Effects of gray wolf-induced trophic cascades on ecosystem carbon cycling

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Abstract. It is predicted that predator-induced trophic cascades could have important impacts on ecosystem carbon cycling. Yet the magnitude and direction of predator impacts on carbon cycling have not been widely quantified for terrestrial ecosystems. Here, we report on analyses of the potential for gray wolves to have cascading impacts on ecosystem carbon cycling. Our goal is to provide reasonable first approximations of their potential role in this fundamental ecosystem process. We find that gray wolves could lead to an increase in net ecosystem productivity (NEP) of 24.0–52.0 g $C \cdot m^{-2} \cdot yr^{-1}$ in Isle Royale's boreal forest, and a decrease in NEP of 30.03–102.88 g $C \cdot m^{-2} \cdot yr^{-1}$ in Yellowstone's grasslands. If such gray wolf impacts scale up to the broader North American boreal and grassland gray wolf range, these estimates suggest a potential for the indirect effects of wolves on yearly carbon fluxes to be on the same order of magnitude as the fossil fuel emissions of 6–20 million passenger cars per year. While considerable heterogeneity and uncertainty in gray wolf effects is likely to exist over both time and space, our results suggest that it may be worth examining in more detail the potential significance of the indirect effects of top predators on terrestrial ecosystem carbon using more systematic landscape-scale sampling in locations with and without wolves.

Key words: *Canis lupus;* carbon sequestration; climate change; Isle Royale; wolves; Yellowstone National Park.

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Introduction

There is a rising call to shift the focus of conservation from protecting single species to a broader focus on protecting species as members of biotic communities and ecosystems (Ray et al. 2005, Soule et al. 2005, Dobson et al. 2006, Sinclair and Byrom 2006, Estes et al. 2011). This call stems from the recognition that species are functionally interdependent through direct and indirect trophic connections within food webs and that these trophic relations can instrumentally determine the structure and functioning of ecosystems (Ray et al. 2005, Soule et al. 2005, Dobson et al. 2006, Sinclair and Byrom 2006, Heithaus et al. 2008, Schmitz et al. 2010, Estes et al. 2011). Because ecosystem functioning (e.g., carbon cycling) can provide important environmental services (e.g., greenhouse gas regulation, ecosystem carbon storage), it stands to reason that any conservation action that ensures that these trophic relations remain intact and endure would accordingly be predicted to sustain vital services that support societal welfare (Flueck

2000, Dobson et al. 2006, Schmitz et al. 2010, Estes et al. 2011).

This issue is especially germane to large carnivore conservation (Ripple et al. 2014). Some of these species are being lost from ecosystems at disproportionately high rates just as we are learning more about their important roles in controlling the functioning of ecosystems (Duffy 2003, Heithaus et al. 2008, Schmitz et al. 2010, Estes et al. 2011, Ripple et al. 2014), leading to increased calls to enhance carnivore protection and restoration in order to safeguard or recover those functions and ensuing services. These calls are predicated on the assumption that carnivore species will influence ecosystem functions in the same way across all ecosystem types, especially via trophic cascades in which they exert strong control over ecosystem functions through direct effects on their prey and indirect effects on their prey's plant resources (Ray 2005, Estes et al. 2011, Ripple et al. 2014). This assumption remains uncertain because scientific insight about the general role that large carnivores play in shaping ecosystem functions is only now accumulating (Ray 2005, Estes et al. 2011). Moreover, the nature and strength of carnivore-induced cascading effects on ecosystem functioning may vary with ecosystem type (Soule et al. 2005, Schmitz et al. 2010), which may mean that the assumption is invalid. We begin to evaluate this assumption with a quantitative assessment of the impact that one large carnivore species—the gray wolf (*Canis lupus*)—may have on one particular ecosystem function—carbon cycling—in different ecosystem types.

