Trophic cascades among wolves (*Canis lupus)*, deer (*Odocoileus virginianus)*, and riparian forb diversity in Northern Michigan and Wisconsin

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Abstract

Overabundance of white tailed deer (*Odocoileus virginianus)* and sustained overbrowsing has been shown to reduce plant diversity in different ecosystems. Through trophic cascades, gray wolves (*Canis lupus)* may have indirect effects on plant populations by altering deer movements, browsing patterns, and foraging behavior. We hypothesized that overabundant white-tailed deer populations may be significantly affecting the diversity of plant communities in riparian habitats, and that wolves may be generating a trophic cascade mitigating these impacts. To assess the potential for a top-down trophic cascade effect, we surveyed 25 riparian bog sites in a Great Lakes forest divided between high wolf-use areas and low-wolf use areas. At each site, the species richness and diversity of forbs were surveyed. The results were consistent with our hypothesis; in areas of high wolf-use, there were significantly more riparian forb species, and there was significantly greater diversity. These findings, combined with previous work in this forest, strongly suggest that top down trophic cascades generated by wolves may be significantly affecting riparian forb communities. This understanding could be important in future conservation and management of riparian habitats.

Introduction

White-tailed deer (*Odocoileus virginianus*) populations have dramatically increased in recent decades. Intensified deer herbivory can affect the growth and survival of many herb, shrub, and tree species. Selective consumption of species can in turn alter vegetation dynamics and reduce diversity (Côte et al. 2004).

The presence of carnivores can have strong direct and indirect effects on herbivore prey communities, such as white-tailed deer, via predator-prey interactions (Estes et al. 2011). In northern mesic forests of the Great Lakes Region, gray wolves (*Canis lupus)*, the primary natural predator of white-tailed deer, have been shown to significantly affect the density and distribution of deer populations (Mech 1977, Flagel et al. *in review*). Around each wolf territory lies a "buffer zone" which wolves avoid entering, creating areas of “high-wolf use” and areas of “low-wolf use” (Mech 1977). Deer usually live throughout wolf territories, but in areas where wolves are present, deer antipredator strategies may include the avoidance of high wolf-use areas (Mech 1997).

Indirect interactions between carnivores and plants, mediated by herbivores, are commonly referred to as trophic cascades (Ripple et al. 2001, Hairston et al. 1960). As seen in the interaction between elk and wolves in Yellowstone, wolves may influence lower trophic levels by both killing deer and altering their behavior (Ripple et al. 2001). Behavioral modifications include changes in diet, alterations of feeding patterns, and spatial changes regarding habitat use, and choices of feeding sites (Ripple et al. 2001). Through trophic cascades, top-down effects by wolves on deer populations may indirectly increase plant biomass by reducing herbivore density and altering herbivore behavior (Terborgh et al. 1999, Ripple et al. 2001, Hebbelwhite et al. 2005, Flagel et al. *in review*). In 2013, Callan et al. found that the presence of wolves may release some understory plant species from deer overbrowsing in northern white cedar habitats, thus stimulating greater understory plant diversity in high-wolf use areas. Flagel et al. (*in review*) found similar results in northern mesic forests. However, no research to our

knowledge has been done to see how these trophic cascades are affecting diversity in riparian plant communities such as bogs.

