ARE WOLVES IN WISCONSIN AFFECTING THE BIODIVERSITY OF UNDERSTORY PLANT COMMUNITIES VIA A TROPHIC CASCADE?

by

RAMANA CALLAN

(Under the Direction of Nathan P. Nibbelink)

ABSTRACT

Wolf recovery in the Great Lakes region is anticipated to generate a top-down trophic cascade by altering white-tailed deer density, habitat selection, and/or foraging behavior. Through these direct impacts on deer, wolves are predicted to trigger additional indirect impacts on chronically browsed plant communities. To detect the signal of top-down effects, we performed vegetation surveys in northern white cedar wetlands to measure species richness (***S***) of understory plants across a gradient of wolf impact. We fit species area-curves of vascular plants grouped by vegetation growth form and duration of wolf occupancy. Sampling at multiple scales revealed that areas consistently occupied by wolf packs were characterized by higher ***S*** of forbs at local scales (1-10 m^2), and higher ***S*** of shrubs at broader scales (10 - 400 m^2). Once we detected the signal of a trophic cascade, we further refined our approach by calculating a weighted wolf occupancy duration index (WWODI) based on historic and current wolf pack territory data. We found strong positive correlations between WWODI and the density and diversity of woody stems 50-100 cm tall. Unpalatable species and size classes above the browse line showed no relationship with WWODI. The characteristic gap in the size structure of woody stems, indicative of over-browsed understories, was less apparent in cedar wetlands with high wolf impact. Finally, we tested three possible hypotheses for observed relationships between ***S*** and WWODI: (1) a top-down trophic cascade, (2) a bottom-up trophic cascade, and (3) non-trophic associations. Using environmental variables, we created multivariate models of ***S*** of forbs, shrubs, tree seedlings and ferns. We used an information theoretic approach to select the best fit models and found that inclusion of WWODI was supported for models of understory plant species known to respond positively to release from herbivory: forbs, shrubs and tree seedlings. When landscape variables associated with wolf habitat selection were used to generate models of plant species richness, these models performed poorly. Evaluated collectively, our results provide little support for either the bottom-up or non-trophic hypotheses. Instead, our results are consistent with wolves triggering a release from browsing pressure by white-tailed deer (a top-down trophic cascade).

INDEX WORDS: trophic cascade, deer browsing intensity, wolf recovery, seedling recruitment, Great Lakes region, northern white cedar, Wisconsin, multivariate models, local and regional variables, understory plant communities, species richness, species-area relationship

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DEDICATION

I would like to dedicate this dissertation to my mom, Mona, who is eternally supportive of all my endeavors.

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CHAPTER 1

INTRODUCTION

Top-down trophic cascades predict a pattern of alternating abundance or biomass across successively lower trophic levels (Paine 1980, Pace et al. 1999, Micheli et al. 2001). Hairston, Smith and Slobodkin (1960) proposed the classic cascade as a simplified tri-trophic system of predators (carnivores), herbivores (consumers) and plants (producers). With top-down control of such an odd numbered food chain, the loss of a predator releases herbivores from predation allowing them to increase in abundance. This shift in trophic structure in turn leads to a decline in plant abundance or biomass. Consequently, the decline of large carnivores has had broad repercussions for the maintenance of lower trophic levels (Crooks and Soule 1999, Miller et al. 2001). In theory, the repatriation of large carnivores may reverse this trend, allowing plants to recover. Conversely, release from over-browsing may not lead to a restored community because of ecological hysteresis (Cote et al. 2004).

White-tailed deer (*Odocoileus viginianus*) populations drastically increased during the 20th century throughout their range in North America (Garrot et al. 1993) due, in part, to the extermination of their primary predator, the wolf (*Canis lupus*) (Estes 1996, Van Deelen et al. 1996, Horsley et al. 2003, Augustine and deCalesta 2003). The long term negative impacts of over-browsing by white-tailed deer on species diversity, species composition, plant biomass, and structure of understory plant communities has been well documented (Frelich and Lorimer 1985, Alverson et al. 1988, Tilghman 1989, Rooney and Waller 2003, Horsley et al. 2003, Rooney et al. 2004, Cote et al. 2004, Holmes et al. 2008). Whether the recent recovery of the Midwest wolf population can mitigate these negative effects is of great interest from both theoretical and resource management perspectives (Rooney and Anderson 2009). Our objective was to test for evidence of such recovery across a gradient of wolf impact.

Prior to European settlement, densities of white-tailed deer in the northern Great Lakes Region were much lower because of extreme winters and extensive coverage of mature hemlock-hardwood forests (Dahlberg and Guettinger 1956, Habeck and Curtis 1959, DelGuidice et al. 2009). The early successional communities and high edge density created by large-scale clear cutting combined with the intentional eradication of large carnivores led to severely inflated deer populations throughout the region. For several decades, understory plant communities of northern Wisconsin have been subject to deer densities that exceed pre-settlement conditions by 350-500% (Rooney and Waller 2003).

Comparisons between deer exclosures and adjacent browsed plots in both Wisconsin and Michigan have shown drastic differences in the survival and reproductive success of preferred browse species (Graham 1954, Dahlberg and Guettinger 1956, Stoeckeler, Strothman, and Krefting 1957). Evidence from manipulative experiments in northern hardwood forests shows a distinctive threshold pattern indicating that the diversity of forbs, shrubs and trees in seedling size classes drastically decreases when deer density increases from moderate to high levels (Tilghman 1989, Horsley et al. 2003). Since current levels of white-tailed deer browsing intensity are degrading habitat quality, then, in theory, recovery of wolves should reduce browse pressure allowing biodiversity of understory plant communities to increase with continued wolf occupancy.

We chose to focus on northern white cedar (*Thuja occidentalis*) stands due to the established link between recruitment failure of cedar and white-tailed deer browsing intensity (Alverson et al. 1988, Van Deelen 1999, Cornett et al. 2000). Northern white cedar is a highly preferred browse species (Beals et al. 1960) and lowland cedar stands have been intensively used by deer during the winter months (Verme 1965) often sustaining deer yard densities from 30-40/km^2. These coniferous wetlands support extremely diverse plant communities (Pregitzer 1990) providing habitat for a variety of rare lilies and orchids (USDA Forest Service 2004). Unique shrub and herbaceous species restricted to conditions found in white cedar wetlands (light regimes and soil chemistry) are equally sensitive to over-browsing. Thus, we anticipated that recovery from over-browsing would be more easily detected in this uniquely diverse and browse-sensitive community type.

With protection under the Endangered Species Act, gray wolves began recolonizing northern Wisconsin in the 1970s, but wolf distribution remained very limited until the 1990s (Wydeven et al. 2009). The wolf is considered a strongly interactive species due to its direct and indirect effects on lower trophic levels (Soulé et al. 2003). Recovery of the gray wolf in the Great Lakes region is thus predicted to generate top-down effects that will contribute to the conservation of regional biodiversity (McShea 2005, Ray 2005). Hoskinson and Mech (1976) reported observations that deer survival is higher on the edges of wolf territories as compared to their centers. Wolves are less likely to hunt in these buffer zones so as to avoid potentially fatal encounters with neighboring wolf packs (Mech 1977). At local scales, the distribution of deer in northeastern Minnesota was found to be negatively correlated with wolf territory extents, and deer were found primarily in buffer zones (Lewis and Murray 1993). Thus buffer zones surrounding wolf pack territories may act as refugia for white-tailed deer (Mech 1994).

Increased vigilance of individual deer that do continue to forage within wolf territories is also likely to reduce local impacts on woody browse species. By forcing deer to increase movement and spend less total time browsing, the presence of wolves may alter the disturbance regime experienced by local plant communities (Ripple and Beschta 2004). Within occupied wolf territories, deer may no longer be able to sit and browse one location until all preferred species become locally rare or extinct. Thus, we hypothesized that the recovery of wolves in Wisconsin has generated a mosaic of deer browsing intensity as deer alter their foraging activity to avoid occupied wolf territories, showing preference for the buffer zones between adjacent packs.

Our first objective was to detect the signal of a top-down trophic cascade (Chapter 2). We performed extensive vegetation surveys in northern white cedar wetlands to measure species richness (S) of understory plant communities across a gradient of wolf impact. We fit species area-curves for understory plant species grouped by vegetation growth form (tree, seedling, shrub, forb, grass, sedge, or fern) and duration of wolf territory occupancy (low or high wolf impact). We also sought to determine if differences in species richness were more or less observable at specific spatial scales ($0.01\ m^2$, $1.0\ m^2$, $10\ m^2$, $100\ m^2$, $400\ m^2$, $1000\ m^2$). In this manner we hoped to aid future studies of terrestrial trophic cascades by suggesting appropriate scales of observation for each vegetation growth form.

Our second objective was to predict the impacts of wolf recovery on future canopy composition of northern white cedar wetlands (Chapter 3). To accomplish this, we first calculated the weighted wolf occupancy duration index (WWODI) based on historic and current wolf territory data from 1995-2009. We then evaluated the relationship between WWODI and woody stem density, species diversity, and species composition. We categorized woody species based on their assumed browse preference and browse sensitivity and explored how canopy cover, demographic inertia, and WWODI influenced woody stem density of each of five size classes (10-50 cm, 50-100 cm, 100-137 cm, 0-1 cm dbh, and 1-2.5 cm dbh). We also compared our index of potential wolf impact with commonly used measures of deer browse intensity.

Finally, in Chapter 4, we tested three alternative hypotheses for observed relationships between plant species richness and wolf impact: (1) a top-down trophic cascade, (2) a bottom-up trophic cascade (effects propagating up through the food web), and (3) a non-trophic association (spurious effects created by landscape level factors known to benefit both plant diversity and wolf habitat quality). Using local and regional variables, we created multivariate models of species richness of forbs, shrubs, seedlings and ferns. To evaluate evidence for the bottom-up hypothesis, we used an information theoretic approach to select the best fit models and examined whether inclusion of WWODI improved model fit. To evaluate evidence in support of the non-trophic association hypothesis, we used variables known to influence wolf habitat selection (mean distance to paved road and mean patch area of forest) to model our vegetation response variables. By accounting for the variability in species richness explained by bottom-up and non-trophic models, we sought to isolate purely top-down trophic effects of wolves on plant species richness.

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CHAPTER 2

SIGNAL DETECTION OF WOLF PACK TENURE IMPACTS ON PLANT SPECIES RICHNESS AT MULTIPLE SPATIAL SCALES IN NORTHERN WHITE CEDAR WETLANDS[1]

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2.0 Abstract

Expansion of the Great Lakes wolf population presents a natural experiment in the long term ecological impacts of a keystone predator recovering from local extinction. Our research explores whether wolves are reducing local browse intensity by white-tailed deer thus indirectly mitigating the biotic impoverishment of understory plant communities. To assess the potential for a top-down trophic cascade effect, we used a vegetation survey protocol based on a spatially and temporally explicit model of wolf territory occupancy in northern Wisconsin. We fit species area-curves for understory plant species grouped by vegetation growth form (based on their predicted response to release from herbivory, i.e., tree, seedling, shrub, forb, grass, sedge, or fern) and duration of wolf territory occupancy (high or low wolf impact). Through this process we were able to evaluate if, and at what spatial scales, plant species richness differs between areas colonized and continuously occupied by wolf packs (high wolf impact areas) and areas never successfully colonized (low wolf impact areas).

As predicted for a trophic cascade response, our results indicate that forb species richness at local scales ($10m^2$) is significantly higher in high wolf impact areas (high wolf impact: 10.7 ± 0.9, low wolf impact: 7.5 ± 0.9, N=16, $p < 0.001$), as is shrub species richness (high wolf impact: 4.4 ± 0.4, low wolf impact: 3.2 ± 0.5, N=16, $p < 0.001$). Also as predicted for a tropic cascade response, percent cover of ferns is higher in low wolf impact areas (high wolf impact: 6.2 ± 2.1, low wolf impact: 11.6 ± 5.3, N=16, $p = 0.05$). However, contrary to expectations, species richness of ferns in high wolf impact areas is in fact higher at the $10m^2$ scale (high wolf impact: 2.99 ± 0.3, low wolf impact: 2.08 ± 0.47, N=16, $p < 0.01$). Also contrary to expectations, species richness of sedges is higher in high wolf impact areas at the smallest spatial scale measured, $0.01m^2$, (high wolf impact: 0.47 ± 0.16, low wolf impact: 0.23 ± 0.14 N=7, $p < 0.05$), but this pattern is not found at any other scale. Associations between wolf impact and other vegetation growth forms (trees, seedlings and grasses) are not apparent. Beta richness of understory plant species did not differ between high and low wolf impact areas, confirming earlier assumptions that deer herbivory impacts species richness primarily at local scales. Sampling at multiple spatial scales revealed that changes in species richness are not consistent across scales nor among vegetation growth forms: forbs show a stronger response at local scales (1-10m^2), while shrubs show a response across broader scales (10m^2 - 400m^2).

These results provide compelling evidence of trophic effects, however, reciprocal relationships between wolves, deer and vegetation are lacking. Indications of the causal mechanisms responsible also remain speculative. In addition, understory vegetation in white cedar stands may be more strongly influenced by local abiotic factors, such as hydrology and edge effects, than by changes in local deer densities and foraging behavior. Continued research directed at ruling out confounding factors and differentiating between top-down vs. bottom-up trophic effects is needed.

Key Words: species-area relationship, trophic cascade, deer browsing intensity, wolf recovery, Wisconsin

2.1. *Introduction*

A decline in rare and uncommon species is contributing to a biotic homogenization of understory plant communities in northern Wisconsin (Frelich and Lorimer 1985, Rooney and Waller 2003, Cote et al. 2004, Wiegmann and Waller 2006). Exclosure studies combined with re-sampling of historic vegetation plots from the 1950's (Curtis 1959) strongly indicate the overabundance of white-tailed deer (*Odocoileus viginianus*) as the causal factor driving local losses in plant diversity (Rooney and Waller 2003, Rooney et al. 2004). Consistent with this pattern, populations of northern white cedar (*Thuja occidentalis*) have suffered region wide recruitment failure due primarily to decades of over-browsing (Alverson et al. 1988). Without recruitment to the canopy, existing mature stands of white cedar may become increasingly isolated as older stands senesce, accelerating the associated loss of understory plant species restricted to cedar stands (Alverson et al. 1988) via the process of 'relaxation' described by Diamond (1975).

White cedar forests are used intensively by deer during the winter months, subjecting the highly nutritious and palatable seedlings to excessive herbivory (Habeck 1960, Van Deelen et al. 1996). Historically, these coniferous wetlands have supported extremely diverse plant communities (Pregitzer 1990) providing habitat for a variety of rare lilies and orchids (USDA Forest Service 2004). Unique shrub and herbaceous species restricted to conditions found in white cedar wetlands are equally sensitive to over-browsing. Protecting cedar wetlands from elevated deer populations is essential for sustaining cedar stands that are comprised of more than "living-dead" canopy trees with species-poor understories (Alverson et al. 1994, Cornett et al. 2000).

Three approaches to restoring the ecological integrity of plant communities sensitive to deer herbivory have been suggested: extensive exclosures, relaxed hunting regulations, and modified habitat management to reduce forage availability (Alverson et al. 1988). Unfortunately, many economic, political and social factors interact to limit implementation of these approaches. Altering forest management practices to a) protect plants with limited economic value, b) drastically decrease white-tailed deer populations, and c) reduce edge and successional habitat, challenges the basic tenets of conventional forest/game management theory. Although these changes were proposed for Wisconsin's National Forests over 20 years ago (Task Force 1986) the widespread application of these principles has met with continued resistance.

