21), neither wolf nor lynx (n = 36)]. Adapted from
524 Melis *et al.* (2009).

525

526

Appendix 1

527 Locations, species, densities of cervids and wolves, predator present/absent, net primary productivity (*NPP*), and plant damage for 42
 528 sites used in analysis; and followed by full citations to table.

<u>Location</u>	<u>Latitude</u>	<u>Longitude</u>	<u>Cervid Species</u>	<u>Cervid Density¹</u>	<u>DE Density²</u>	<u>Wolf Density³</u>	<u>Human</u>	<u>Bear</u>	<u>NPP⁴</u>	<u>Plant Damage⁵</u>	<u>Ref. #</u>
Cent. Sweden	59.5N	12.37E	moose	2.6	15.6	A	P	A	2.10	yes	1
Elk Island NP ⁶ , Cent. Alberta	53.63N	112.85W	moose	1.5	9	A	P	A	1.19	N/A	2
Riding Mt NP, S. Manitoba	50.76N	100.24W	moose	0.94	5.6	P	A	P	1.69	N/A	3
Gaspésie Park, E. Quebec	48.9N	66.40W	moose	1.9	11.4	A	A	P	2.10	no	4
S.W. Yukon	61.25N	138.67W	moose	0.17	1	P	P	P	1.29	N/A	5
Denali, Cent. Alaska	63.60N	151.50W	moose	0.26	1.6	5.6	A	P	1.78	N/A	6,7
E.Cent. Alaska	64N	142W	moose	0.09	0.5	8	P	P	0.82	no	8
Pukaskwa NP, S.Cent. Ontario	48.25N	85.92W	moose	0.3	1.8	14.9	A	P	2.39	N/A	9
S.W. Quebec (MW area)	47.1N	76.7W	moose	0.27	1.6	13.8	rare	P	1.60	N/A	10
N.E. Alberta (AOSERP area)	57.19N	111.64W	moose	0.26	1.6	6.6	P	P	1.03	N/A	11
E. Alaska	64.25N	148W	moose	0.2	1.2	15.6	P	P	0.93	N/A	12
Papineau-Labelle, S. Quebec	46.17N	75.50W	deer	3	3	28	A	P	1.89	N/A	13
E.Cent. Ontario	45.92N	78.97W	deer	5.8	5.8	40.2	A	P	2.44	N/A	14
N.Cent. Minnesota	47.75N	93.25W	deer	6.3	6.3	39	P	P	1.83	N/A	15
Wind Cave NP W. South Dakota	43.6N	103.45W	elk	3.3	9.9	A	P	A	1.14	no	16
Olympic NP, W. Washington	47.78N	123.93W	elk	6.8	20.4	A	A	P	2.10	yes	17
Cent. Scotland	57.13N	3.93W	elk	9.3	27.9	A	P	A	1.66	yes	18
N.W. Michigan	46.77N	89.75W	deer	6	6	A	P	P	1.64	yes	19
N. Pennsylvania	41.60N	79W	deer	12.6	12.6	A	P	P	2.45	no/yes	20,21
S.Cent. Sweden	60.5N	13.60E	moose	1.3	7.8	A	P	A	1.96	yes	22
Karelia Russia	63.50N	33.1E	moose	0.25	1.5	P	P	P	1.56	no	22
N. New York	44.15N	74.15W	deer	12.2	12.2	A	A	P	2.52	yes	23
Cent. Quebec (MCW area)	52.50N	73.00W	moose	0.03	0.2	6.7	P	P	1.77	N/A	10
N.E. France	47.83N	6.97E	elk	8.2	24.6	A	P	A	2.40	yes	24

N.E. Wisconsin	45.87N	88.70W	deer	14.5	14.5	rare	P	P	2.07	yes	25
E.Cent. Sweden	61.00N	17.00E	moose	3.4	20.4	A	P	A	1.85	yes	26
Canaan Park , West Virginia	39.07N	79.52W	deer	32.4	32.4	A	A	P	2.49	yes	27
Mauricie Park, S.E. Quebec.	46.80N	78W	moose	0.4	2.4	P	A	P	2.53	N/A	28
Chapleau N.E. Ontario	47.90N	83.40W	moose	0.35	2.1	P	A	P	2.40	N/A	29
Voyageurs NP, N. Minn.	48.5N	92.9W	deer	8.4	8.4	33	A	P	2.15	N/A	35
Bashkirsky, Russia	53.33N	58.00E	moose	0.4	2.4	20.8	A	P	0.95	N/A	30
Darvinsky, Russia	58.74N	37.90E	moose	0.3	1.8	12	A	P	2.27	N/A	30
Laplandsky, Russia	67.95N	31.87E	caribou	1.4	2.8	rare	A	P	0.84	N/A	30
Pechoro-Ilychsky, Russia	62.46N	58.72E	moose	0.05	0.3	2.3	A	P	0.85	N/A	30
Tver Region, Russia	56.48N	32.9E	moose	0.17	1	P	P	P	2.18	N/A	31
Kostroma Region, Russia	58.11N	44.E	moose	0.15	0.9	4.4	P	P	1.19	N/A	32
E.Cent. Finland	64.50N	29.12E	moose	0.31	1.9	P	P	P	1.49	N/A	33
E.Cent. Ontario	46N	80.1W	deer	3.1	3.1	35.7	P	P	2.22	N/A	34
N.E. Wisconsin	45.87N	88.70W	deer	20.8	20.8	rare	A	P	2.07	yes	25
N.E. Minnesota	47.67N	91.56W	moose	0.56	3.4	28	P	P	2.01	N/A	35
Kenai Alaska	59.78N	150.71W	moose	0.8	4.8	14.2	P	P	1.78	N/A	36
N. British Columbia	59.00N	131.67W	Moose	0.34	2.0	10.0	P	P	1.06	N/A	37

529 Footnotes to above table: ¹Cervid densities are #/km², ²deer equivalent (DE) densities are #/km² (deer = 1 DE, caribou = 2 DE, elk = 3 DE, moose = 6 DE), ³wolf densities are #

530 km², P = present, A = absent, ⁴kg of dry mass/m²/yr, ⁵effects of herbivory on plants: yes = plant damage described in article; low/no = little or no plant damage described in artic

531 N/A = herbivory effects not a subject covered in the article, ⁶ NP=National Park.

532 **Full References to Appendix 1 Table**

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