We focus on the gray wolf for several reasons. In conservation circles, its restoration to a grassland ecosystem to which it historically belonged is celebrated as a successful recovery of a trophic cascade (Smith et al. 2003, Marris 2014). Gray wolf populations also remain or have expanded throughout other parts of the species' range (Ripple et al. 2014). And, of all studies of large carnivore effects on ecosystems, the most comprehensive insights arguably come from the analysis of gray wolf-induced trophic cascades (McLaren and Peterson 1994, Hebblewhite et al. 2005, Ripple et al. 2014). This includes studies in both grassland and boreal ecosystems, enabling the comparison of its potential effects in different ecosystem types.

We focus on carbon cycling because wolves might impact the amount of CO_2 exchanged between ecosystems and the atmosphere. This is contentious, as ecosystem science has long held that plants, microbes, and fire, not animals, exert primary control over carbon exchange between ecosystems and the atmosphere (Schmitz et al. 2014). A decided lack of accounting for animal effects continues even for our focal ecosystems (e.g., Potter et al. 2011). Yet, animals may play equally significant roles (Schmitz et al. 2014), in some cases via carnivore-induced trophic cascades (Schindler et al. 1997, Wardle et al. 2007, Wilmers et al. 2012, Atwood et al. 2013, Strickland et al. 2013). Whether or not trophic cascades lead to consistent outcomes in different ecosystems remains uncertain, however (Schmitz et al. 2010, 2014). But, given the looming threat to many large carnivores worldwide, the mere potential to have important ecosystem effects compels arguments for policy to take precautionary conservation actions (Ripple et al. 2014).

In the interest of advancing evidence-based conservation on this issue (Ray 2005, Soule et al. 2005), we synthesize data to evaluate the potential magnitude of gray wolf impacts on ecosystem carbon cycling via trophic cascades, and whether or not these impacts are consistent across grassland and boreal ecosystems. Our estimates are intended to provide reasonable approximations in order to assess the potential for wolves to influence regional carbon budgets. But their effect on net ecosystem carbon uptake or release is context dependent and might only be realized over long timescales. We conclude that conservation science can provide needed context-dependent insights about when, where, and how carnivore-induced trophic cascades influence ecosystem functions and services.

Methods and Results

We brought together data from previous studies on predator–prey and herbivore–plant interactions, as well as on ecosystem carbon fluxes to account for the impacts of gray wolves on carbon cycling within a grassland and boreal ecosystem. We estimated net primary productivity (NPP) in g C·m^{-2}·yr^{-1} as the difference between carbon taken up by photosynthesis (i.e., gross primary productivity) and plant respiration

(Chapin et al. 2012). We also debited from NPP the carbon released by heterotrophic (animal and soil microbial) respiration to estimate net ecosystem productivity (NEP), that is, the net carbon retained in the ecosystem (Chapin et al. 2012). Our budget was estimated for cases when wolves were present vs. absent to account for gray wolf effects mediated by their direct interactions with their herbivore prey and hence their indirect interactions with plants and the soil. In boreal forest of North America, wolves prey primarily on moose (*Alces alces*), a dominant browser of woody vegetation (Smith et al. 2003). In the grasslands of the Rocky Mountains, wolves prey primarily on elk (*Cervus elaphus*) (Smith et al. 2003), a dominant grazer of grasses and herbaceous vegetation. Our calculations result in partial budgets because the focal species are a subset of the larger food webs in their respective ecosystems (Smith et al. 2003) and information is currently lacking to explicitly account for the effects of other species. Nevertheless, the enclosure designs in the studies used to calculate gray wolf effects include other species effects as part of the background environmental variation. We thus conservatively assess whether wolves are even capable of causing appreciable changes to ecosystem functioning, given the inherent food web complexity. Moreover, by focusing just on these species, we are also following suggestions (Soule et al. 2005) to consider the dominant, strong interactors as the starting point for assessments of the conservation implications of interacting species.

