

Digging Further into Wolf-Deer Interactions: Food Web Effects on Soil Nitrogen Availability in a Great Lakes Forest

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Source: The American Midland Naturalist, 176(1):147-151.

Published By: University of Notre Dame

DOI: <http://dx.doi.org/10.1674/0003-0031-176.1.147>

URL: <http://www.bioone.org/doi/full/10.1674/0003-0031-176.1.147>

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Notes and Discussion Piece

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ABSTRACT.—The negative impacts of herbivore consumption on plants are well known, but impacts on ecosystem processes are not. Herbivores can alter soil nutrient availability through herbivory and waste deposition. If predators significantly reduce herbivory, they may impact some soil ecosystem processes. Gray wolves may regulate white-tailed deer herbivory in Great Lakes forests, and this may impact soil nitrogen availability. Deer enclosure/control plots in high- and low-wolf use forest patches were employed to determine whether wolves and/or deer affect nitrogen availability. Despite evidence for deer affecting soil nitrogen availability in other forests and wolves affecting it in grasslands, we found no such effects in this forest. Given the context dependence of top-down impacts on nutrient dynamics, we encourage further inquiry.

Key words: ammonium, deer, ecosystem processes, forest, Great Lakes, indirect effects, nitrate, nitrogen, soil, wolf

INTRODUCTION

Top-down impacts on ecosystem processes, such as nutrient cycling, are well-characterized in aquatic communities but not terrestrial communities (Bardgett and Wardle, 2003; Schmitz *et al.*, 2010). Studying the influences of herbivory on differences in nitrogen availability is particularly important in some systems if we are to better understand and maintain ecosystem integrity (Gilliam, 2006). Herbivory can be significant in terrestrial nitrogen cycling (Pastor *et al.*, 1993; Frank and Groffman, 1998; Belovsky and Slade, 2000; Singer and Schoenecker, 2003; Murray *et al.*, 2013). Herbivores may alter nitrogen dynamics through several mechanisms. Reductions in plant biomass and herbivory-stunted growth can reduce the amount of aboveground nutrient uptake, increasing soil nutrient levels (Bressette *et al.*, 2012). Preferential feeding could also shift dominance between low-quality plants producing slow-decomposing litter and high-quality plants producing fast-decomposing litter (Pastor *et al.*, 1993; Côte *et al.*, 2004; Harrison and Bardgett, 2004). Dung/urine deposition can also increase nutrient availability either by transporting them between systems (Seagle, 2003) or shortcutting litter decomposition (Frank and Groffman, 1998; Bardgett and Wardle, 2003).

Intensified herbivory by predator-free ungulates has substantially impacted many forest communities, reducing plant growth and shifting species compositions (Côte *et al.*, 2004; Ripple *et al.*, 2010). Ungulates are expected to reduce nitrogen availability in forest ecosystems as a result of such effects (Pastor *et al.*, 2006). White-tailed deer (*Odocoileus virginianus*) have particularly impacted eastern forest plant communities (Côte *et al.*, 2004; Rooney, 2009), and as a result may be affecting soil nutrient dynamics (Ritchie *et al.*, 1998; Bressette *et al.*, 2012).

Recovered gray wolves (*Canis lupus*) in turn could mitigate these ungulate impacts by limiting ungulate herbivory (Frank, 2008; Ripple *et al.*, 2010; Schmitz *et al.*, 2010; Callan *et al.*, 2013; Flagel *et al.*, 2016). Deer have been observed to change their distributions as well as foraging behaviors in relation to wolves (Mech, 1977; Flagel *et al.*, 2016), which in turn appears to be reducing deer herbivory impacts on Great Lakes forest plants, including increased sapling growth and understory forb diversity (Callan *et al.*, 2013; Flagel *et al.*, 2016). Wolves meanwhile in Rocky Mountain systems reduce herbivory impacts by lowering grazing ungulate populations (Hebblewhite and Smith, 2010), potentially altering soil nitrogen dynamics in grasslands (Frank, 2008). However, no studies to date have investigated the interaction of wolves and soil nitrogen availability in forests outside carcass distribution (Bump *et al.*, 2009).