This lack of research is unfortunate, as riparian areas support some of the most diverse and productive of all plant communities. Through the interaction of soils, hydrology, and biotic communities, riparian areas maintain many important physical, biological, ecological functions that are important for wildlife, aquatic systems, and social benefits (Klapproth and Johnson 2009). Sustained ungulate browsing could affect riparian environments by changing, reducing, or eliminating vegetation (Platts 1979, Klapproth and Johnson 2009). The loss of native riparian vegetation can negatively affect wildlife, soils, water quality, and stream quality. Deer have been shown to forage on several riparian species in eastern U.S. habitats, including *Aster divaricatus, A. prenanthoides, Chelone glabra, Impatiens capensis, Pilea pumila, Polygonum virginianum* and *Ranunculus hispidis* (Mosbacher and Williams 2011). Mitchell (1997) also demonstrated that deer grazing in the Hudson Valley led to a steep decline in orchid populations. Browse-intolerant orchid species such as the Calypso orchid (*Calypso bulbosa*), showy lady's slipper (*Cypripedium reginae*), large roundleaf orchid (*Platanthera orbiculata*), and ram's head lady's slipper (*Cypripedium arietinum*) are now primarily rare or threatened in the Great Lakes Region due to overbrowsing (Rooney et al. 2002). Meanwhile, there is evidence that wolves reduce deer browse on willows in riparian areas (C. Bendel and D. Flagel unpublished data). Therefore, it is possible that overabundant white-tailed deer populations may be significantly affecting the diversity of plant communities in riparian habitats, and that wolves could generate a trophic cascade mitigating these impacts by reducing deer herbivory.

To test this hypothesis, we compared the biodiversity of riparian forbs surrounding bogs in high and low-wolf use areas in Northern Wisconsin and Upper Michigan. Because the presence of predators such as gray wolves can affect the density and distribution of deer populations, and deer herbivory can influence plant biodiversity, we expected to see a lower riparian plant biodiversity in low-wolf use areas compared to high-wolf use areas.

Methods

Study Site

This study took place at The University of Notre Dame Environmental Research Center (UNDERC), located near Land O' Lakes, Wisconsin. The UNDERC habitat consists of a patchy mosaic of forests and wetlands. UNDERC was an ideal study site because of the large number of wetland environments, as well as high white-tailed deer numbers (7-12 per km^2), and the recent re-colonization of wolves to the area (WI DNR estimates).

Because wolf packs establish and occupy territories that are patchily distributed across the landscape, study sites were chosen in areas of high-wolf use and low-wolf use across the UNDERC property (Callan et al. 2013). Previous studies defined the areas of UNDERC which are occupied and used by wolves (Flagel et al. *in review*).

Vegetation Survey

Twenty-five bogs were haphazardly selected throughout UNDERC property and the surrounding riparian area surveyed during the month of July 2014. Thirteen sites were

located in high-wolf use areas, and 12 were located in low-wolf use areas. A 20m x 2m transect was surveyed on solid ground riparian habitat at each site, totaling an area of 40 m^2 surveyed for each site. Along each transect, the total number of different species of forbs, and the total number of individuals of each species were counted. We avoided sampling sphagnum mats, as these low diversity floating mats differ substantially in vegetation from other riparian habitats (personal observation) and the wettest areas may be avoided by deer (Ratcliffe and Walker 1958).

Statistical Analysis

Unbalanced, student's t-test were used in order to determine if there was a significant difference in plant species richness as well as species evenness between high and low wolf use areas. The evenness of plant species (H') was calculated using the Shannon Diversity Index.

$$H' = -\sum_{i=1}^{S}\left[\left(\frac{n_i}{n}\right)\ln\left(\frac{n_i}{n}\right)\right]$$

Results

Species richness of riparian forbs (mean ± ISE) was significantly higher in high-wolf use areas (11.54 ± 0.8807) compared to low wolf use areas (7.83 ± 0.8744) ($t = 3.0859$, $df=23$, $p=0.005$) (Figure 1). There was also significantly greater species diversity in riparian forbs between high (1.512 ± 0.0973) and low (1.005 ± 0.1453) wolf use areas ($p=0.004$, $df=23$, $t=3.233$) (Figure 2).

Discussion

As predicted, both species richness and species diversity of riparian forbs were significantly lower in low-wolf use areas. The results showed that the mean number of species in high-wolf area was 11.54, which was significantly higher than the mean of 7.83 found in low-wolf area. These results are consistent with Callan et al. (2013) and Flagel et al. (*in review*) who found significantly greater diversity of understory forb species with wolves in the Great Lakes forest habitats.