Boreal carbon budget

Boreal NPP.—Estimates of moose impacts on boreal forest NPP were based on data from exclosure experiments conducted in Isle Royale National Park, Michigan, USA, by McInnes et al. (1992) with specifics of the analysis presented in Appendix A of Schmitz et al. (2014). Net primary productivity of trees inside moose exclosures averages 8×10^8 g·km^{-2}·yr^{-1}. Moose browsing causes a decline in NPP from 0.7 to 1.5×10^8 g·km^{-2}·yr^{-1} per moose (McInnes et al. 1992). Empirical analysis of 27 studies of gray wolf–moose predator–prey relationships revealed that moose populations will stabilize at ~2 moose/km^2 without predators and at 1.3 moose/km^2 with wolves (Messier 1994). Combining these results

yields an estimate of boreal forest NPP of 5.0–6.6 $\times 10^8$ g·km^{-2}·yr^{-1} without wolves and 6.05–7.09 $\times 10^8$ g·km^{-2}·yr^{-1} with wolves. The gray wolf effect, taken as the difference in these two quantities, is 0.49–1.05 $\times 10^8$ g·km^{-2}·yr^{-1} or 49–105 g·m^{-2}·yr^{-1}. Trees are comprised of approximately 50% carbon (Schmitz et al. 2014); thus, wolves indirectly increase the carbon uptake in NPP by 24.5–52.5 g C·m^{-2}·yr^{-1} in boreal forest.

Boreal NEP.—We estimated the impacts of wolves on boreal forest NEP as NPP—soil respiration—moose respiration. This assumes that respiration by other animals is small and/or unlikely to vary substantially between scenarios with and without wolves. We linearly interpolated the reported soil respiration rates assuming moose densities that ranged from 0.5 to 1.5 moose/km^2 (McInnes et al. 1992, Schmitz et al. 2014) to yield the estimates of soil respiration of 3.25 and 3.875×10^4 g C·km^{-2}·yr^{-1} with and without wolves, respectively. Moose metabolic rate during the more active nonwinter months is 552 KJ/kg$^{0.75}$ (Regelin et al. 1985). Given an average moose body mass of 359 kg, we estimated moose respiration to be 4.55×10^4 KJ·ind^{-1}·d^{-1}. Assuming a conversion of 41 KJ/g C (see Appendix A in Supplemental material in Schmitz et al. 2014), this leads to moose respiration rates of 5.2×10^5 g C·km^{-2}·yr^{-2} with wolves and 8×10^5 g C·km^{-2}·yr^{-1} without wolves. Net ecosystem productivity therefore ranges from 3.02 to 3.54 $\times 10^8$ g C·km^{-2}·yr^{-1} with wolves and from 2.5 to 3.3 $\times 10^8$ g C·km^{-2}·yr^{-1} without wolves. The total gray wolf effect is to increase NEP by 2.4–5.2 $\times 10^7$ g C·km^{-2}·yr^{-1}, or 24–52 g C·m^{-2}·yr^{-1}.

We next extrapolated gray wolf indirect contributions to carbon cycling to the whole North American boreal forest in which both wolves and moose co-occur using area estimates from Schmitz et al. (2014). We appreciate that large variations in the nature and strength of species interactions are likely to occur over such a vast area, leading to spatial variation in the magnitude of ecosystem carbon uptake. In addition, gray wolf densities were higher in Isle Royale (during the period for which the data we extrapolated from here were collected) where they enjoy full protection than they are elsewhere in the Boreal. As such, this extrapolation should not be viewed as a precise evaluation of gray wolf impacts on carbon cycling, but rather as an order-of-magnitude

first approximation of their potential landscape-scale effects prior to their extensive exploitation by humans. Intact boreal forest currently covers 1.89×10^6 km^2 of North America (Schmitz et al. 2014). Applying our estimates of NEP to the North American boreal forest where gray wolves and moose co-occur yields a gray wolf impact on carbon sequestration of $4.6–9.9 \times 10^{13}$ g C/yr. To put these numbers in perspective, the U.S. EPA estimates that the average yearly emissions from a passenger vehicle are 5.1 metric tons of CO_2 or 1.39×10^6 g C/yr. Thus, the indirect impact of wolves on boreal forest carbon sequestration might have once been equivalent to reducing the tailpipe emissions of $3.3–7.1 \times 10^7$ passenger cars per year.