In this study we analyzed nitrogen levels within paired deer enclosure and control plots in high- and low-wolf use areas to evaluate wolf and deer impacts on soil nitrogen availability in forests. We expected excluding deer herbivory would increase nitrogen uptake by plants, thus decreasing soil nitrogen levels. We also expected that deer herbivory reduction by wolves would have a similar effect, with soil nitrogen levels higher in high-wolf use areas than low-wolf use.

STUDY AREAS

Most of this work was done at the ~3200 ha University of Notre Dame Environmental Research Center (UNDERC, Land O' Lakes, Wisconsin, 46°13'N, 89°31'W). Habitat is mostly comprised of northern mesic forest patches scattered among bogs and conifer swamps. The forest is dominated by maples (*Acer* spp.), with balsam fir (*Abies balsamea*) less abundant. We also used the 2500 ha Dairymens Inc. game preserve (Boulder Junction, Wisconsin; 46°9'N, 89°51'N), which has similar habitat (although more eastern hemlock; *Tsuga canadensis*). Current white-tailed deer densities at both sites are 7-12 per km² based on Wisconsin Department of Natural Resources estimates. Wolves recolonized these areas in the early 2000s (Rooney, 2009; Flagel *et al.*, 2016). Soils are mostly sandy loam varieties.

Wolf use has been spatially defined as high or low at UNDERC based on collar telemetry and wolf sign surveys. In 2009, 144 m² exclosures were constructed in scattered forest patches to protect plants from deer browsing. Adjacent control plots which deer could browse were also established < 10 m from their respective exclosures so that forest composition was as similar as possible. Ten paired exclosures-controls were built; five each in low- and high-wolf use areas. Maple sapling growth and forb species richness has become significantly greater in low-wolf use exclosures compared to controls, and are also greater in high-wolf use areas versus low-wolf use areas, suggesting a trophic cascade (Flagel *et al.*, 2016).

At Dairymens Inc., four similar ≥196 m² exclosures were constructed in 1990. No pre-exclosure data for these exists, but the understory is thought to have been sparse (Rooney, 2009). Wolf sign has never been detected by the Dairymens exclosures (T. P. Rooney, pers. comm.), therefore we assume these are in an area of low-wolf use. Woody browse and forbs are now nearly absent in Dairymens controls as a result of deer, compared to substantial changes in structure and composition in exclosures (Rooney, 2009).

METHODS

Five 20 cm soil cores spaced ≥ 7 m apart (center and corners) were collected from each deer exclosure and control using a 2.5 cm corer. Cores were collected during the peak growing season (July 9-11, 2013) and after the growing season (before leaf fall; September 28-29, 2013). This was done to assess whether plant phenology (high growth vs. senescence) interacted with wolf/deer impacts (Pastor *et al.*, 1993, Ritchie *et al.*, 1998). An index of ionic nitrogen (ammonium and nitrate) available during the growing season was obtained using buried ion-exchange resin bags. Bags were made by placing 7.5 g of resin beads (Rexyn®, Fisher Scientific Inc., Pittsburgh, Pennsylvania) into 2.5 cm nylon stocking sections (see Binkley *et al.*, 1986). On June 14, 2013, three bags were buried 5 m apart and 5 cm deep along a transect bisecting each UNDERC exclosure or control. Resin bags were collected September 28-29, 2013.

Once collected, cores and resin bags were pooled by exclosure/control, stored in a vacuum-sealed plastic bag, and frozen. Chemical analysis was done by the University of Wisconsin-Madison Soil Testing Laboratories (Verona, Wisconsin). Total nitrogen (%) was quantified by flow injection analysis (FIA) acid digested soil core solution (Lachat QuickChem 8000; Loveland, Colorado). To quantify ammonium and nitrate (ppm), nitrogen was released from resin beads in 2 N KCl, and the solution was then analyzed by FIA.