The recovery of Wisconsin's wolf population (*Canis lupus*) may provide an alternative (or complementary) approach to protecting sensitive plant species from excessive deer herbivory. Indirect interactions between carnivores and plants, mediated by herbivores, are commonly referred to as trophic cascades (Paine 1980, Carpenter et al. 1985). Such interactions are frequently used to justify carnivore conservation, despite limited experimental evidence of trophic cascades involving large mammalian predators (Carroll et al. 2001, Miller et al. 2001, Ray 2005). Recent studies of species interactions in Yellowstone National Park (YNP) suggest that the recovery of wolf populations can naturally ameliorate ungulate-caused ecosystem simplification (Ripple and Beschta 2004, White and Garrot 2005). Examining whether this pattern is observed in other regions with different ecological characteristics, such as the Great Lakes Region, will contribute to our growing understanding of how trophic cascades involving mammalian predators behave in terrestrial systems.

Unlike in Yellowstone, where elk (*Cervus elaphus*) are the primary prey species of gray wolves, wolves in the Great Lakes Region prey mainly on white-tailed deer [although prior to

European settlement, the Great Lakes Region also contained diverse populations of ungulate species (DelGuidice et al. 2009)]. Based on land and forest cover conditions, pre-settlement white-tailed deer densities in northern Wisconsin are thought to have ranged between 4 and 6/km^2 (McCaffery 1995). Since deer prefer early successional habitat and landscapes with high edge density, extensive clearing and fragmentation of forests for agriculture and timber extraction have led to dramatic increases in forage availability. Predator extirpation, when combined with protective hunting laws and habitat management, has contributed to current deer densities ranging between 4 and 15/km^2 (Wi DNR 2008). Alverson et al. (1988) prescribed densities as low as 1-2 deer/km^2 to improve recruitment of sensitive plant species. Is the recovering wolf population in Wisconsin even capable of maintaining deer densities this low?

In the Great Lakes Region, wolves require 15-18 deer 'equivalents' per wolf per year (Fuller 1995). Hence the current Wisconsin wolf population, which has grown to ~690 individuals (in winter) since their placement on the endangered species list (Wydeven and Wiedenhoeft 2010), has the capacity to take ~12,000 deer per year. Given that there are an estimated 390,000 deer in the Northern Forests of Wisconsin (posthunt), region-wide effects of wolf recovery on deer populations are unlikely to manifest in the short term (Pers. comm. Keith McCaffery 2008). In addition, whether wolf kills represent primarily compensatory or additive mortality for white-tailed deer is in part dependent on stochastic environmental variables (Mech and Peterson 2003). However, localized influences on deer populations are more probable, and drastic local reductions have been observed in Minnesota (Nelson and Mech 2006).

Wolves began recolonizing northern Wisconsin in the 1970s, but wolf distribution remained very limited until the 1990s (Wydeven et al. 1995, Wydeven et al. 2009). Depending on pack size and prey density, wolf territories in the Great Lakes Region can range in size but average approximately 136 km^2 (Wydeven et al. 2009). Hoskinson and Mech (1976) reported that deer survival is higher on the edges of wolf territories as compared to their centers. Wolves are less likely to hunt in these buffer zones so as to avoid potentially fatal encounters with neighboring wolf packs (Mech 1977). At local scales, the distribution of deer in northeastern Minnesota was found to be negatively correlated with wolf territory extents, and deer were found primarily in buffer zones (Lewis and Murray 1993). Thus buffer zones surrounding wolf pack territories may act as refugia for white-tailed deer (Mech 1994).

Ecological processes (such as trophic cascades) are likely to manifest differentially over a range of spatial and temporal scales (Levin 1992, Polis 1999, Bowyer and Kie 2006). Historically, ecological studies have often failed to address the issue of scale or have sampled patterns at an inappropriate scale for the process being investigated (Dayton and Tegner 1984, Wiens 1989, Menge and Olson 1990, Levin 1992, 2000). Size, generation time, reproductive characteristics, and dispersal ability of the organisms involved determine the scale(s) at which they perceive and respond to environmental change (Levin and Pacala 1997). Variation in these life history traits necessitates sampling at multiple spatial scales to accurately interpret responses to top-down processes. Additionally, the effects of trophic cascades are likely to be dampened by spatial heterogeneity (van Nes and Scheffer 2005). Habitat refugia combined with spatial and temporal variability in species’ distributions allow prey to escape predation (Halaj and Wise 2001), potentially creating a mosaic of impact intensity across the landscape. Few, if any, attempts have been made to explicitly incorporate spatial scale into studies of terrestrial trophic cascades.

Previously documented trophic cascades in temperate terrestrial systems represent species-level as opposed to community-level cascades (Polis 1999). These studies tested how predators affect productivity of one or occasionally several plant species (McLaren and Peterson 1994, Ripple et al. 2001, Berger et al. 2001, Ripple and Beschta 2003, Hebblewhite et al. 2005), but failed to test if predator manipulations affect species richness of entire plant communities. It has been argued that terrestrial cascades (when compared to aquatic cascades) are principally species-level phenomena, due to comparatively nonlinear food web structure, trophic complexity and effective plant defense mechanisms (Halaj and Wise 2001). However, studies in terrestrial systems often fail to measure community level responses, making inferences gained from these types of meta-analyses somewhat speculative.

Recolonization by wolves of portions of their historic range in North America may provide appropriate experimental conditions for improving our understanding of trophic cascades in terrestrial systems (Hebblewhite et al. 2005). Wolf recovery in the Great Lakes Region over the past three decades has been closely monitored by the respective Departments of Natural Resources (DNR) in Minnesota, Wisconsin and Michigan. The Wisconsin DNR (WiDNR) has incorporated radiotelemetry, snow track surveys, howl surveys, and public observations to annually map wolf pack territories in Wisconsin since 1979. The high quality of this dataset provided the information we needed to examine the spatial and temporal patterns in wolf occupancy throughout the state. Use of this dataset enabled us to investigate the potential for a top down trophic cascade and to answer the following question: is the recovery of wolves releasing some understory plant communities from over-browsing by white-tailed deer?

The simplified tri-trophic cascade that we are testing for is comprised of wolves, white-tailed deer, and understory plant communities (Figure 2.1). The objectives of this study were to develop species-area curves to test if differences in species richness occur between areas of high and low potential wolf impact. Due to differences in life history traits, such as longevity, reproductive rate, dispersal ability and resource allocation to physical and chemical defenses, species can differ vastly in their response to herbivory. For example, tree seedlings, shrubs, and forbs are highly preferred by white-tailed deer and are thought to respond negatively to high browsing pressure. In contrast, ferns, grasses, and sedges are generally avoided by white-tailed deer and thought to respond positively (though indirectly) to high browsing pressure, as they are released from competition with more sensitive species (Stromayer and Warren 1997, Cooke and Farrell 2001, Boucher et al. 2004). Thus, we anticipated that understory plants would vary in their response to release from browsing pressure dependent on the vegetation growth form in question (trees, seedlings, shrubs, forbs, grasses, sedges, and ferns).

Based on previous studies of deer influence on terrestrial plant communities (Frelich and Lorimer 1985, Stromayer and Warren 1997, Cooke and Farrell 2001, Rooney and Waller 2003, Boucher et al. 2004, Cote et al. 2004, Wiegmann and Waller 2006), we anticipated that high wolf impact areas would be subject to reduced browse pressure and thus be characterized by increased percent cover of forbs, shrubs and seedlings. We further predicted that ferns, grasses and sedges would demonstrate the opposite response to wolf recovery (decreased percent cover in high wolf impact areas). The relationship between disturbance and species diversity (Figure 2.2) described by Denslow (1985) predicts that species richness of seedling, shrub and forb species should be higher at high wolf impact areas (since browsing pressure should be lower and closer to historic levels). We also sought to determine if differences in species richness were more or less observable at specific spatial scales (0.01 m^2, 1.0 m^2, 10 m^2, 100 m^2, 400 m^2, 1000 m^2). In this manner we hoped to aid future studies of terrestrial trophic cascades by suggesting appropriate scales of observation for each vegetation growth form.

2.2. *Methods*

2.2.1 STUDY SITE

Data were collected throughout the Chequamegon-Nicolet National Forest, as well as various state and county forests spanning 7 counties in north-central Wisconsin (Figure 2.3). The forests of northern Wisconsin are transitional between deciduous forests to the south and boreal forests to the north (Pastor and Mladenoff 1992, Mladenoff et al. 1993). Northern white cedar wetlands occupy 5% of the forested landscape (WiDNR 1998). This community type develops on poorly-drained sites with a slight through-flow of groundwater, producing elevated pH and nutrient richness of the soil (Black and Judziewicz 2008). Mature stands of white cedar are densely shaded with nearly closed canopies. The combination of these characteristics provide the unique light regimes and soil chemistry required by species restricted to this community type (see below).

Co-dominant trees in white cedar wetlands include balsam fir (*Abies balsamea*), yellow birch (*Betula alleghaniensis*) and black ash (*Fraxinus nigra*). Tag alder (*Alnus incana* subsp. *rugosa*), hollies (*Ilex mucronata* and *I. verticillata*), hazelnuts (*Corylus* spps.) and honeysuckles (*Lonicera* spps.) are common understory shrubs. Cedar wetlands are rich in sedges (e.g. *Carex disperma*, *C. trisperma*), ferns (e.g. *Dryopteris* and *Gymnocarpium* spps.) and numerous wildflowers. Common wildflowers are goldthread (*Coptis trifolia*), starflower (*Trientalis borealis*), wild sarsaparilla (*Aralia nudicaulis*), naked miterwort (*Mitella nuda*), blue-bead lily (*Clintonia borealis*), bunchberry (*Cornus canadensis*), Canada mayflower (*Maianthemum canadense*), and trailing “sub-shrubs” such as creeping snowberry (*Gaultheria hispidula*), dwarf red raspberry (*Rubus pubescens*) and twinflower (*Linnea borealis*). Orchids include yellow lady’s slipper (*Cypripedium parviflorum*), heart-leaved twayeblade (*Listera cordata*), lesser rattlesnake plantain (*Goodyera repens*), and blunt-leaved bog orchid (*Platanthera obtusata*).

2.2.2 DATA COLLECTION

Wolf packs establish and occupy territories that are patchily distributed across the landscape (Mladenoff et al. 1999). The effect of wolves on deer abundance and foraging behavior is likely to be limited to locations continuously occupied by wolf packs. Presumably, the impact of wolves increases with the size of the pack and the number of years the territory has been consistently occupied. Since pack size and territory extent vary from year to year, this creates a mosaic of potential impact intensity across the landscape. WiDNR population estimates of wolves were ascertained by live-trapping and radio tracking (Mech 1974, Fuller and Snow 1988), howl surveys (Harrington and Mech 1982), and winter track surveys (Thiel and Welch 1981, Wydeven et al. 1995). Territory extents are delineated using minimum convex polygons based on radiolocations of collared wolves and other wolf sign (Wydeven et al. 1995).

Using GIS, we overlaid current wolf territories with historic territory extents (Wiedenhoeft and Wydeven 2008) to delineate areas which have been continuously occupied for ~10 years. A similar process was employed to select areas which have apparently remained unoccupied since wolf recolonization of the region. Only sites within the Chequamegon-Nicolet National Forest, state forest or county forest boundaries were selected. Although wolves have established territories outside of public lands, these territories are often located in agricultural or industrial forest landscapes, and anthropogenic sources of landscape change are likely to confound any potential trophic effects of wolf recolonization.

We used the Combined Data Systems (CDS) data for the Chequamegon-Nicolet National Forest (USDA 2001) and various state and county forest datasets to select stands characterized as northern white cedar wetlands. White cedar stands within consistently occupied wolf territories were then paired with the closest unoccupied white cedar stand of similar stand area and stand age. In this way, plots were assigned to either high wolf impact (8-10 yrs of recent wolf occupancy) or low wolf impact (0-3 yrs of recent wolf occupancy) categories and paired high and low wolf sites were within a few kilometers of each other (Figure 2.4). This process was intended to control for spatial auotocorrelation and limit the potential for confounding variables to produce false associations.

Hawth's Analysis Tools add-on for ArcGIS (Beyer 2004) was used to randomly place one vegetation plot within each pre-selected white cedar stand. We surveyed a total of 32 cedar stands (16 in low and 16 in high wolf impact areas). Fourteen plots were completed in 2008 and 18 plots were completed in 2009. An additional six plots representing moderate potential wolf impact were also surveyed, but these data are not analyzed here (see Chapters 3 and 4). Vegetation surveys followed the Carolina Vegetation Survey (CVS) protocol developed by Peet et al. (1998). Plots consist of 10 modules (10 X 10 meters) in a 2 X 5 array (1000 m^2 total). Four of the ten modules are treated as intensive modules because they are intensively sampled while the remaining plots are surveyed for additional species occurrences only. Two corners in each of the intensive modules were sampled for presence of vascular plant species (trees, shrubs, seedlings, ferns, forbs, grasses and sedges) using a series of nested quadrats (increasing incrementally in size from 0.01 m^2 to 10 m^2). Percent cover data was estimated visually for each 100 m^2 module based on the following cover classes: 0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95%, 95-100%. Identification of forbs conforms to Black and Judziewicz

(2008), other plant species names conform to Gleason and Cronquist (1991). Due to extensive time requirements, species identification of grasses and sedges was discontinued for the second field season.

2.2.3 DATA ANALYSIS

Percent cover of all plant species in each growth form (tree, shrub, seedling, forb, fern, grass, sedge) was assigned the geometric mean of the cover class to which they were visually assigned. Geometric mean values for each of the four intensive modules were then averaged to provide one value for each plot. Simple student's t-tests were used to compare percent plant cover between high and low wolf impact areas and across all vegetation growth forms.

Species richness at each scale (0.01 m^2, 1.0 m^2, 10 m^2, 100 m^2, 400 m^2, 1000 m^2) was calculated for each plot by averaging subsamples. The number of subsamples varied depending on the scale sampled (0.01 m^2 -10 m^2, n=8, 100 m^2, n=4, and 400 m^2 -1000 m^2, n=1). Again, student's t-tests were used to compare species richness between high and low wolf impact areas and across all vegetation growth forms and spatial scales. The multi-scale nested structure of the CVS protocol also facilitates the construction of species-area curves. Species–area curves describe the rate at which species numbers increase with increases in the area sampled (Rosenzweig 1995). We fit averaged species richness values to the power function to determine y-intercept and slope values (c and z-values). We chose the power model because it was shown to outperform the exponential model when evaluated using Akaike Information Criterion (AICc) (Barnett and Stohlgren 2003). The power model has an equation of the form:

$$S = cA^z$$

where S represents the number of species, A represents the area, and c and z are constants.

For this type of analysis, the power function is often manipulated to log–log form:

$$\log(S)=z\log(A)+\log(c)$$

Calculation of *c* and *z* values, where *c* = species richness at one unit of area (α- richness) and *z* = the rate at which species richness increases with area (β- richness), allow us to predict the direction and magnitude of differences in species richness. We grouped species-area curves for low and high wolf impact sites (n=16) to compare α- and β- richness between these two treatments. Species-area curves were generated for all vegetation growth forms separately (note that grass and sedge species richness data are from the first year of the study only and are based on a reduced sample size, n =7). T-tests and 95% confidence intervals were used to determine significant differences in *c* and *z* values as well as to indicate at which scales differences are most easily detected.