There are several possible reasons for this pattern. Reduced browse intensity in high wolf areas could be limiting the ability of a few browse-resistant forb species to become locally dominant, thus increasing species richness and evenness (Callan et al. 2013). Deer could also be preferentially foraging on palatable, browse-intolerant species such as lady slipper orchids or trillium, thus lowering species richness in low wolf use areas (Mitchell 1997, Rooney et al. 2002). It is predicted that trophic cascades will continue to cause the significant difference in riparian forb diversity to increase over time. Future experiments could look at the long-term effects of trophic cascades on the diversity of riparian communities.

The results from this study indicate that top down trophic cascades generated by the recovery of the Great Lakes wolf population may not only affect understory forest communities, but may also be significantly affecting riparian environments such as bogs. If top predators are key components to the diversity of ecological communities, as suggested by this study, it will be important to retain top predators in ecosystems (Terborgh et al. 1999). This understanding could have many important implications for riparian management.

Riparian environments serve as critical transitions between terrestrial and aquatic ecosystems, and play a major role in maintaining healthy streams (Klapproth and Johnson 2009). Further research could be done to determine how a loss in plant diversity affects other aspects of riparian systems such as water quality, animal behavior, or aquatic interactions. Understanding the relationships between top predators, herbivores, and plant communities is important for maintaining riparian plant diversity, and could serve a critical role in future conservation and management of riparian ecosystems.

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Tables and Figures

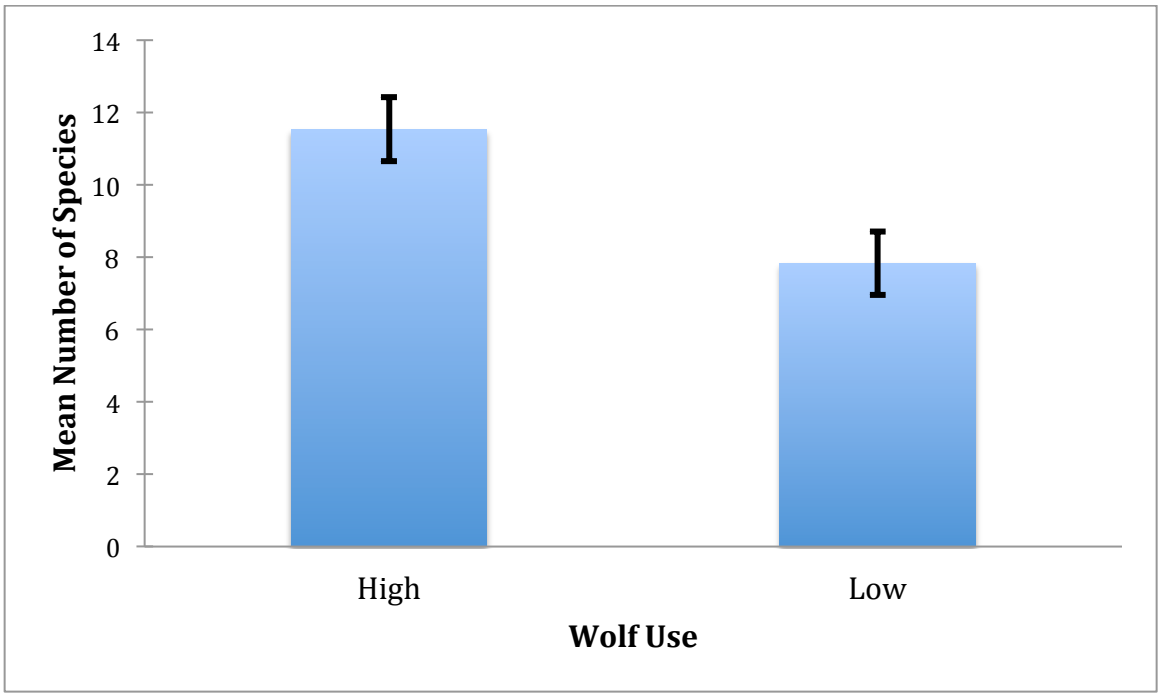

Figure 1. **Species richness in high and low wolf use areas**. In areas of high-wolf use, species richness of riparian forbs was significantly higher ($t = 3.0859$, $df=23$, $p=0.005$). The mean number of species in high-wolf areas was 11.54 (I= 0.8807), while the mean number of species in low-wolf use areas was 7.83 (I= 0.8744).