Statistical analyses.—We used a repeated-measures ANOVA for total % nitrogen (arcsine square-root transformed), with wolf use (high vs. low), deer use (control vs. exclosure), and growing season time (July vs. September) as factors. For Dairymens total nitrogen, we had no wolf factor (uniform). We examined ammonium, nitrate, and total ionic nitrogen (ammonium + nitrate) availability (ppm) using 2×2 ANOVAs, with wolf use and deer use as factors (square-root transformed).

RESULTS

UNDERC total nitrogen (%) did not differ with wolf ($F_{1,8} = 2.38$, $P = 0.161$) or deer use ($F_{1,8} = 0.221$, $P = 0.651$), although growing season time approached significance ($F_{1,8} = 4.63$, $P = 0.064$; Figs. 1A and 1B). Total nitrogen at Dairymens did not differ with deer use ($F_{1,8} = 0.931$, $P = 0.406$) or growing season time ($F_{1,3} = 0.140$, $P = 0.736$; Fig. 1C). Total ionic nitrogen at UNDERC was likewise not affected by wolf ($F_{1,8} = 0.056$, $P = 0.829$) or deer use ($F_{1,8} = 0.976$, $P = 0.352$; Fig. 1D). Ammonium was not affected by wolf ($F_{1,8} = 0.241$, $P = 0.637$) or deer use ($F_{1,8} = 0.696$, $P = 0.428$) (Fig. 1E) and neither was nitrate (wolf