2.3. ***Results***

2.3.1 PERCENT COVER BY STRATA

We identified a total of 190 vascular plant species: 23 species of tree, 31 species of shrub, 98 species of forb, 12 species of fern, five species of fern ally, 16 species of sedge, seven species of grass, two species of vine, one species of rush, and four non-native species (see Appendix 1). Sites with high wolf impact tended to have a diverse understory community with complex vertical structure. In contrast, low wolf impact sites had a very limited herbaceous layer and almost no woody-browse. Some low wolf impact sites were characterized by an understory dominated by ferns, sedges and grasses but still lacking in forbs, shrubs and tree seedlings.

Percent cover of forbs was higher in high wolf impact areas (high wolf impact: 15.0 %± 4.4%, low wolf impact: 8.8% ± 2.5%, N=16, $p = 0.05$) as were shrub and tree seedling cover combined (high wolf impact: 11.2% ± 4.3%, low wolf impact: 6.1% ± 2.1%, N=16, $p = 0.05$), while cover of ferns was lower (high wolf impact: 6.2 ± 2.1, low wolf impact: 11.6 ± 5.3, N=16, $p = 0.05$) (Figure 2.5). Surprisingly, the percent cover of grasses was equivalent in low and high wolf impact areas (high wolf impact: 0.50% ± 0.22%, low wolf impact: 0.59% ± 0.50%, N=16, $p = 0.32$), and sedge cover tended to be higher in wolf areas, though not significantly so (high wolf impact: 7.4 ± 4.0, low wolf impact: 4.5 ± 1.8, N=16, $p = 0.10$).

2.3.2 SPECIES-AREA RELATIONSHIPS

Slopes and intercepts of species-area curves in continuously occupied wolf areas tended toward higher alpha richness (c) for all species combined (Table 2.1, Figure 2.6) but this difference was not significant ($p = 0.10$). Beta richness (z) ranged from 0.27-0.35 across all sites but was consistently similar between low and high wolf impact areas. When species richness of understory plants was broken down into vegetation growth forms based on their hypothesized response to herbivory, differences between high and low wolf impact areas were more pronounced (Table 2.1). Alpha richness of forbs was much higher in high wolf impact areas ($p< 0.001$) as was alpha richness of shrubs ($p< 0.05$). Surprisingly, alpha richness of ferns was in fact higher in high wolf impact areas ($p<0.05$), and alpha richness of sedges tended to be higher in high wolf impact areas, but this difference was not significant ($p<0.10$). Again, beta richness was equivalent between high and low wolf impact areas across all vegetation growth forms.

As predicted for a trophic response, forb species richness at local scales ($10m^2$) was significantly higher in high wolf impact areas (high wolf impact: 10.7 ± 0.9, low wolf impact: 7.5 ± 0.9, N=16, $p < 0.0001$), as was shrub species richness (high wolf impact: 4.4 ± 0.4, low wolf impact: 3.2 ± 0.5, N=16, $p < 0.001$). Again, contrary to expectations, species richness of ferns was higher at the $10m^2$ scale (high wolf impact: 2.99 ± 0.3, low wolf impact: 2.08 ± 0.47, N=16, $p < 0.01$). Species richness of sedges was higher in high wolf impact areas at the smallest spatial scale measured, $0.01m^2$, (high wolf impact: 0.47 ± 0.16, low wolf impact: 0.23 ± 0.14 N=7, $p < 0.05$), but this pattern was based on a limited sample size and was not observed at other spatial scales. Species richness of trees, seedlings and grasses was similar between low and high wolf impact areas across all scales.

2.4. *Discussion*

As predicted, percent cover of forbs was 70% higher on average in high wolf impact areas, and species richness of forbs was 43% higher (at the $10m^2$ scale). Shrubs showed a similar pattern with 84% higher percent cover for seedlings and shrubs grouped and 39% higher species richness for shrubs alone. Percent cover of ferns was 47% lower in high wolf impact areas. Although we predicted greater species richness of tree seedlings in high wolf impact areas (Tilghman 1989), this pattern was not observed. The presence of seedling species may be more related to proximity to seed sources (adults in the canopy) and perhaps seedling density, not richness, will show a stronger response to wolf occupancy (see Chapter 3).

The similarity in percent cover of grasses in high and low wolf impact areas was inconsistent with our predictions for a top-down trophic response since previous studies indicated an indirect positive relationship between deer browsing pressure and the percent cover of grass species. Almost all visual estimates of grass cover fell in the same cover class: 0-1%. This area represents approximately one square meter of a $100m^2$ module. Percent cover of grasses and sedges may need to be estimated at finer scales than the $100m^2$ module. Evidence does suggest that sedges may actually be more abundant in high wolf impact areas. It is possible that sedges in northern white cedar swamps respond negatively to white-tailed deer grazing even though they have been shown to respond positively in other vegetation types. Alternatively, a higher proportion of high wolf impact sites may, by chance, have been located in wetlands with abiotic conditions more conducive to sedge growth and survival. If, by chance, the abiotic conditions between high and low wolf impact areas differ significantly, this could result in false associations between potential wolf impact and all of the vegetation response variables measured (see Chapter 4).

Plant species richness is determined by linked processes that act differentially across small, intermediate, and large spatial scales (Schmida and Wilson 1985). Species richness at small scales ($<1m^2$) is a consequence of direct competition and niche relations (variability in resource utilization and allocation). At intermediate scales ($1m^2$ - $100m^2$), species richness is more a consequence of microhabitat heterogeneity promoting the coexistence of species with different habitat requirements. At scales beyond $100m^2$, species richness is more likely determined by immigration of seeds from source habitats ('mass effect' dynamics, Schmida and Whitaker 1981). At this scale, the extent to which the plant community is linked to the regional species pool becomes the dominant process determining local recruitment and ultimately species richness (Rogers et al. 2009).

Our results indicate apparent associations between potential wolf impact and vegetation response variables at local scales (alpha richness). The similarity in *z*-values (beta richness) between high and low wolf impact sites suggests that herbivory may have little or no impact on species turnover, habitat heterogeneity or mass effects. Although we observed consistent differences at broader scales, these may be due to local differences propagating up through higher scales of observation. Reduced browse intensity limits the ability of a few browse resistant species to become locally dominant thus increasing species richness at local scales. Additionally, increased species richness may be closely linked to increased density of individuals at local scales. This pattern has been observed in both temperate and tropical plant communities (Denslow 1995, Busing and White 1997, Hubbell 2001, Schnitzer and Carson 2001).

Had we surveyed at scales greater than 1000m^2 we might expect a point at which species richness between high and low wolf impact areas would converge. However, patch occupancy of cedar stands and metapopulation dynamics of individual plant species could become dominant processes at this scale, superseding species-area relationships, and strengthening or weakening differences in species richness values between high and low wolf impact areas.

Top-down and bottom-up forces are both critical for maintaining biodiversity and ecological integrity of ecosystems, but it is not well understood how the relative strengths of these processes vary in space and time. Carnivores may cause herbivores to switch habitats or change their foraging behavior, resulting in net-positive indirect effects on some plant populations and net-negative indirect effects on other plant populations (Polis 1999). Similarly, increases in species richness at certain locations may be offset by decreases in species richness at other locations. Therefore, it is important to ascertain the proper spatial scale at which to measure the effects of a given trophic cascade.

By sampling at multiple scales, we revealed that our ability to detect differences in species richness was not consistent among vegetation growth forms. Based on means and 95% confidence intervals, forbs show a stronger response at local scales (1-10m^2), while shrubs show a response across broader scales (10m^2 - 400m^2). The design of future research should incorporate the proper scale in order to effectively detect top-down effects. Many vegetation studies survey at the scale of 1m^2, which is likely to miss significant differences in shrub species richness. Whether these scales are appropriate for community types other that northern white cedar wetlands is unknown. However, it is likely that the relevant scales are determined by the process of deer herbivory itself and should be consistent across vegetation community types.

2.5. *Conclusion*

There has been limited experimental evidence of trophic cascades initiated by vertebrate predators in temperate terrestrial ecosystems, partly due to the difficulty in administering and monitoring such large scale manipulations (Shurin et al. 2002). Recent attempts to infer top-down effects of predators have drawn on comparisons across areas with and without predators (Berger et al. 2001), or correlative studies of vegetation response following predator restoration (Ripple et al. 2001, Ripple and Beschta 2003). One of the most well known examples of a terrestrial trophic cascade is the wolf -moose (*Alces alces*)–balsam fir system on Isle Royale (McLaren and Peterson 1994). Despite its historical significance, experimental ecologists view cause and effect in the Isle Royale system as speculative due to the studies correlative nature and lack of replication or comparable control sites (Eberhardt 1994, Schmitz et al. 2000).

Whether trophic cascades are considerably weaker in terrestrial systems as compared to aquatic systems continues to be debated (Strong 1992, Polis 1999, Halaj and Wise 2001, Shurin et al. 2002). Recent evidence from experimental manipulations of herbivores and carnivores in old field ecosystems supports the theory that the effects of predators in terrestrial systems are much stronger on plant species diversity than on plant biomass, and that these changes in species composition and evenness may have strong effects on ecosystem properties (Schmitz 2006). Thus, total trophic-level biomass, a sufficient response variable for aquatic systems, may be an inappropriate response variable with which to measure trophic responses in terrestrial systems.

Our data from northern white cedar wetlands support Schmitz's argument that we need to rethink how we address trophic cascades in terrestrial systems instead of considering them as weaker examples of aquatic cascades.

The impacts of overabundant deer populations on understory plant community structure and composition have been well established (Alverson et al. 1988, Tilghman 1989, Peek and Stahl 1997, Crete 1999, Rooney 2001, Rooney and Waller 2003, Horsley et al. 2003, Rooney et al. 2004, Holmes et al. 2008). However, only a limited number of studies have examined how the recovery of wolves might moderate these effects. Our results provide compelling correlative evidence of top-down trophic effects generated by the recovery of Wisconsin's wolf population. By addressing wolf impact at the scale of wolf territory extents, instead of presence/absence of wolves for entire regions, we were able to have both replication of "treatments" (n=16) and comparable local control sites (n=16).

Our results support earlier unpublished work by Anderson et al. as well as a recent M.S. thesis (Bouchard 2009). Anderson et al. showed that the biomass of forb and woody-browse species in cedar wetlands of Wisconsin and Michigan increased toward the center of wolf pack territories (unpublished data). Combined with a decrease in graminoid species, these factors suggest a reduction in browsing pressure. In support of this hypothesis, Anderson et al. observed a simultaneous reduction in browsing of woody plant species of cedar swamps near wolf territory centers. A similar pattern was not observed in other forest-cover types (coniferous forest, deciduous forest and mixed forest), leading the authors to conclude that trophic cascades in this region are more detectable in areas with low productivity and high species richness (such as cedar swamps).

Unfortunately, reciprocal relationships between trophic levels, like those found by McLaren and Peterson (1994) between wolves, moose and balsam fir on Isle Royale, are lacking in Wisconsin. At present, deer data is available for the past several decades, but only at the very coarse scale of deer management blocks (WiDNR 2008). Since most low and high wolf impact areas in our study were within the same deer management unit, existing deer data was considered unsuitable for the scale of this study. Future research should focus on monitoring deer abundance and/or foraging behavior concurrent with wolf occupancy and vegetation response.

Several factors that benefit both plant diversity and wolf habitat quality, irrespective of deer density and any sort of trophic effects, could result in the correlation that we documented. In particular, road density has been shown to be negatively correlated with both plant diversity (Findlay and Houlahan 1997, Watkins et al. 2003) and wolf habitat selection (Mladenoff et al. 1995). In addition, understory vegetation in white cedar stands may be more influenced by hydrology and edge effects than by changes in local wolf or deer densities. Landscape level connectivity between cedar stands is likely to influence mass effects as discussed above. A bottom-up effect could also be responsible for observed patterns. Areas with high plant biomass and diversity may attract and maintain higher deer densities which in turn support successful establishment by wolf packs. Continued research directed at ruling out confounding factors and differentiating between top-down vs. bottom-up effects is needed.

If the methods employed here were applied across other forest types, we could predict long-term, region-wide effects of reintroducing top predators to this and other terrestrial systems. In addition, the spatially hierarchical sampling design developed to analyze wildlife census data in conjunction with vegetation data provides a template for addressing other broad scale ecological impacts. Regardless of the process in question, multi-scale approaches allow us to determine the scale at which a pattern becomes detectable. The ability to detect such signals above the ambient noise of ecological variation is essential to understanding the relationship between pattern and process.

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Table2.1. Slope (z or Beta richness), intercept (c or alpha richness), and correlation coefficient (r^2) values by vegetation growth form for species-area curves of northern white cedar stands with low and high potential wolf impact. Values in parentheses represent 95% confidence intervals.

	Low Potential Wolf Impact			High Potential Wolf Impact		
	z	*c*	r^2	*z*	*c*	r^2
All Species	**0.32** (0.30-0.35)	**8.98** (7.34-10.99)	**0.94**	**0.32** (0.30-0.35)	**10.82** (9.16-12.79)	**0.96**
Forbs	**0.24** (0.22-0.26)	**3.82** (3.33-4.39)	**0.91**	**0.24** (0.22-0.26)	**5.42** (4.84-6.05)	**0.93**
Shrubs	**0.30** (0.29-0.31)	**1.35** (1.20-1.51)	**0.95**	**0.32** (0.31-0.33)	**1.57** (1.40-1.76)	**0.95**
Seedlings	**0.26** (0.25-0.27)	**1.20** (1.04-1.37)	**0.96**	**0.27** (0.25-0.29)	**1.25** (1.00-1.54)	**0.93**
Trees	**0.22** (0.21-0.23)	**0.76** (0.60-0.93)	**0.87**	**0.21** (0.19-0.23)	**0.78** (0.63-0.95)	**0.86**
Ferns	**0.22** (0.20-0.24)	**0.94** (0.71-1.20)	**0.81**	**0.24** (0.23-0.25)	**1.24** (1.09-1.41)	**0.94**
Grasses	**0.20** (0.16-0.24)	**0.52** (0.42-0.62)	**0.83**	**0.21** (0.18-0.24)	**0.60** (0.36-0.92)	**0.77**
Sedges	**0.23** (0.20-0.26)	**1.37** (1.00-1.83)	**0.86**	**0.21** (0.23-0.25)	**1.80** (1.41-2.27)	**0.91**

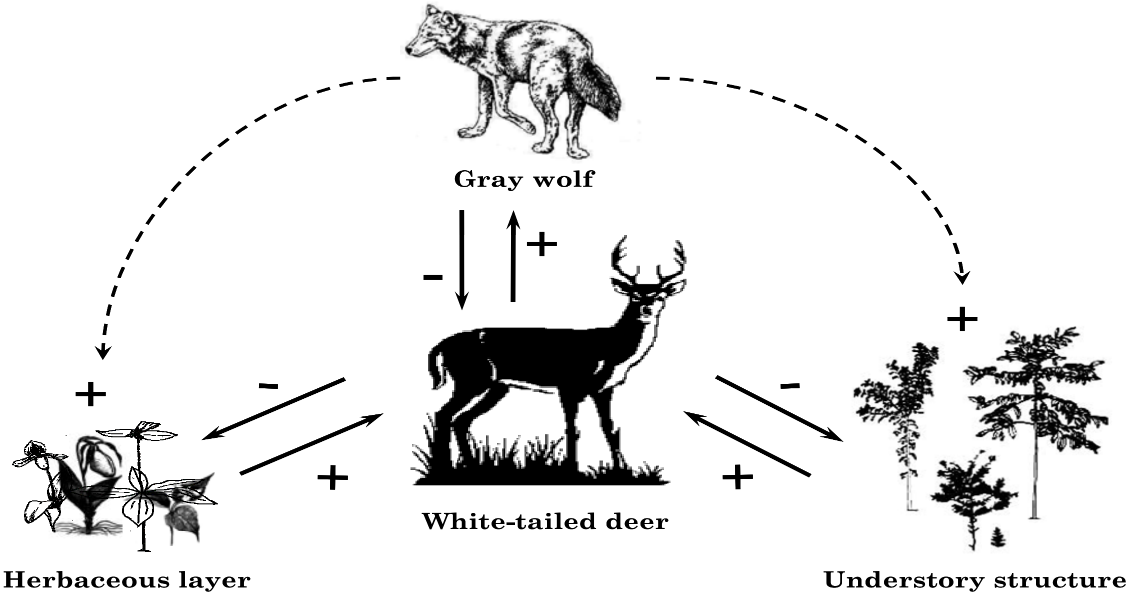


Figure 2.1 Diagram of assumed tri-trophic interactions in northern Wisconsin forests. Solid arrows represent direct positive and negative interactions. Dashed arrows represent hypothesized indirect positive interactions between wolves and plants.