Grassland carbon budget

Grassland NPP.—Frank et al. (2002) showed experimentally that grazers in Yellowstone National Park, especially elk, have a stimulative effect on grassland NPP by enhancing nutrient cycling rates, which is a function of the amount of grassland biomass consumed. Stimulation of NPP (Stim, g·m^{-2}·yr^{-1}) was related linearly to consumption (g/m^2) and given by

$$\text{Stim} = 6.5 + 4.1 \times \text{consumption} \qquad (1)$$

Frank (2008) compared grazer consumption rates before and after gray wolf reintroduction and found that grazer consumption rates had declined post-gray wolf reintroduction for similar levels of mean aboveground net primary productivity (ANPP). Specifically, pre-gray wolf grazer consumption rates were given by

$$\text{Consumption}_{w/o\,wolves} = 0.44 \times \text{ANPP} - 15.4 \qquad (2)$$

while post-gray wolf grazer consumption rates were given by

$$\text{Consumption}_{w/wolves} = 0.56 \times \text{ANPP} - 0.001 \times \text{ANPP}^2 - 33.2. \qquad (3)$$

Combining Eqs. 2 or 3 with Eq. 1 yields estimated relationships for the stimulative effects of grazers on NPP for varying levels of ANPP with and without wolves. Specifically, stimulation of NPP without and with wolves is given by

$$\text{Stim}_{w/o\,wolves} = 6.5 + 4.1 \times (0.44 \times \text{ANPP} - 15.4) \qquad (4)$$

and

$$\text{Stim}_{w\,wolves} = 6.5 + 4.1 \times (0.56 \times \text{ANPP} - 0.001 \times \text{ANPP}^2 - 33.2) \qquad (5)$$

respectively.

At low levels of ANPP (75 g/m^2), this leads to estimates of NPP stimulation of 19.5 and 78.7 g·m^{-2}·yr^{-1} with and without wolves, respectively, for a net gray wolf effect of -59.1 g·m^{-2}·yr^{-1}. At high levels of ANPP (250 g/m^2), estimates of NPP stimulation are 188.1 and 394.4 g·m^{-2}·yr^{-1} with and without wolves, respectively, for a net gray wolf effect of -206.2 g·m^{-2}·yr^{-1}. Assuming that carbon content of vegetation is 50% of dry weight, wolves indirectly decrease NPP by 29.55–103.1 g C·m^{-2}·yr^{-1}.

Grassland NEP.—We estimated the impacts of wolves on grassland NEP as NPP—soil respiration—elk respiration with and without wolves. Average elk population sizes were 17,725 and 13,227, respectively, during the pre- and post-gray wolf periods during which Frank (2008) measured the grassland productivity. Other large grazer populations (pronghorn and bison) declined during that period from 600 to 240 pronghorn and from 2800 to 2400 bison, respectively, but these changes were unlikely to be related to wolves (White et al. 2007, Frank 2008). Elk account for 85–96% of gray wolf prey depending on season, whereas bison only account for 1.3–4.1% and pronghorn are <1% (Metz et al. 2012). While the decline of elk, pronghorn, and bison is suggestive of some other factor causing declines in all three species, the simultaneity of the decline in all three species might be coincidental. Bison have since increased almost twofold, while elk have continued to decline, and pronghorn in the southern part of the GYE have increased with gray wolf reintroduction because wolves are suppressing their main predator, coyotes (Berger et al. 2008). Frank et al. (2002) reported NPP from grazed grassland as varying from 325 to 565 g C/m^2. We assumed an average elk body mass of 277 kg (Greer and Howe 1964) and estimated a respiration rate of 217 g C·ind^{-1}·d^{-1} using a metabolic rate of 0.32 kcal/kg (Wickstrom et al. 1984). Assuming a Northern Range area of 1530 km^2 (Lemke et al. 1998), this leads to a respiration rate of 0.92 g·m^{-2}·yr^{-1} pre-gray wolf