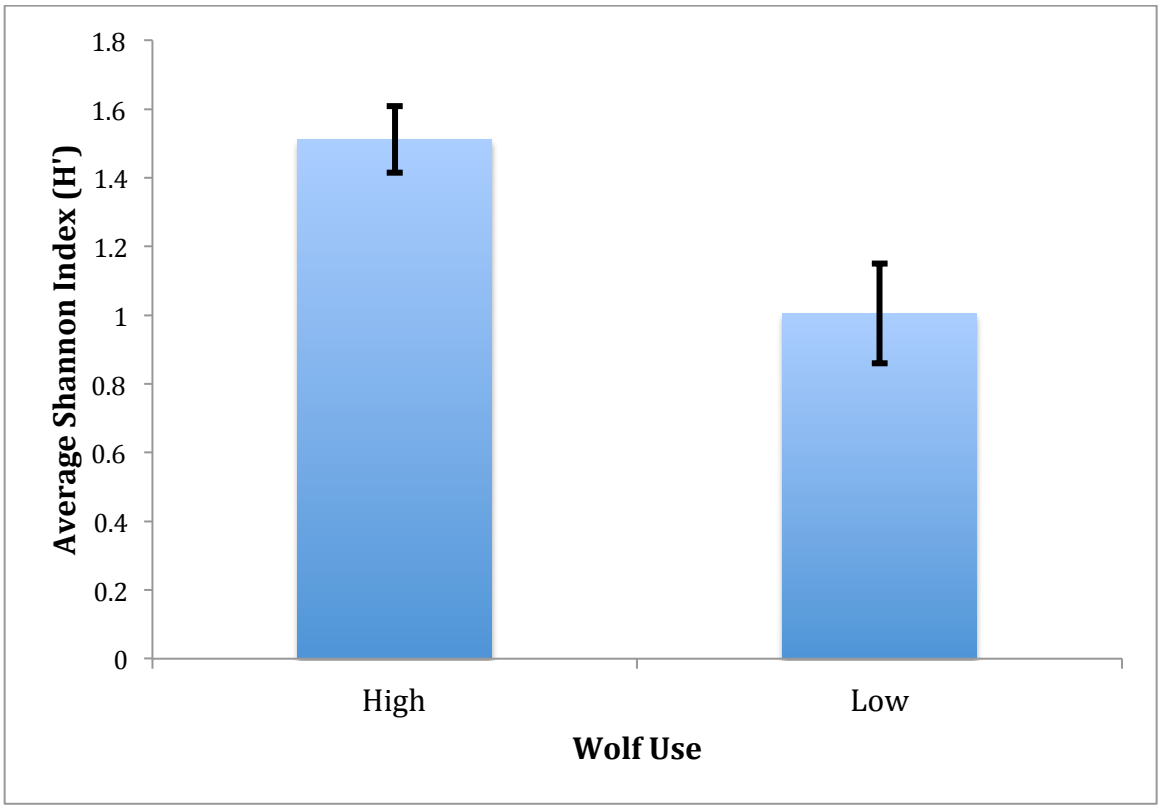

Figure 2. **Species diversity in high and wolf use areas**. High-wolf use areas showed significantly greater species diversity in riparian forbs when compared to low-wolf use areas (t=3.233, df=23, p=0.004,). H' was 1.512 (I=0.0973) in high-wolf use areas compared to a mean of 1.005 (I=0.1453) in low wolf use areas.