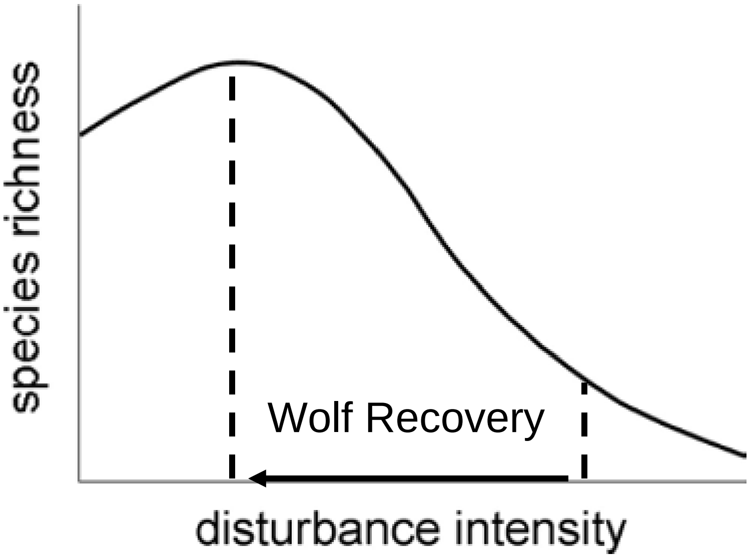


Figure 2.2 Proposed relationship between deer browsing intensity (disturbance) and species richness of understory plants. Wolf recovery should limit browsing intensity, thus releasing plants from browse pressure and increasing species richness.

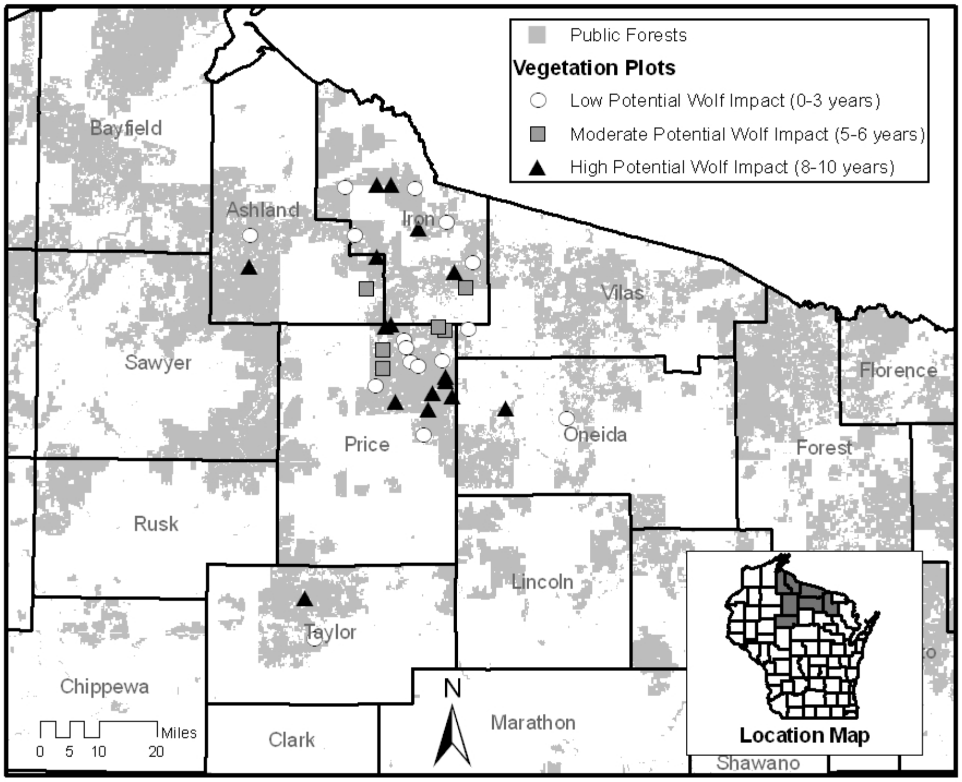


Figure 2.3 Study areas in northern Wisconsin. Black triangles indicate vegetation plots located in high potential wolf impact areas.

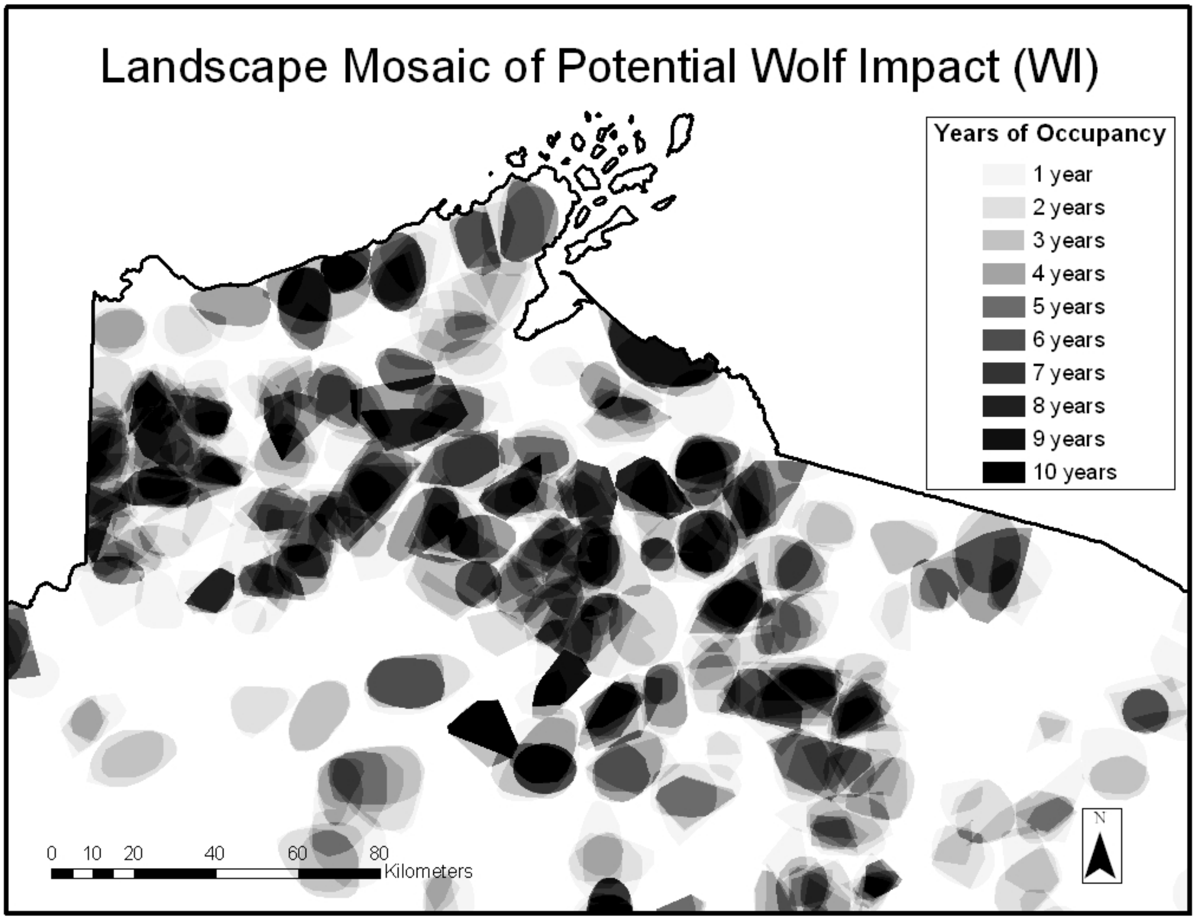


Figure 2.4 Surface of potential wolf impact based on 10 years (1998-2008) of wolf pack territory data (WiDNR). Years of occupancy represent the duration of wolf pack tenure. High potential wolf impact areas = 8-10 years of occupancy, low potential wolf impact = 0-3 years of occupancy.

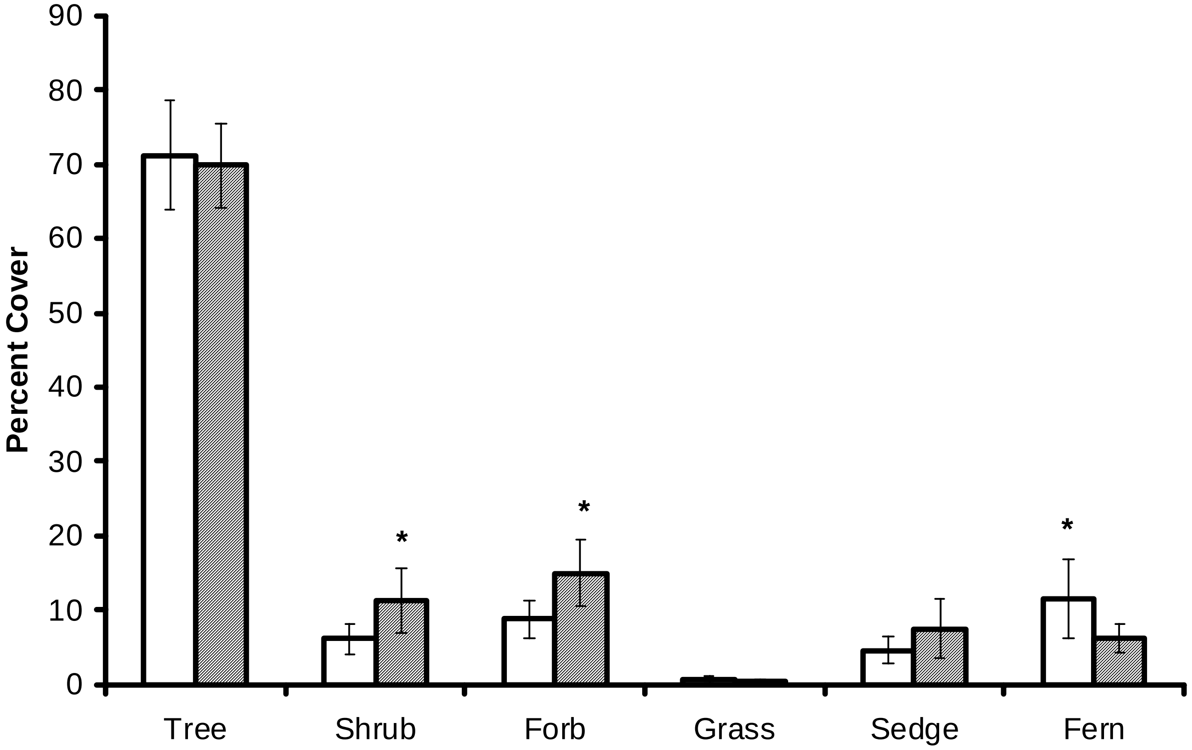
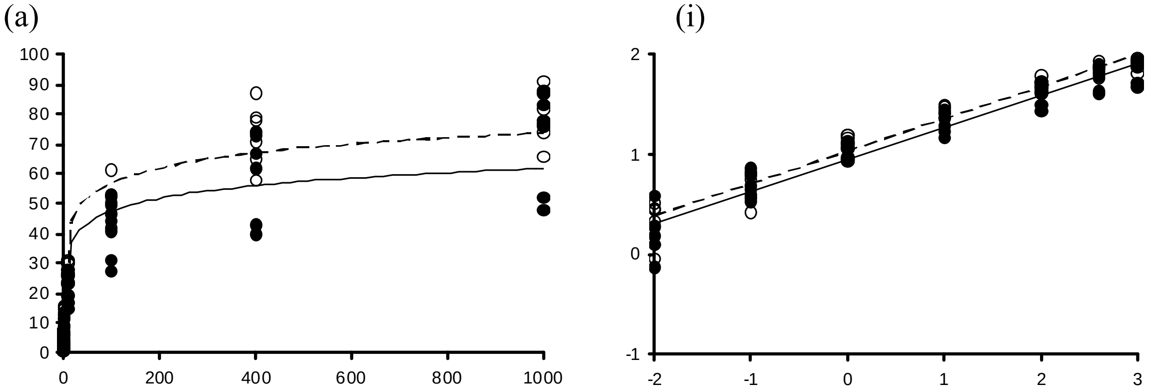
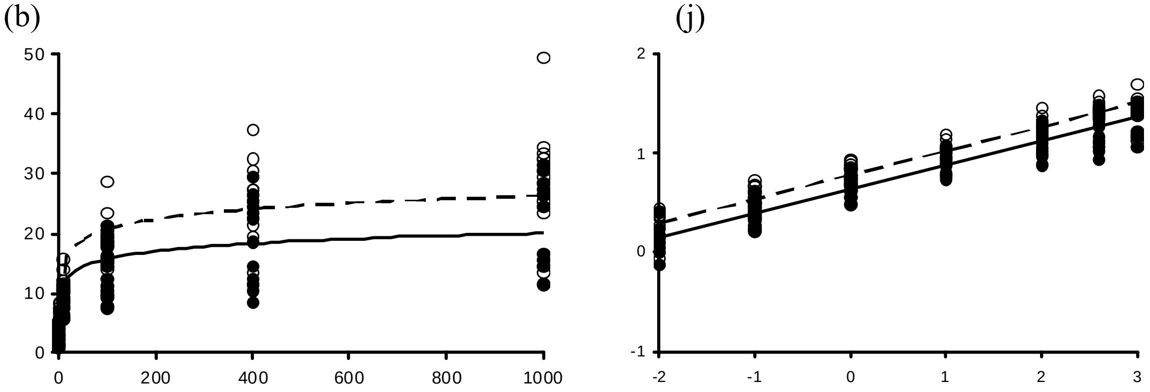


Figure 2.5 Average percent cover of high and low potential wolf impact plots of six vegetation growth forms (forbs, shrubs, trees, ferns, grasses and sedges) with 95% confidence intervals. Values are averaged geometric means of cover classes (0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95%, 95-100%). Hatched bars represent areas with high potential wolf impact. Asterisks indicate significant differences ($p < 0.05$).