and 0.68 g·m^{-2}·yr^{-1} post-gray wolf. We extrapolated the yearly soil respiration from the monthly values taken at full light during the growing season months by Risch and Frank (2006). We incorporated the diurnal variation in soil respiration using data from Risch and Frank (2010). Finally, we assumed that soil respiration during the months of the year that are typically covered with snow was 25% of the average during the growing season (Sommerfeld et al. 1993). This led to an estimated yearly soil respiration rate of 228 g C·m^{-2}·yr^{-1}. Data were not available to estimate the differences in soil respiration in the presence and absence of wolves, so we conservatively assumed soil respiration to be constant across both scenarios. We calculated an NEP of 66.77–233.22 g C·m^{-2}·yr^{-1} with wolves and 96.08–336.1 g C·m^{-2}·yr^{-1} without wolves. The change in NEP from before to after wolf reintroduction was thus 30.03–102.88 g C·m^{-2}·yr^{-1}.

Again, to evaluate the potential larger-scale impacts, we calculated the areas of North American grassland in which wolves overlap with elk by taking the intersection of the gray wolf's current range (IUCN 2013) with a montane grassland coverage layer for North America (2005). This resulted in 2.94×10^5 km^2 of grassland in the gray wolf's range. Applying our estimates of NEP to these areas yields a negative impact of wolves on carbon sequestration of 8.8×10^{12}–$3.0 \geq 10^{13}$ g C/yr or the equivalent of adding the average emissions of 6.3–21.6×10^6 cars per year.

Discussion

Our analyses indicate that wolves are unlikely to have the same net impact on ecosystem–atmosphere carbon exchange in the different ecosystems despite inducing trophic cascades in both. Rather, the nature of the effect depends upon the biological pathways through which their indirect effects manifest resulting in more carbon sequestered in one ecosystem (boreal) and less in the other (grassland).

In boreal ecosystems, moose suppress forest productivity by selectively browsing on hardwoods and releasing conifer, which subsequently decreases the litter nitrogen return to the soils (Pastor et al. 1993). Wolves partially suppress the impacts of moose on forest dynamics

leading to an increase in NPP. The food web in the boreal ecosystem is simpler than in the grassland, making it easier to ascribe a potential causal link of effects (Smith et al. 2003). In many grasslands, grazing stimulates both below- and aboveground productivity of grassland plants (McNaughton 1976, Frank et al. 2002, Ziter and MacDougall 2013). Grazing is thought to stimulate production by removing the aboveground leaf and stem tissue that have high maintenance costs and shade actively growing leaf tissue, thus allowing assimilated carbon to be allocated toward growth (McNaughton 1984, Frank et al. 2002).

Although the impacts of wolves on Yellowstone's elk population remain controversial, an emerging consensus is building that the reintroduction of wolves has played a significant role in the decline of the Northern Yellowstone elk herd (White and Garrott 2013, Peterson et al. 2014). Human harvest, drought, and other large carnivores have also likely played a role in the decline of Yellowstone elk, but at this time it is not possible to disentangle the relative contributions of each factor on the overall elk population decline. Our analyses, however, are based on a decline in elk population of only 25.4% (from 17,725 and 13,227), while the population of elk has declined by over 79% in total since gray wolf reintroduction (from over 19,000 to <4000). So while we cannot precisely quantify how much of the elk decline was due to gray wolves, our estimates as to their indirect effects on carbon cycling are likely to be conservative. Still, it should be recognized that other factors contributing to the decline in elk, such as other predators and climate, also have impacts on ecosystem carbon cycling. Our focus here has been on wolves, because they are strong interactors in these ecosystems, and their reintroduction/recolonization is likely to have changed the dynamics of carbon cycling.

Our accounting for the grassland ecosystem does not include the potential cascading impacts of wolves on stands of woody vegetation that are interspersed throughout these grasslands (Ripple and Larsen 2000, Ripple and Beschta 2007). Gray wolf effects could cause carbon buildup in willow, aspen, and cottonwood that appear to have undergone resurgence in growth due to decreased elk herbivory following the gray wolf reintroduction (Beyer et al. 2007, Ripple and

Beschta 2007, Beschta and Ripple 2014). Such effects could compensate for carbon losses from grassland (Schmitz et al. 2014). However, these impacts to date have likely been localized, with a small contribution to regional carbon budgets. Willow covers less than 1.8% of the land area covered by the focal grassland on the Northern Range of Yellowstone (Savage and Lawrence 2010), and while some areas have undergone willow recovery, most have not because of hysteresis due to lowering of water tables within streams that formerly supported luxuriant willow production (Marshall et al. 2013). Aspen cover 4.8% of the land area in the region (Savage and Lawrence 2010), but for the mid-2000's period from which we have drawn our inferences on grasslands, it is debated whether aspen production was significantly influenced by wolves (Kauffman et al. 2010), thereby causing uncertainty about the effects on NEP.