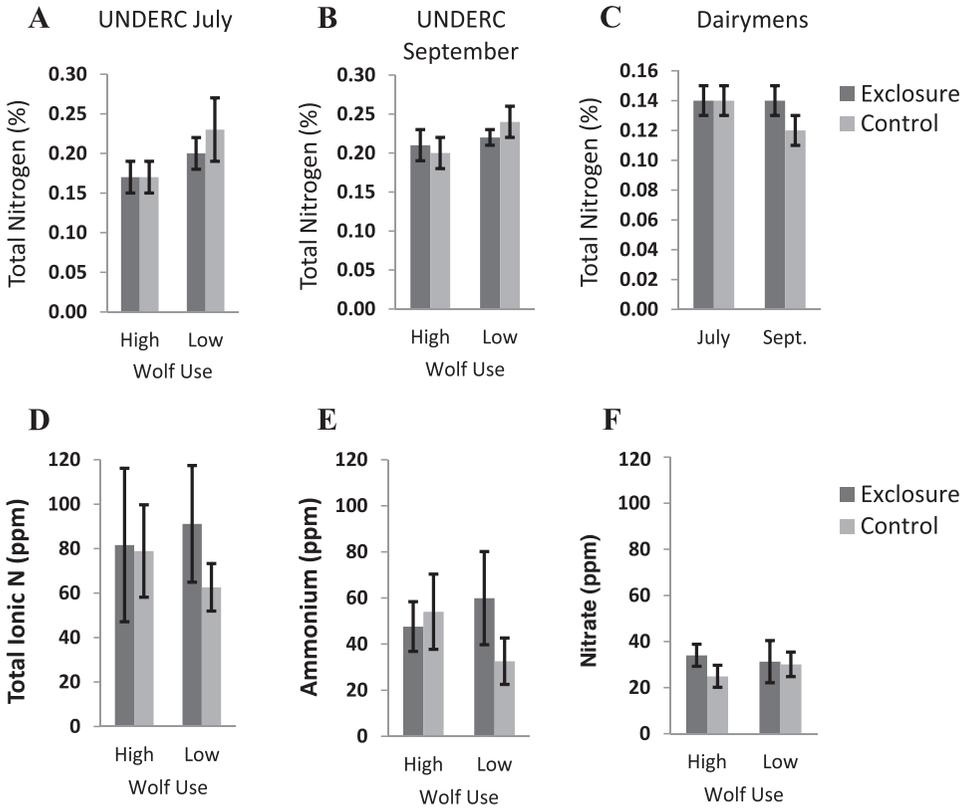


FIG. 1.— Total nitrogen on UNDERC (A and B) and Dairymens (C) deer exclosures and controls as derived from July and September (Sept.) 2013 soil cores, and 2013 growing season ionic nitrogen values (D–F) for UNDERC deer exclosures as derived from resin bags (A) represents UNDERC July core values, whereas (B) represents UNDERC September values. Bags were buried from early-mid June through late September. UNDERC also has the additional factor of varying wolf use. There were no significant differences based on wolf use to report. There were also no significant differences between paired exclosure and control plots. Graphs represent plot means ± 1 SE. Note difference in y-axis scales between UNDERC and Dairymens graphs

use: $F_{1,8} = 0.004$, $P = 0.953$; deer use: $F_{1,8} = 0.639$, $P = 0.447$; Fig. 1F). None of the interactions was significant ($P \geq 0.201$).

DISCUSSION

We did not find any differences in total nitrogen or ionic nitrogen (ammonium, nitrate, or combined) between any treatments at UNDERC or Dairymens. This suggests that neither wolves nor deer cause significant changes in nitrogen availability on these study areas. The lack of significant deer use impacts on nitrogen is not likely due to study time as our results were similar for both short-term (UNDERC) and long-term (Dairymens) exclosures. Growing season time approached significance for UNDERC total nitrogen, which is likely the result of seasonal declines in microbial activity and plant growth (Harrison and Bardgett, 2004).

Observable nitrogen effects may require substantially higher levels of herbivory and/or different plant species compositions (Pastor *et al.*, 1993; Singer and Schoenecker, 2003; Schmitz, 2008). Ritchie *et al.*

(1998) and Bressette *et al.* (2012) found significant deer impacts on forest nitrogen with 3-4 times higher deer densities than those at UNDERC. However, Dairymens enclosures were subject to periods of substantially higher deer densities (>16 per km²) (Rooney, 2009) than UNDERC, but we still found no nitrogen difference. Meanwhile, previous studies which found significant ungulate effects (*i.e.*, Pastor *et al.*, 1993; Ritchie *et al.*, 1998; Bressette *et al.*, 2012) did so in forests with substantially different species compositions (boreal, oak savannah, and oak-hickory, respectively) than UNDERC. Given the prevalence of maple at UNDERC, it is possible that leaf litter inputs dramatically outweigh the impacts of understory changes on soil nitrogen availability (Lovett *et al.*, 2004). We suggest that herbivory level may not be as important as species composition, and future work should take this into account.

Kitchell *et al.* (1979) called for further research on the effects of predators on nutrient dynamics over 30 y ago, but this topic remains largely ignored and grossly undervalued (Schmitz, 2008, Schmitz *et al.*, 2010). Wolves affect soil nitrogen in Rocky Mountain grasslands through altering levels of ungulate herbivory (Frank, 2008), but our study failed to find evidence for nitrogen effects in a Great Lakes forest. This site-specificity begs for further inquiry. Predator re-introductions are controversial and difficult to manage; therefore, it is important that we are able to predict the food web effects of these events (Licht *et al.*, 2010). Hence, both ecology and management benefit from more studies, such as ours, which look beyond the impacts of predators on plants and consider the potential impacts on ecosystem processes (Maron *et al.*, 2006).

Acknowledgments.—We thank Dairymens Inc. and T. P. Rooney for field site use, and D. Tamblyn, L. Sancomb, and D. A. Fligel for field help. We also thank J. McLachlan, E. Archie, T. Van Deelen, W. Carson, J. Belovsky, M. Cramer, C. Mattison, L. Herrera, A. Laws, J. Bump, J. Vucetich, A. Wydeven, D. Beyer, and E. Kistner for assistance/advice. This project was largely funded by the American Museum of Natural History Theodore Roosevelt Memorial Fund and the Sigma Xi Scientific Society. Additional funding was provided by UNDERC and the University of Notre Dame.

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