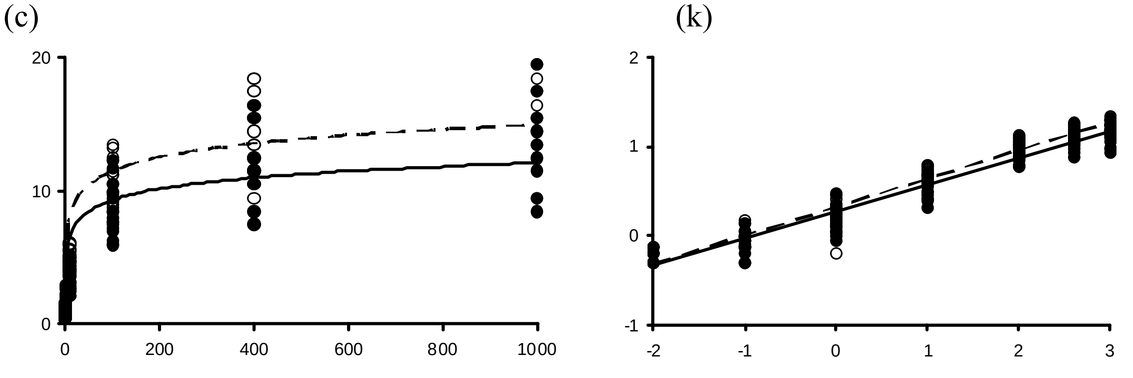
All Understory Plant Species (n=7)



Forbs (n=16)

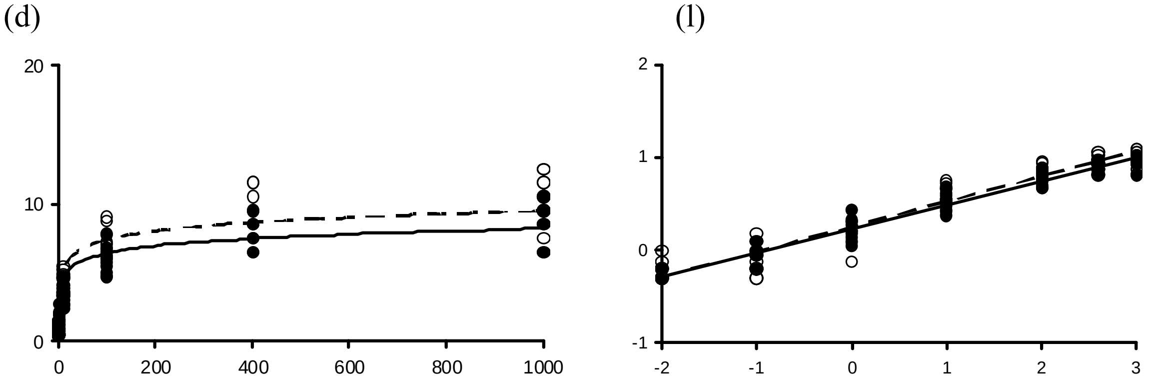


Shrubs (n=16)

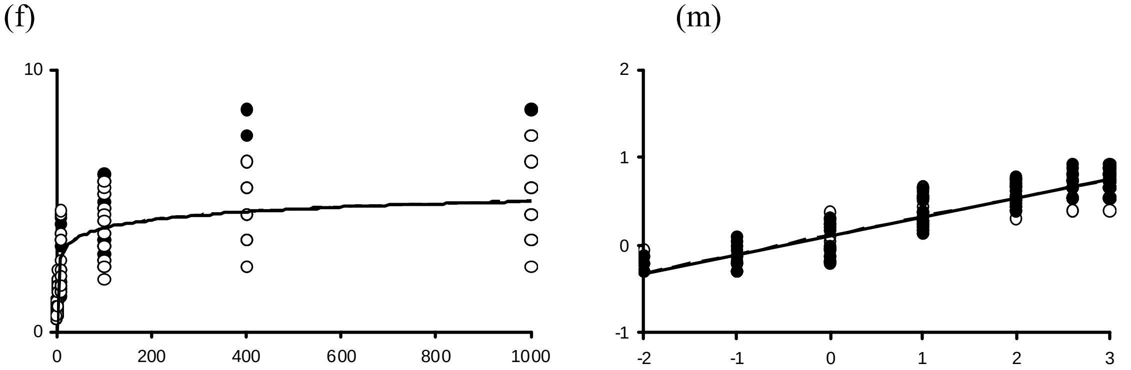


Area (m^2)

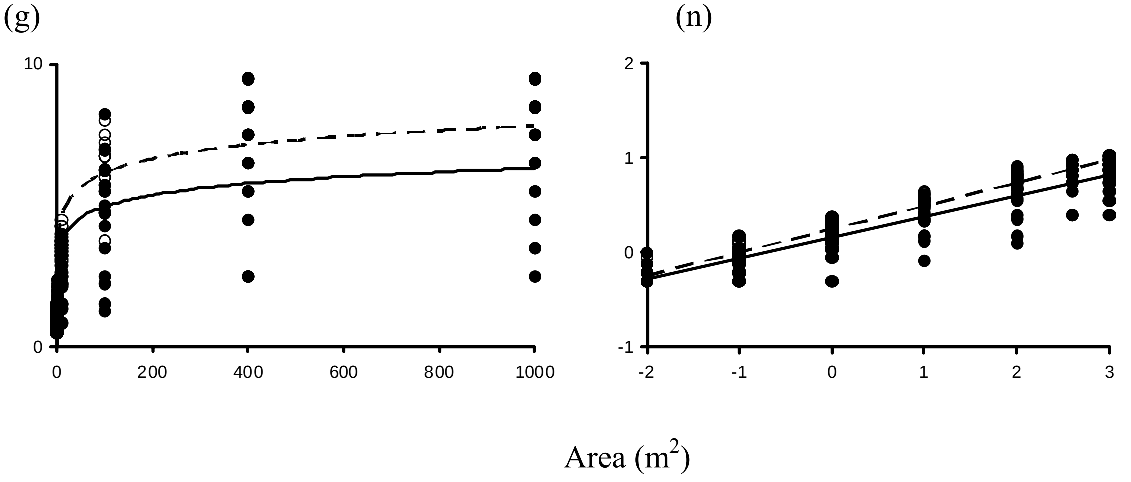
Seedlings (n=16)



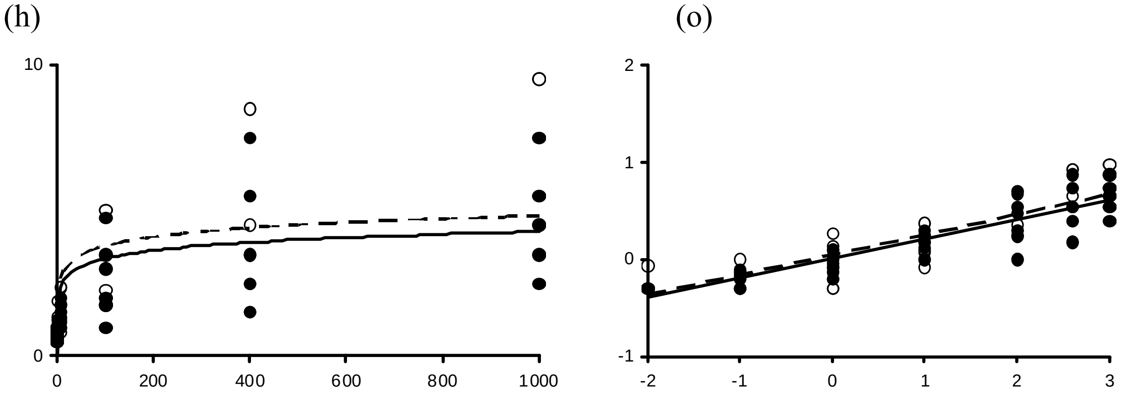
Trees (n=16)



Ferns (n=16)



Grasses (n=7)



Sedges (n=7)

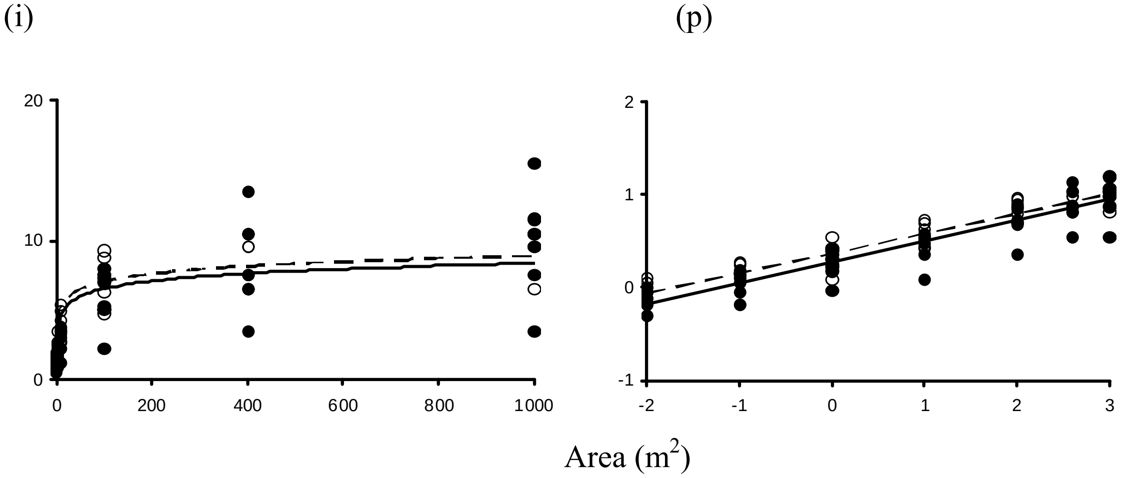


Figure 2.6 High and low potential wolf impact species-area curves displayed on arithmetic (a-h) and logarithmic (i-p) scales for all plant species together (a,i) and in each of seven vegetation growth forms (forbs, shrubs, seedlings, trees, ferns, grasses and sedges). High potential wolf impact data points are represented by open circles and dashed lines. Data points are the mean number of species at each scale from each plot. Scales on y-axis (number of plant species) vary depending on maximum species richness for each vegetation growth form. Sample size for all species, grasses and sedges are reduced because identification of sedges and grasses was not performed on all plots.

CHAPTER 3

WOLF RECOVERY AND THE FUTURE OF WISCONSIN'S FORESTS: A TROPHIC LINK?[2]

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[2] Callan, R. and N. P. Nibbelink *to be submitted to*

Forest Ecology and Management spring 2011

3.0 Abstract

The negative impacts of overabundant white-tailed deer (*Odocoileus viginianus*) populations on understory plant community structure and species composition have been well established. However, few studies have examined how the recovery of gray wolves (*Canis lupus*) might moderate these effects. Wolves, which have been recolonizing central Wisconsin since the early 1990s, are known to alter both the foraging behavior and local density of white-tailed deer. To test for evidence of indirect effects of wolves on understory woody plants, we first calculated an index of potential wolf impact based on historic and current wolf territory data: the Weighted Wolf Occupancy Duration Index (WWODI). We then performed intensive vegetation surveys (n=38) in northern white cedar wetlands across a gradient of wolf impact. Our objective was to evaluate the relationship between wolf pack tenure and woody stem density and species diversity in this highly browse sensitive and speciose community. In addition, we evaluate the potential for wolf recovery to alter the future canopy composition of northern white cedar wetlands.

Spearman rank correlations show the continuous presence of a wolf pack to be positively and significantly correlated with seedling density ($\rho = 0.602$, $p < 0.0001$) species richness ($\rho = 0.601$, $p < 0.0001$), and Shannon's diversity index ($\rho = 0.584$, $p < 0.0001$) of woody stems in the 50-100 cm height class. Surprisingly, moderately browsed species showed a stronger relationship with WWODI than severely browsed species ($\rho = 0.635$, $p < 0.0001$ vs. $\rho = 0.353$, $p < 0.05$). We propose two possible explanations for this discrepancy: 1) that even a few deer are able to prevent recruitment of highly preferred species, and/or 2) sensitive species are now so rare that a response to reduced browsing pressure is difficult to detect because of limited sample sizes. Unpalatable or insensitive species showed no relationship with WWODI. Size classes above the browse line also showed no relationship with WWODI.

Density of wild sarsaparilla (*Aralia nudicaulis*) and nodding trillium (*Trillium cernuum*), two perennial forb species known to decline with increased deer density, were strongly positively correlated with WWODI ($\rho = 0.462$, $p < 0.005$ and $\rho = 0.479$, $p < 0.005$ respectively). Other measures of browse pressure (scape height of the blue-bead lily, *Clintonia borealis*, red maple browse index, and deer density DMU^{-1}) were unrelated to WWODI. Site specific estimates of deer density continue to be a challenge in deer-vegetation studies, but our pilot study of un-baited infrared digital trail cameras demonstrated a potential for providing deer visitation rates and unambiguously confirmed substantial use of cedar stands by deer during spring and summer months.

The gap in the size structure of woody stems characteristic of over-browsed understories is less apparent in cedar wetlands with high wolf impact. However, regardless of wolf impact, recruitment of cedar in our study area is very limited. As the mature cedar and other co-dominants senesce, it is likely that these remnant forests will be replaced by balsam fir (*Abies balsamea*) stands and speckled alder (*Alnus incana* subsp. *rugosa*) thickets.

Key Words: cedar wetlands, trophic cascade, deer browsing, wolf recovery, seedling recruitment, demographic inertia, Wisconsin

3.1. *Introduction*

Top-down trophic cascades predict a pattern of alternating abundance or biomass across successively lower trophic levels (Paine 1980, Pace et al. 1999, Micheli et al. 2001). Hairston, Smith and Slobodkin (1960) proposed the classic cascade as a simplified tri-trophic system of predators (carnivores), herbivores (consumers) and plants (producers). With top-down control of such an odd numbered food chain, the loss of a predator releases herbivores from predation allowing them to increase in abundance. This shift in trophic structure in turn leads to a decline in plant abundance or biomass. Consequently, the decline of large carnivores has had broad repercussions for the maintenance of lower trophic levels (Crooks and Soule 1999, Miller et al. 2001). In theory, the repatriation of large carnivores may reverse this trend, allowing plants to recover. Conversely, release from over-browsing may not lead to a restored community because of ecological hysteresis (Cote et al. 2004).

White-tailed deer (*Odocoileus viginianus*) populations have drastically increased in recent decades throughout their range in North America (Garrot et al. 1993) due, in part, to the extermination of their primary predator, the wolf (*Canis lupus*) (Estes 1996, Van Deelen et al. 1996, Horsley et al. 2003, Augustine and deCalesta 2003). The long term negative impacts of over-browsing by white-tailed deer on the species composition, biomass, and structure of understory plant communities has been well documented (Frelich and Lorimer 1985, Alverson et al. 1988, Tilghman 1989, Rooney and Waller 2003, Horsley et al. 2003, Rooney et al. 2004, Cote et al. 2004, Holmes et al. 2008). Whether the recent recovery of the Midwest wolf population can mitigate these negative effects is of great interest from both theoretical and resource management perspectives (Rooney and Anderson 2009). Our objective was to test for evidence of such recovery across a gradient of wolf impact.