More recent data from 2012 are now showing extensive sapling recovery in 26–65% of Northern Yellowstone aspen stands (Painter 2013). Cottonwood trees, which cover approximately 1.6% of the land area occupied by grassland (Savage and Lawrence 2010), have undergone a resurgence of young sapling growth in half of their range (Beschta and Ripple 2014). Taken together, these newer findings suggest that if the recovery of woody vegetation (particularly that of aspen) continues, the cascading effect of wolves on woody vegetation could be sufficient enough to offset the negative impact of wolves on grassland carbon cycling. Given that grassland area was recently measured to exceed deciduous forest cover by a factor of 12.13 (Savage and Lawrence 2010), an average increase in woody plant NEP of 364–1247 g $C \cdot m^{-2} \cdot yr^{-1}$ would be required to balance the negative indirect effect of wolves on herbaceous NEP. This is within the growing potential of these species, particularly if there is a concurrent increase in their spatial extent (Grant et al. 2006).

Our estimates indicate that at broad geographic scales, the indirect effects of predators could be large. Extrapolating our results from Isle Royale to the whole boreal forest indicates that the indirect effect of wolves on ecosystem carbon cycling might once have been as large as an increase in NEP equivalent to the emissions of 33–71 million passenger vehicles per year. Clearly, Isle Royale is only one small site in the vast and heterogeneous boreal forest. As such, our extrapolation of gray wolf effects could be greater or smaller than the true amount. Our results indicate, however, that the impact of wolves on carbon cycling was once and may still be significant at the biome scale. This depends on the extent to which gray wolf population densities have declined, together with how other factors such as land-use change now influence moose populations. In the areas with heavy human control of gray wolf populations or where gray wolves have a smaller percentage of large herbivores in their diet, gray wolf impacts on carbon cycling are likely to be attenuated. Extrapolating our results from Yellowstone to North American grasslands within the current range of gray wolves and elk results in a decrease in NEP equivalent to the emissions of 6–21 million vehicles. These estimates will likely increase as gray wolves continue to recolonize the portions of their former range. Again, this result should be interpreted cautiously as considerable differences in ecological processes can exist from one grassland to another. Our estimates are based on accounting for systematic differences in predator abundance or presence. Better scientific inferences could be made if large predators were experimentally excluded from the areas to assess their causal effects on whole ecosystem functioning, but performing experiments with large carnivores is logistically difficult given the required spatial extent and ethical issues associated with manipulating their abundance in the face of their looming declines. Nevertheless, the degree of precision and accuracy in our estimates are on par with estimates of other sources and fates of carbon in the global carbon budget (Schmitz et al. 2014) and therefore give reasonable approximations of the potential direction and order of magnitude of the impact that wolves may once have had on boreal forest and grassland carbon cycling (Fig. 1).

As keystone species, the impact of large carnivores on ecosystems often stands to be quite large relative to their biomass representation within ecosystems (Schmitz et al. 2010, Estes et al. 2011). Accordingly, their ecosystem service values are often used to justify their conservation or restoration to ecosystems (Fluek 2011). Our analyses here offer a cautionary note for policy makers that the ecosystem service benefits provided by large carnivores, even the same
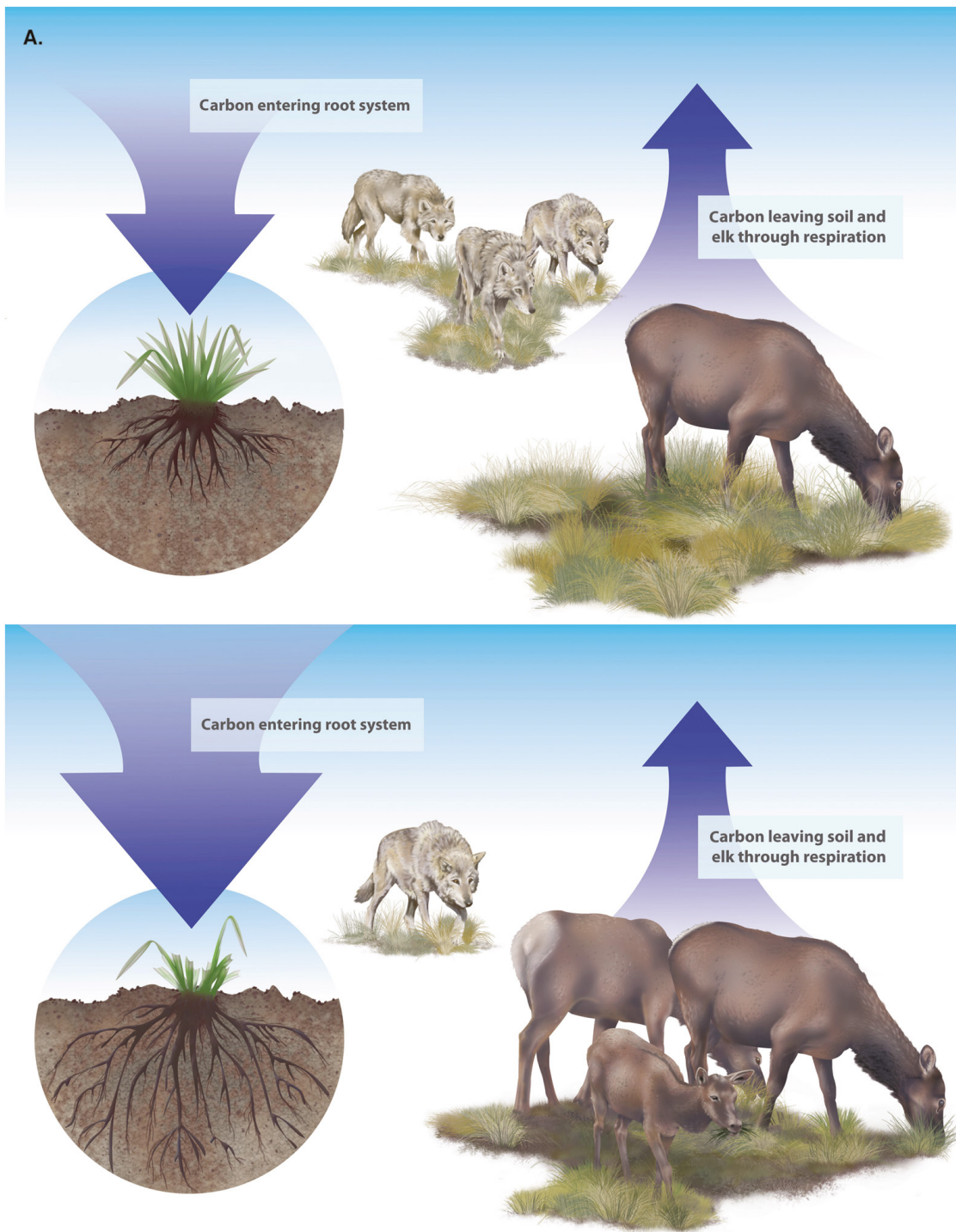
Fig. 1.   Idiosyncratic impacts of wolves on ecosystem carbon cycling. (A) In grasslands, few wolves lead to an increase in herbivory, which stimulates root growth and overall grassland productivity, leading to an increase in net ecosystem productivity (NEP; illustrated