Prior to European settlement, densities of white-tailed deer in the northern Great Lakes Region were much lower because of extreme winters and extensive coverage of mature hemlock-hardwood forests (Dahlberg and Guettinger 1956, Habeck and Curtis 1959, DelGuidice et al. 2009). The early successional communities and high edge density created by large-scale clear cutting caused drastic increases in forage availability. Agriculture, deer baiting and fertilized lawns and gardens have amplified these positive impacts on habitat quality for white-tailed deer. When combined with the intentional eradication of large carnivores, these environmental changes have led to severely inflated deer populations throughout the region. For most of the 20th century, understory plant communities of northern Wisconsin have been subject to deer densities that exceed pre-settlement conditions by 350-500% (Rooney and Waller 2003).

Comparisons between deer exclosures and adjacent browsed plots in both Wisconsin and Michigan have shown drastic differences in the survival and reproductive success of preferred browse species (Graham 1954, Dahlberg and Guettinger 1956, Stoeckeler, Strothman, and Krefting 1957). Exclosure studies can be difficult to interpret because they provide only two points of reference, comparing extremely high browsing pressure to non-existent browsing pressure (Hobbs et al. 1996). Because deer-plant interactions were hypothesized to have non-linear dynamics, more recent correlative (Alverson et al. 1988, Alverson and Waller 1997, deCalesta 1997, Augustine and Jordan 1998, Cote et al. 2004, Holmes et al. 2008) and manipulative studies (Tilghman 1989, Horsley et al. 2003) have explored variation in white-tailed deer density across a gradient of deer impact in both space and time.

Evidence from these manipulative experiments in northern hardwood forests shows a distinctive threshold pattern indicating that the diversity of forbs, shrubs and trees in seedling size classes drastically decreases when deer density increases from moderate to high levels

(Tilghman 1989, Horsley et al. 2003). However, levels of browse intensity are relative and must often be explicitly determined for a range of habitat types and initial conditions. This relationship between browse intensity and woody species diversity is consistent with the concept that species diversity is maximized when disturbance conditions match the historic disturbance regimes under which plant communities developed (Denslow 1985). Since current levels of white-tailed deer browsing intensity are degrading habitat quality, then, in theory, recovery of wolves should reduce browse pressure allowing biodiversity of understory plant communities to increase with continued wolf occupancy.

Numerous mechanisms for reduced species diversity under high browse pressure have been proposed. The most obvious explanation is that chronic browsing leads to recruitment failure, mortality and ultimately local extinction of preferred species. An alternate explanation implicates the thick stands of insensitive or unpalatable species that form under high browsing pressure. By producing dense shade, these species are able to suppress more sensitive species while capturing all resources, a phenomenon commonly referred to as competitive exclusion (de la Cretaz and Kelty 2002). Both of these explanations may be confounded by the fact that the reduction in seedling density itself may produce reduced species diversity via the direct effect of density on species richness (Denslow 1995, Hubbell 2001). Whether these explanations represent alternate or complementary hypotheses is not clear.

Of the trees found in our study area, northern white-cedar (*Thuja occidentalis*), hemlock (*Tsuga canadensis*) and yellow birch (*Betula alleghaniensis*) are considered preferred deer browse species that may suffer reduced recruitment under even light levels of deer browse (Stoekeler et al. 1957). On the Apostle Islands, hemlock, cedar and yellow birch declined with increased deer density across the otherwise homogenous archipelago (Beals et al. 1960). In

Michigan deer yards, Van Deelen et al. (1996) documented drastic declines in cedar, hemlock, and yellow birch recruitment with concurrent increases in balsam fir (*Abies balsamea*), poplar (*Populus* spp.), and maple (*Acer* spp.).

We chose to focus on northern white cedar stands due to the established link between recruitment failure of cedar and white-tailed deer browsing intensity (Verne and Johnson 1986, Alverson et al. 1988, Heitzman et al. 1999, Van Deelen 1999, Cornett et al. 2000, Rooney et al. 2001, Forester et al. 2008). Northern white cedar is a highly preferred browse species (Beals et al. 1960, Ully et al. 1968) and lowland cedar stands have been intensively used by deer during the winter months (Verme 1965) often sustaining deer yard densities from 30-40/km^2. Thus, we anticipated that recovery of shrubs and seedlings would be more easily detected in this uniquely diverse and browse-sensitive community type.

With protection under the Endangered Species Act, wolves have been recolonizing northern Wisconsin since the early 1970s, but had very limited distribution until the 1990s.(Wydeven et al. 1995, Wydeven et al. 2009). Hoskinson and Mech (1976) reported observations that deer survival is higher on the edges of wolf territories as compared to their centers. Wolves are less likely to hunt in these buffer zones so as to avoid potentially fatal encounters with neighboring wolf packs (Mech 1977). At local scales, the distribution of deer in northeastern Minnesota was found to be negatively correlated with wolf territory extents, and deer were found primarily in buffer zones (Lewis and Murray 1993). Thus buffer zones surrounding wolf pack territories may act as refugia for white-tailed deer (Mech 1994).

Increased vigilance of individual deer that do continue to forage within wolf territories is also likely to reduce local impacts on woody browse species. By forcing deer to increase movement and spend less total time browsing, the presence of wolves may alter the disturbance regime experienced by local plant communities. Within occupied wolf territories, deer may no longer be able to sit and browse one location until all preferred species become locally rare or extinct.

We hypothesized that the recovery of wolves in Wisconsin has generated a mosaic of deer browsing intensity as deer alter their foraging activity to avoid occupied wolf territories, showing preference for the buffer zones between adjacent packs. Our first goal was to calculate an index of potential wolf impact based on historic data of wolf pack territory extents. Our primary objective was to test for a relationship between this index of potential wolf impact and the structure, density, species diversity and species composition of woody stems in understory communities of northern white cedar wetlands. Our secondary objective was to compare our index of potential wolf impact with commonly used measures of deer browse intensity. Our final objective was to predict future changes in canopy species composition of lowland cedar stands.

3.2. ***Methods***

3.2.1 STUDY SITE

Data were collected throughout the Chequamegon-Nicolet National Forest, as well as various state and county forests spanning 7 counties in north-central Wisconsin. The forests of Northern Wisconsin are transitional between deciduous forests to the south and boreal forests to the north (Pastor and Mladenoff 1992, Mladenoff et al. 1993). Annual air temperature in northern Wisconsin averages 4° C, and mean annual precipitation ranges between 76 and 86 cm. The freeze free period averages ~80 days, making for a short growing season. Snowfall accumulation frequently exceeds 76 cm and this snow cover provides insulation for ground vegetation (NOAA 1982).

Glaciation strongly influenced the soils and topography of Wisconsin. Soils are derived from sandy loam glacial till, silt covered glacial till, and sandy outwash. With a maximum elevation of 550 m, there is little topographic relief. The gently rolling terrain is inundated with thousands of lakes and numerous wetlands. Terrestrial landscapes are comprised of 40% deciduous forest types (dominated by sugar maple, *Acer saccharum* and paper birch, *Betula papyrifera*), 9% coniferous, (dominated by white pine, *Pinus resinosa*, red pine, *Pinus strobus*, and balsam fir, *Abies balsamea*), 8% mixed-coniferous-deciduous, and 7% early successional (dominated by aspen, *Populus tremuloides*). Forested and emergent wetland communities cover an additional 26% of the area (dominated by tamarack, *Larix laricina* and black spruce, *Picea mariana*, and Labrador-tea, *Ledum groenlandicum* and leather leaf *Chamaedaphne calyculata*, respectively). Northern-white cedar wetlands occupy less than 5% of the landscape but support a large proportion of the regional biodiversity (WiDNR 1998).

Northern-white cedar wetlands develop on poorly-drained sites with a slight through-flow of groundwater. These conditions elevate the pH and nutrient richness of the soil (Black and Judziewicz 2008). Mature stands of white cedar are densely shaded with nearly closed canopies. The combination of these environmental characteristics produces unique light regimes and soil chemistry required by species restricted to this community type. Co-dominant trees in white cedar wetlands include balsam fir, yellow birch (*Betula alleghaniensis*) and black ash (*Fraxinus nigra*). Speckled alder (*Alnus incana* subsp. *rugosa*), hollies (*Ilex mucronata* and *I. verticillata*), hazelnuts (*Corylus* spps.) and honeysuckles (*Lonicera* spps.) are common understory shrubs.

3.2.2 WOLF DATA

Wisconsin Department of Natural Resources (WiDNR) population estimates of wolves were ascertained by live-trapping and radio tracking (Mech 1974, Fuller and Snow 1988), howl surveys (Harrington and Mech 1982), and winter track surveys (Thiel and Welch 1981, Wydeven et al. 1995). Territory extents were delineated using minimum convex polygons based on radiolocations of collared wolves and other wolf sign (Wydeven et al. 1995, Wydeven et al. 2009). Depending on pack size and prey density, wolf territories in the Great Lakes Region can range in size but average approximately 136 km^2 (Wydeven et al. 2009). Wolf packs establish and occupy territories that are patchily distributed across the landscape (Mladenoff et al. 1999). The negative effect of wolves on deer abundance and foraging behavior is likely to be limited to locations continuously occupied by wolf packs. Presumably, the impact of wolves increases with the number of years the territory has been consistently occupied. Since pack size and territory extent vary from year to year, this creates a mosaic of wolf impact intensity across the landscape.

Using GIS, we overlaid current wolf territories with historic territory extents back to 1995 (Wydeven and Wiedenhoeft 2008). Only sites that fell within the Chequamegon-Nicolet National Forest, state or county forest boundaries were selected. Although wolves have established territories outside of public lands, these territories are often located in agricultural or industrial forest landscapes and anthropogenic sources of landscape change are likely to confound any potential trophic effects of wolf recolonization. It was also difficult to locate and obtain access to northern white cedar stands on private property. We categorized locations that had been occupied for 0-3 years as low potential wolf impact areas, locations that had been occupied for 5-6 years as moderate potential wolf impact areas and locations that had been occupied for more than 8 years as high potential wolf impact areas.

Weighted wolf occupancy duration Index (WWODI) values were calculated by summing the most recent 15 years of DNR wolf territory extent data (1993-2007 for vegetation plots surveyed in 2008 and 1994-2008 for plots surveyed in 2009). Recent years were weighted more strongly given the assumption that wolf occupancy in the distant past would have a weaker impact on current browse intensity and therefore a weaker indirect effect on understory plant communities. The most recent year of wolf occupancy (presence/absence of a wolf pack at each location) was divided by 1, the next most recent year was divided by 1.1, and so on. Thus:

$$\mathbf{WWODI = Y_t/1 + Y_{t-1}/1.1 + Y_{t-2}/1.2 + \ldots\ldots.. Y_{t-15}/2.4}$$

where $\mathbf{Y_t}$ is the current year of wolf occupancy and $\mathbf{Y_{t-15}}$ is the wolf occupancy 15 years ago. Although we had hoped to calculate wolf density by dividing territory area by the number of wolves in each pack, pack size data was not consistently collected for all years and all packs.

3.2.3 DEER DATA

White-tailed deer density data were obtained for each deer management unit (DMU) for the year in which vegetation data were collected, either 2008 or 2009 (WiDNR 2009). WiDNR calculates initial deer density estimates using the sex-age-kill method and then corrects for the proportion of the DMU that is considered deer habitat (Millspaugh et al. 2006). Wisconsin DMUs are vastly larger in area than the cedar stands and wolf pack territories they contain. Since a deer density estimate for a given DMU is a single value intended to represent an average across a very large heterogeneous area, it is unlikely that these values represent the site specific deer density influencing the understory of isolated cedar stands. Unfortunately, this was the only region-wide data available.

Un-baited infrared triggered cameras (ITCs) have been successfully used to estimate local abundance of white-tailed deer (Roberts et al. 2006). In the early spring of 2009 (17th of April), we set up 14 ITCs in vegetation plots that had been surveyed in 2008 (one camera per plot). The cameras were faced into the plot to record deer visitations. All cameras were checked in early summer (June 10th-12th) and removed from the field by August 21st. Observations were divided into two sessions: spring (April 17th-June 10th), and summer (June 10th – August 21st). Only 7 of the 14 cameras remained functional until they were retrieved in late summer. Leaf River© digital trail cameras failed to capture images of deer due to a considerable delay between animal detection and camera activation. Cuddeback© trail cameras performed very well. The total number of deer captured by each Cuddeback© was then divided by the total number of days the camera was operational for spring and summer sessions. Leaf River© trail cameras did not produce usable data, reducing our sample size to n=7.

We measured site specific browse intensity on each vegetation plot for plots surveyed in 2008 (n=14). Browse intensity indices conformed to the sugar maple browse index (SMBI) developed by Frelich and Lorimer (1985). Unfortunately, sugar maple seedlings were rare in the northern white cedar wetlands and we attempted to substitute a red maple browse index (RMBI). We collected data for additional indicators of browsing intensity such as flower scape height in the blue-bead lily (*Clintonia borealis*), density of wild sarsaparilla (*Aralia nudicaulis*) and density of nodding trillium (*Trillium cernuum*) at all plots (n=32). These forb species have been shown to decline in areas of high deer density (Balgooyen and Waller 1995, Augustine and deCalesta 2003). Scape height of blue-bead lily and the density of wild sarsaparilla and nodding trillium are negatively related to browsing pressure, and so, according to a trophic cascade response, should be positively related to WWODI. In contrast, Red Maple Browse index, deer density DMU^{-1} and deer visitation day^{-1} are positively associated with browsing pressure and so should be negatively correlated with WWODI.

3.2.4 VEGETATION DATA

We used the Combined Data Systems (CDS) data for the Chequamegon-Nicolet National Forest (USDA 2001) and various state and county forest datasets to identify stands characterized as northern white cedar wetlands. White cedar stands of similar area and stand age were selected. We used Hawth's Tools to randomly place one vegetation plot within each pre-selected white cedar stand. We surveyed a total of 38 cedar stands, 14 plots were completed in summer 2008 and 24 plots were completed in summer 2009.

Vegetation surveys follow the Carolina Vegetation Survey (CVS) protocol developed by Peet et al. (1998). Understory woody stem surveys consisted of two 10 X 10 m modules per 200 m^2 plot. For each module, woody stems were identified to species when possible, but sometimes only to genus. Scientific names conform to Gleason and Cronquist (1991). Tallies of stems in each height class for seedlings (10-50 cm, 50-100 cm, 100-137 cm) and each diameter class for saplings and mature trees (0-1 cm, 1-2.5 cm, 2.5-5 cm, 5-10 cm, 10-15 cm, 15-20 cm, 20-25 cm, 25-30 cm, 30-35 cm, 35-40 cm and > 40 cm) were recorded for each module. For trees greater than 40 cm d.b.h. we measured the exact d.b.h. to the nearest centimeter. Data from the 2 modules were then averaged to provide a single value for each plot (the average number of stems of each species per size class). Basal area per plot was calculated for each tree species and scaled up to basal area per hectare.

To compare the diversity of woody stem species with WWODI, we calculated the species diversity index per plot, averaging values from the two modules. Diversity of woody species for each size class was calculated using the Shannon-Weiner diversity index ($H' = -[\Sigma(p_i)(\ln p_i)]$). A simple linear regression model was fit to test for a relationship between species diversity and the strength of potential wolf impact (WWODI).

3.2.5 LITERATURE REVIEW OF SPECIES SPECIFIC BROWSING RESPONSE

When assessing browsing response, it is important to consider both browse preference (the relative desirability of the plant species to foraging white-tailed deer) and browse sensitivity (the physical response of plant species to browsing events) of each species. For example, more sensitive, preferred species such as red oaks (*Quercus rubra*), have displayed drastic differences in seedling mortality rate, 34.6% for exposed seedlings compared to 3.2% for seedlings protected from deer herbivory (Stange and Shea 1998). In contrast, sugar maple (*Acer saccharum*) also a preferred species, can survive high browse pressure for many years without mortality (Switzenberg et al. 1955, Stoeckler, Strothman, and Krefting 1957). At the extreme end, balsam fir is rarely browsed and may in fact experience a competitive advantage when deer browsing levels are high (Graham 1954). Understanding browse preference is complicated by the fact that preference is relative and dependent on the available species in the area. For example, balsam fir is not a preferred species in cedar wetlands, where it replaces cedar under high browsing pressure, but is preferred on some islands where more palatable species are rare.

Table 3.1 shows a list of tree and shrub species found in northern white cedar stands of north-central Wisconsin. Based on a review of the available literature, we assigned a browsing response value to each species. Species that were observed to be browsed more often than their abundance in the community would suggest were considered to be preferred. Species that were more abundant inside exclosures were considered sensitive to deer browsing. Response values ranged from -4 (recruitment failure) to +3 (competitive advantage). With few exceptions, browse preference and sensitivity information for shrub species was limited. These browsing response scores were used in the following analyses to determine which groups of woody stem species showed a relationship with potential wolf impact.

3.3. ***Results***

3.3.1 SPECIES RICHNESS AND POTENTIAL WOLF IMPACT

A one-way ANOVA was used to test for woody stem species richness differences among high, moderate and low potential wolf impact (Figure 1). Species richness differed significantly across the three levels of wolf impact for the three seedling size classes: 10-50 cm, F (2, 35) = 5.72, p = 0.007, 50-100 cm, F (2, 35) = 10.71, p < 0.0001, and 100-137 cm, F (2, 35) = 3.37, p = 0.05. Species richness did not differ for the two sapling size classes: 0-1 cm d.b.h., F (2, 35) = 1.41, p = 0.257, and 1-2.5 cm d.b.h., F (2, 35) = 0.32, p = 0.729.

3.3.2 WEIGHTED WOLF OCCUPANCY DURATION INDEX (WWODI)

The weighted wolf occupancy duration index ranged from 0.00 – 9.47 with an average value of 4.66. These data are not normally distributed so they were compared to other variables using Spearman rank correlations. Figure 3.2 shows the linear relationship ($y = 0.0934x + 0.798$, $r^2 = 0.379$, $p<0.0001$) between weighted wolf occupancy index values and Shannon's diversity index of all woody species 50-100cm in height at the plot level (n=38). Relationships between WWODI and the diversity of woody stems in the other size classes were weaker, similar to the species richness comparisons above. Despite considerable variability among sites, this strong positive relationship was consistent and suggests an indirect positive trophic response to wolf recovery. While a simple cumulative occupancy index, which ranged from 0-15, had a similar relationship with diversity of woody species 50-100 cm ($y = 0.0593x + 0.829$, $r^2 = 0.356$, $p<0.0001$), the weighted index provided a slightly improved fit and was considered a logical compromise between underestimating and overestimating the effect of historic wolf occupancy. Time-weighted averages are a useful tool for reducing data to a single value for use in regression analyses (Vanni and Layne 1997, Mörschel 1999).

3.3.3 SPECIES COMPOSITION

Northern white cedar averaged 84.5% of the total basal area (TBA) of all 38 vegetation plots but ranged from 36.8%-99.0% (Table 3.2). Balsam fir, black ash, yellow birch, paper birch and red maple comprised the majority of the remaining TBA (13.1% collectively). Black ash and red maple were clearly co-dominant at some sites representing up to 49.1% and 35.7% of the TBA respectively. Scattered eastern hemlock, black spruce, eastern white pine, tamarack and white spruce occurred in a few plots but did not consistently constitute a significant portion of the canopy.

The understory was often dominated by speckled alder or balsam fir. Hollies (*Ilex* spp.), honeysuckles (*Lonicera* spp.), dogwoods (*Cornus* spp.), gooseberries (*Ribes* spp.), hazelnuts (*Corylus* spp.), blueberries (*Vaccinium* spp.) and Labrador tea (*Ledum groenlandicum*) were common in the understory but contributed little to basal area as few of them reached breast height (with the exception of *Ilex* spp.). Sugar maple (*Acer saccharum*), mountain maple (*Acer spicatum*), red oak (*Quercus rubra*), mountain ash (*Sorbus* spp.), American basswood (*Tilia americana*), and American elm (*Ulmus Americana*) were found occasionally as seedlings in the understory but were not found in the canopy.

3.3.4 CANOPY COVER, DEMOGRAPHIC INERTIA, AND WWODI INFLUENCE ON SEEDLING DENSITY

Spearman rank correlations of all woody species suggest that the density of woody stems in the first size class (10-50cm in height) is related primarily to canopy cover ($\rho = -0.559$, $p < 0.0005$) and secondarily to WWODI ($\rho = 0.404$, $p < 0.05$) which we associate with a potential reduction in browsing pressure (Table 3.3a). Canopy cover is inversely related to available light explaining the strong negative relationship between woody stem density and canopy cover. At the second size class (50-100cm in height), WWODI has the strongest relationship with woody stem density ($\rho = 0.602$, $p < 0.0001$) followed by demographic inertia ($\rho = 0.496$, $p < 0.005$). Demographic inertia is the density of woody stems in the preceding size class (size class 1 in this case). At this stage, canopy cover is no longer an important factor suggesting that light availability influences germination success but demographic inertia and disturbance intensity (*i.e.* browsing pressure) determine establishment and recruitment. As the woody stems escape the browse line, beyond size class 3 (100-137cm in height), demographic inertia surpasses WWODI and continues to be the dominant factor driving woody stem density for the sapling size classes (0-2.5cm dbh).

We anticipated that the species likely to experience recruitment failure at high levels of browsing pressure (*i.e.* yellow birch, red oak, hemlock and cedar) would have an even stronger relationship with WWODI than moderately browsed species. However, the relationship was in fact weaker, but still significant for the 2nd and 4th size classes (Table 3.3b). When we grouped species likely to gain a competitive advantage from browsing pressure (balsam fir, speckled alder and spruce) the previously observed relationship with WWODI disappeared completely (Table 3.3c). The density of browsing insensitive species appear entirely dependent on canopy cover and demographic inertia. The strongest relationship with WWODI was in fact found with the woody stem density of moderately impacted species (the species scoring between 1and -2 for browsing response in Table 3.1). The positive relationship between density of saplings in size class 5 and canopy cover is likely due to saplings of this size contributing to canopy cover and providing additional shade at the height at which densiometer readings were taken.

When we separated shrub species from tree species (having removed species that are likely to experience a competitive advantage with increased browse pressure: balsam fir, speckled alder and spruce), additional patterns emerged. Density of shrubs in size class 1 is much more strongly related to canopy cover than tree seedlings of the same size ($r = -0.643$, $p < 0.0001$ compared to $r = -0.078$, $p = 0.643$). This likely reflects the fact that most of the tree species are shade tolerant. WWODI is the only variable strongly correlated with shrub density at size class 2 ($r =0.626$, $p < 0.0001$). In contrast, while the relationship between WWODI and seedling stem density is somewhat weaker ($r = 0.415$, $p < 0.01$), it transmits up through to the 4th size class. Few individual shrubs reach size class 4 so this difference may be due to a smaller sample size.

When we analyzed species independently, and compared the density of woody stems of each species to WWODI, more specific associations became apparent (Table 3.4). More than half of the shrub species were strongly related to WWODI, while less than a third of the tree species showed a significant correlation. The densities of quaking aspen (*Populus tremuloides*) , velvet-leaf blueberry (*Vaccinium myrtilloides*), and mountain holly (*Ilex mucronata*) were negatively correlated with WWODI implying that they may in fact gain a competitive advantage with high browsing pressure. Among the tree species, the density of woody stems of sugar maple, striped maple, yellow birch, and black ash were significantly positively correlated with WWODI. Among the shrubs, densities of red osier dogwood (*Cornus stolonifera*), American and beaked hazelnut (*Corylus americana and C. cornuta*), American and swamp fly honeysuckle

(*Lonicera canadensis*, and L. *oblongifolia*), alder-leaf buckthorn (*Rhamnus alnifolia*), and gooseberry species (*Ribes* spp.) were significantly positively correlated with WWODI.

Few studies have addressed the relative browsing preference and sensitivity of shrub species (see Table 3.1). Our data suggest that they may be even more sensitive than many tree species (assuming an indirect effect of wolves on plants via a trophic cascade mechanism). Given that shrub species do not benefit from a constant seed rain from the canopy, over-browsing of these species could quickly lead to local stand-level extinction. Some species may simply have been too rare to show a definite relationship with WWODI one way or the other. Density of alder and balsam fir may reflect historic browsing pressure and represent an aspect of the community that will not change with reduced browsing pressure (consistent with the theory of ecological hysteresis).

3.3.5 RELATIONSHIP BETWEEN WWODI AND BROWSING INTENSITY

Table 3.5 shows Spearman rank correlations between WWODI and six commonly used measures of browse intensity. The lack of a relationship between WWODI and deer density DMU^{-1} ($r = -0.019$, $p = 0.909$) is not surprising given the disparity in scale between these two variables. High impact wolf sites were intentionally paired with the closest low wolf sites during the first season so most high and low wolf impact sites are located within the same DMU (which explains the U-shaped pattern in Figure 4d). The variation in local deer density within a DMU is likely to be great given the average size of DMUs in Wisconsin (1,200 km^2) and the variability in available forage and (presumably) predator pressure.

The red maple browse index (based on the proportion of browsed stems relative to available stems) also had no apparent relationship with WWODI ($r = -0.197$, $p = 0.540$). Not all of the plots had enough red maple to calculate a browse index (n=12). The index only varied from 0.707 to 0.879 suggesting that all red maple seedlings were heavily browsed regardless of wolf occupancy. The high wolf impact areas had a slightly lower browse index on average (0.783 compared to 0.794), but the difference was not significant. Red maple may not be as good of an indicator of browsing intensity as sugar maple. Many of the low wolf impact sites had no red maple, and it is possible that red maple is more likely to suffer mortality under heavy browse pressure compared to sugar maple. For future studies, it may be preferable to measure browse intensity in an adjacent stand with sufficient sugar maple to calculate SMBI.

The camera surveys indicated a negative relationship between deer visitation day^{-1} and WWODI (Figure 4), but the relationship was not significant ($\rho = -0.270$, $p = 0.558$) most likely due to the small sample size (n=7). Local resource managers expressed the opinion that deer would not be found in cedar stands during spring and summer because these habitats were primarily used by deer during the winter months. Our camera survey showed irrefutable evidence that deer are using these habitats in the spring and summer. Our images also confirmed that deer are browsing both woody stem and herbaceous growth in these habitats throughout the growing season. Sixty-four images of deer were captured by the 7 Cuddeback trail cameras in the 128 days that the cameras were on.

Average scape height of the blue bead lily was also unrelated to WWODI ($\rho = 0.378$, $p = 0.279$). Only 10 of the 38 plots contained flowering blue-bead lilies making it a poor indicator species. In contrast, density of sarsaparilla and nodding trillium were strongly positively correlated with WWODI ($\rho = 0.462$, $p < 0.005$ and $\rho = 0.479$, $p < 0.005$ respectively). The relationship between density of these sensitive species and WWODI appears curvilinear indicating a threshold in time (between 6 and 7 years of wolf occupancy) beyond which these species begin to recover from browsing.

3.3.6 WOLF RECOVERY AND FUTURE CEDAR STAND COMPOSITION

On average, there was no significant difference in cedar seedling density between high and low wolf impact areas across all size classes (Figure 4a). Even at the smallest size class cedar density was more related to canopy cover ($\rho = -0.617$, $p < 0.0001$) than to WWODI ($\rho = 0.187$, $p = 0.261$). Black ash, which is not considered a highly preferred species, shows a clear pattern suggesting a release from browse pressure in high wolf impact areas (Figure 4b). Black ash woody stems in the first 4 size classes were 200-300% more abundant in high wolf impact areas, however the difference was only significant at the smallest size class (High wolf = 780 ha^{-1}, and Low wolf = 197 ha^{-1}, $p = 0.05$). Historically, black ash has been replaced by northern white cedar since the adults are less shade tolerant than the slower growing but shade tolerant white-cedar (Gates 1942). A similar but even stronger pattern is seen for yellow birch, a more preferred species (Figure 4c). For this species, the first two size classes show significantly higher densities of woody stems in high wolf impact areas. No difference was observed in the density of balsam fir between high and low wolf areas (Figure 4d). Although black spruce, an unpalatable species, appears more abundant in low wolf areas across early size classes, these differences were not significant (Figure 4e).

3.4. ***Discussion***

Top down effects are likely to attenuate (Schmitz et al. 2000), showing strong direct effects (of carnivores on herbivores) but weaker indirect effects (of carnivores on plants and other trophic levels). Some evidence suggests that more complex food webs typically dampen the strength of trophic cascades (Polis and Strong 1996). The recovery of a top predator may cause an initial pulse of environmental change that eventually subsides. Alternatively, it may take many years to reverse the impacts of decades of chronic browsing by ungulates maintained at population densities far above their historic numbers. Additionally, ecologically effective densities of wolves may only recently have been reached (Soule et al. 2003).

We found that moderate wolf impact sites (5-6 years of wolf pack occupancy) had woody stem species richness values intermediate between high and low wolf sites but that these sites were not significantly different from either low or high wolf impact sites (Figure 1). Thus, a time lag of at least 8 years may be required before trophic effects of wolf recovery manifest in an easily detectable way. Will changes continue at the same pace, accelerate or asymptote? Nonlinear dynamics can often develop with plant-herbivore interactions contingent upon historical events and associated time lags (Cote et al. 2004). White cedar wetlands are relatively sensitive to browsing by white-tailed deer and it is likely that other forest-cover types will display lag times of different lengths. These lag times in trophic effects will depend on the relative sensitivity and resilience of forest-cover types and their individual constituent species to browsing pressure.

Regeneration of canopy dominants in the Great Lakes Region is strongly dependent on the probability that their seedlings will survive browsing by white-tailed deer. White-tailed deer browse the apical meristem of preferred seedlings which stunts plant growth and prevents seedlings from escaping the browse zone (Gill and Beardall 2001). Browsing also reduces root carbon reserves that are normally allocated to chemical defenses and future growth (Bryant et al. 1983). Chronic browsing can therefore produce a positive feedback loop since seedlings are maintained at accessible heights and lack chemical defenses (Peinetti et al. 2001). As fewer and fewer individuals survive past the seedling size classes, a gap develops in the population structure of sensitive species, a pattern which is characteristic of heavily browsed forests (Leopold et al. 1943, Whitney 1984). We anticipated that this gap would be more pronounced in areas with high browsing pressure and by extension (given indirect effects) low potential wolf impact.

Under high browsing pressure, early successional forests may also transition toward dominance by nitrogen-fixing species such as *Alnus* spp. (Kill and Bryant 1998). Forested wetlands in Wisconsin often develop thick understories of speckled alder (*Alnus incana* ssp. *rugosa*) an actinorhizal shrub that forms a symbiotic relationship with N2-fixing actinomycetes of the genus *Frankia* (Furlow 1979). It is likely that areas with historically higher browse pressure will in fact have greater densities of speckled alder which serves to suppress other understory species. Once these stands develop, it is unlikely that reducing browse pressure will reverse this state. Indeed, densities of speckled alder had no relationship with WWODI across all size classes. As the cedar and other co-dominants senesce, it is likely that these remnant lowland cedar forests will be replaced by balsam fir stands and alder thickets.