as the difference in the thickness of the arrows). (B) In boreal forests, fewer wolves lead to increased moose browsing on deciduous trees leading to increased dominance of spruce, less leaf litter, lower net primary productivity, and an overall decrease in NEP.
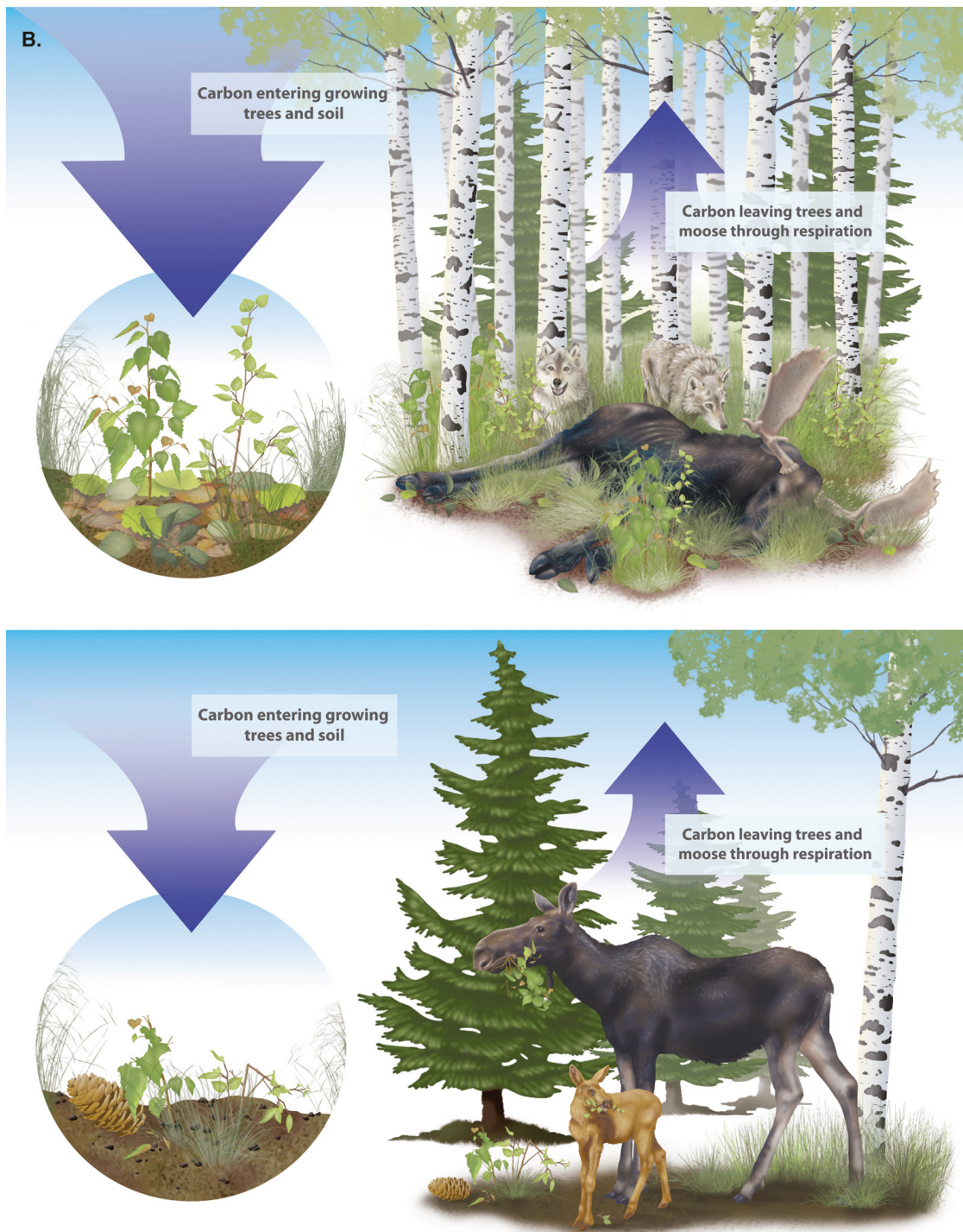
Fig. 1.   Continued.

species of carnivore, may differ across ecosystem types because the nature and strength of effects depends importantly on ecosystem context and is subject to long time lags. Nevertheless, our analyses suggest that it would be an important and worthwhile effort to begin more detailed accounting of these large carnivore effects in the analyses of regional carbon budgets.

Acknowledgments

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