Complicating the issue of recovery from browsing disturbance is the fact that ecological systems display the potential for multiple stable states (Holling 1973, May 1977). Early indications of alternate stable states and their potential drivers arose from investigations of degraded rangelands (Noy-Meir 1975, Hart and Norton 1988). In the range management literature, a degraded state is defined as a lower or less desirable state that can not be returned to its former state without intensive management effort (Friedel 1991). Once a system has crossed the threshold into an alternate stable state, simply reducing the disturbance intensity (grazing pressure) may be insufficient to achieve management goals (Laycock 1991). While these concepts developed out of range science, they are likely applicable to deer-vegetation relationships as well (Stromayer and Warren 1997).

Despite this positive relationship between WWODI and woody stem density and WWODI and species diversity, few of the canopy species in our vegetation plots appear to be successfully recruiting individuals into the sapling size classes (with the exception of balsam fir) (Figure 4a-e). In particular, cedar recruitment is extremely low. Lowland cedar may be slow to respond to release from browse pressure simply because cedar seedlings grow extremely slowly, typically requiring 10 years to reach 30 cm in height and 30 years to attain 3 m (Rooney et al. 2001). Based on their study of upland cedar stands in Minnesota, Cornett et al. (2000) recommend protecting cedar seedlings from deer herbivory for 30-50 years in order to allow them to escape the browse zone and successfully recruit seedlings taller than 2.1 meters.

Recruitment failure of cedars implies that recovery of northern white cedar stand understories may not be possible and indicates future stand level replacement by balsam fir and speckled alder. Mladenoff and Stearns (1993) have argued that the region-wide decline of hemlock is unlikely to be a result of any one factor but instead a suite of interacting factors including disturbance regimes, climate change, hemlock life history, ecosystem processes and historical land use. They suggest that the effects of deer browsing are simply a local phenomenon where deer are heavily concentrated. Their caveat against assuming a single cause of recruitment failure may apply in part to northern white-cedar as well, but browsing clearly poses a major constraint (Rooney et al. 2001). For example, Cornett et al. (2000) showed that browsing by white-tailed deer was the major factor driving the lack of cedar seedlings greater than 25 cm tall. Over a period of three years, Cornett et al. (2000) recorded that 76% of planted northern white cedar seedlings in upland stands of northeastern Minnesota had been browsed at least once. Except in exclosures, cedar seedlings between 30 cm and 1.3 m tall, representing the range of seedling heights subject to deer browsing (Beals et al. 1960, Saunders and Puettman 1999), were completely absent.

Woody species which are both highly preferred by deer and sensitive to deer browsing may now be so rare that we can no longer detect their response to changes in browse pressure (Russell et al. 2001). In addition, there is evidence that even low deer densities can keep preferred species from recruiting because deer will always preferentially feed on these species (Kamler et al. 2010). This may explain why we observed a stronger association between WWODI and moderately browsed species than between WWODI and species likely to experience recruitment failure with chronic browsing (cedar, hemlock, yellow birch).

At this time, it appears that the restructuring of understory communities caused by decades of chronic deer herbivory may have resulted in an alternate stable state (Stromayer and Warren 1997, Augustine et al. 1998, Carpenter 2001, Scheffer et al. 2001). Ecosystem changes in deer yards such as soil compaction, increased peat decomposition and decreased water retention have led to hydric forest conditions being replaced by mesic forest conditions (Van Deelen et al. 1996). These associated changes are likely to have strong effects on understory plant communities that may not be reversible even under reduced browsing conditions (Van Deelen et al. 1996). However, areas with high potential wolf impact do seem to support understory communities more similar to historic plant communities as described by Curtis (1959) in that the continuous presence of a wolf pack was associated with higher species diversity.

Site specific estimates of deer density continue to be a challenge in deer-vegetation studies. Our camera surveys displayed great potential for detecting local variability in browsing pressure. With a grid or array of cameras at multiple sites, combined with comparisons with thermal infrared sensing techniques to calibrate density estimates, we believe these un-baited low maintenance infrared triggered camera surveys can generate a very useful dataset. More extensive ITC surveys of deer combined with the vegetation surveys and wolf territory data used here would provide us with the ability to test for reciprocal relationships between wolves, deer and vegetation which are needed to show definitive evidence of a trophic cascade.

3.5. *Conclusion*

The loss of wolves as a keystone predator has contributed to a less desirable state for understory plant communities in northern white-cedar wetlands. Our data suggests that the recovery of wolves in northern Wisconsin can partially reverse this trend, at least in specific community types where wolf packs have been continuously present for at least 8 years. Whether these observed differences in vegetation patterns are due to direct predation on ungulates (density mediated indirect effects) or to the indirect effect of wolves on deer foraging behavior (trait mediated indirect effects) continues to be hotly debated (Ripple and Beschta 2004, Beyer et al. 2007, Creel and Christianson 2009, Kaufmann et al. 2010) and is beyond the scope of this study.

We suspect, however, that density mediated indirect effects may be unlikely given that the current Wisconsin wolf population, which has grown to ~620 individuals (Wydeven and Wiedenhoeft 2009), has the capacity to take only ~11,000 deer per year. There are an estimated 390,000 deer in the northern forests of Wisconsin (posthunt), so region-wide effects of wolf recovery on deer populations are unlikely to manifest in the short term. The reintroduction of wolves to Yellowstone National Park (YNP) has shown that foraging prey species alter their spatial use of available habitat in the presence of top predators (Ripple et al. 2001, Ripple and Beschta 2003) and also reduce the amount of time allocated to foraging activities due to increased vigilance (Lima and Dill 1990, Laundré et al. 2001). Thus, trait mediated indirect effects may be the more likely mechanism responsible for higher density and diversity of woody stems in high impact wolf areas.

Total trophic-level biomass, a sufficient response variable for aquatic systems, may be an inappropriate response variable with which to measure trophic responses in terrestrial systems. Recent evidence suggests that the indirect effects of predators in terrestrial systems are much stronger on plant species diversity than on plant biomass, and that these changes in species composition and evenness have strong effects on ecosystem properties (Schmitz 2006). Thus, we need to rethink how we address trophic cascades in terrestrial systems as opposed to characterizing them as weaker examples of aquatic cascades (*sensu* Strong 1992, Halaj and Wise 2001, Shurin et al. 2002). If we fail to do so, we risk measuring the wrong plant response variables and missing evidence of ecologically important trophic cascades in terrestrial systems.

For northern white-cedar wetlands, we found density and species diversity of woody stems 50-100cm tall to be ideal plant response variables with which to measure release from browsing pressure, especially when allowances were made for variability in species specific browsing response. The gap in the size structure of woody stems characteristic of over-browsed understories was less apparent in cedar wetlands with high potential wolf impact. However, regardless of WWODI, recruitment of cedar in lowland cedar stands in our study area continues to be very limited. Alverson et al. (1988) concluded that deer densities need to be maintained below 1-2/km^2 in order to sustain the diversity of native Wisconsin plants. In our study area, maximum deer densities of 13/km^2 and above are common. It is unlikely that the recovery of the wolf population alone will reduce the deer population to densities recommended by Alverson et al. (1988). However, as the proportion of early successional forests decreases across the Great Lakes Region, reduced forage, when combined with predation, may cause deer densities to naturally decline.

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Table 3.1 List of tree and shrub species identified in northern white cedar stands of north-central Wisconsin. Browsing response classes based on existing literature for the region. Unidentified and singular occurrence species were assigned to ‘Other’. Browsing response is the sum of browsing preference and sensitivity where Preferred = -2, Browsed = -1, Not preferred = 1, Sensitive = -2, Insensitive = 2 and Unclear = 0. ‘Unclear’ indicates either limited or conflicting data.

Tree spp.	**Browsing preference***	**Browsing sensitivity**	**Browsing response**
Abies balsamea	Not Preferred [1,2,4]	Insensitive [1,7,10]	Competitive advantage (3)
Acer rubrum	Preferred [1,3]	Unclear [1,10]	Reduced recruitment (-2)
Acer saccharum	Browsed [1,5]	Insensitive [1,6,7,10]	Relatively unaffected (1)
Acer spicatum	Preferred [1,2]	Insensitive [1]	Relatively unaffected (0)
Betula alleghaniensis	Preferred [1]	Sensitive [1,6,10]	Recruitment failure (-4)
Betula papyrifera	Browsed [1,4]	Unclear	Relatively unaffected (-1)
Fraxinus nigra	Unclear	Unclear	Relatively unaffected (0)
Larix laricina	Unclear	Sensitive [7]	Reduced recruitment (-2)
Picea spp.	Not Preferred [4]	Insensitive [7,8]	Competitive advantage (3)
Populus tremuloides	Browsed [1,3]	Insensitive [7]	Relatively unaffected (1)
Quercus rubra	Preferred [5]	Sensitive [9]	Recruitment failure (-4)
Sorbus spp.	Preferred [1,2]	Unclear	Reduced recruitment (-2)
Thuja occidentalis	Preferred [1,4]	Sensitive [7,8,9]	Recruitment failure (-4)
Tilia americana	Preferred [1,5]	Unclear	Reduced recruitment (-2)
Tsuga canadensis	Preferred [1,4]	Sensitive [6,7,9]	Recruitment failure (-4)
Ulmus americana	Browsed [5]	Unclear	Relatively unaffected (-1)

Shrub spp.	**Browsing preference***	**Browsing sensitivity**	**Browsing response**
Alnus incana ssp. rugosa	Not Preferred [1,2]	Insensitive [7]	Competitive advantage (3)
Amelanchier spp.	Browsed [1,2,4]	Insensitive [8,10]	Relatively unaffected (1)
Cornus stolonifera	Preferred [2,5]	Unclear	Reduced recruitment (-2)
Corylus spp.	Browsed [1,2,3]	Unclear	Relatively unaffected (-1)
Ilex mucronata	Unclear	Unclear	Relatively unaffected (0)
Ilex verticillata	Unclear	Unclear	Relatively unaffected (0)
Ledum groenlandicum	Unclear	Unclear	Relatively unaffected (0)
Lonicera canadensis	Preferred [1]	Insensitive [10]	Relatively unaffected (0)
Lonicera oblongifolia	Unclear	Unclear	Relatively unaffected (0)
Lonicera villosa	Unclear	Unclear	Relatively unaffected (0)
Rhamnus alnifolia	Unclear	Unclear	Relatively unaffected (0)
Ribes spp.	Browsed [2,5]	Unclear	Relatively unaffected (-1)
Rubus idaeus	Unclear	Unclear	Relatively unaffected (0)
Vaccinium angustifolium	Unclear	Unclear	Relatively unaffected (0)
Vaccinium myrtilloides	Unclear	Unclear	Relatively unaffected (0)
Other	Unclear	Unclear	Relatively unaffected (0)

*** 1 = Dahlberg and Guettinger 1956, 2 = Wetzel et al. 1975, 3 = Stormer and Bauer 1980, 4 = Conover and Kania 1988, 5 = Strole and Anderson 1992, 6 = Anderson and Katz 1993, 7 = Van Deelen et al. 1996, 8 = Cornett et al. 2000, 9 = Rooney and Waller 2003, 10 = Holmes et al. 2008**

Table 3.2 List of tree and shrub species from vegetation plots in descending order by total basal area.

Common Name	**Species Name**	**% of TBA**	**Range**
Northern White Cedar	*Thuja occidentalis*	84.526%	36.758-99.047%
Balsam Fir	*Abies balsamea*	5.444%	0.000-16.856%
Black Ash	*Fraxinus nigra*	3.920%	0.000-49.110%
Yellow Birch	*Betula alleghaniensis*	1.902%	0.000-15.061%
Paper Birch	*Betula papyrifera*	1.448%	0.000-12.520%
Red Maple	*Acer rubrum*	1.282%	0.000-35.730%
Eastern Hemlock	*Tsuga canadensis*	0.481%	0.000-18.290%
Speckled Alder	*Alnus incana ssp. rugosa*	0.400%	0.000-7.618%
Black Spruce	*Picea mariana*	0.338%	0.000-6.986%
Eastern White Pine	*Pinus strobus*	0.116%	0.000-4.390%
Tamarack	*Larix laricina*	0.078%	0.000-2.805%
Sugar Maple	*Acer saccharum*	0.041%	0.000-1.493%
Common Winterberry	*Ilex verticillata*	0.014%	0.000-0.335%
Mountain Maple	*Acer spicatum*	0.005%	0.000-0.080%
White Spruce	*Picea glauca*	0.002%	0.000-0.081%
Mountain Holly	*Ilex mucronata*	0.001%	0.000-0.040%

Table 3.3 Spearman rank correlation (ρ) values and associated P-values for woody stem density across five size classes. Demographic inertia represents the correlation between the density of individuals in each size class and the density of individuals in the preceding size class. Calculation of the weighted wolf occupancy duration index (WWODI) is described in the text. Values in bold with asterisks are considered significant. P-values are Gaussian approximations. With Bonferroni corrections significant p-values are reduced from 0.05 to 0.00167 (α/30).

Size Class	Canopy Cover	Demographic Inertia	WWODI
A) Density of all woody stem species			
1 (10-50cm)	ρ = **-0.559***, p < 0.0005		ρ = **0.404***, p < 0.05
2 (50-100cm)	ρ = -0.107, p = 0.523	ρ = **0.496***, p < 0.005	ρ = **0.602***, p < 0.0001
3 (100-137cm)	ρ = -0.221, p = 0.182	ρ = **0.776***, p < 0.0001	ρ = **0.354***, p < 0.05
4 (0-1cm dbh)	ρ = -0.213, p = 0.199	ρ = **0.793***, p < 0.0001	ρ = 0.156, p = 0.348
5 (1-2.5cm dbh)	ρ = -0.198, p = 0.233	ρ = **0.760***, p < 0.0001	ρ = 0.009, p = 0.955
B) Density of woody stem species likely to exhibit recruitment failure with high browsing pressure: yellow birch, red oak, hemlock, cedar			
1 (10-50cm)	ρ = **-0.416***, p < 0.01		ρ = 0.230, p = 0.164
2 (50-100cm)	ρ = -0.089, p = 0.597	ρ = **0.416***, p <0.01	ρ = **0.353***, p < 0.05
3 (100-137cm)	ρ = 0.005, p = 0.976	ρ = **0.555***, p < 0.0005	ρ = 0.150, p = 0.367
4 (0-1cm dbh)	ρ = 0.142, p = 0.394	ρ = 0.159, p = 0.340	ρ = **0.334***, p < 0.05
5 (1-2.5cm dbh)	ρ = -0.021, p = 0.900	ρ = **0.356***, p < 0.05	ρ = 0.084, p = 0.618
C) Density of woody stem species experiencing a competitive advantage from browsing pressure: balsam fir, speckled alder and spruce			
1 (10-50cm)	ρ = **-0.584***, p < 0.0001		ρ = 0.113, p = 0.499
2 (50-100cm)	ρ = **-0.391***, p < 0.05	ρ = **0.751***, p < 0.0001	ρ = 0.171, p = 0.305
3 (100-137cm)	ρ = **-0.610***, p < 0.0001	ρ = **0.773***, p < 0.0001	ρ = 0.143, p = 0.390
4 (0-1cm dbh)	ρ = **-0.567***, p < 0.0005	ρ = **0.763***, p < 0.0001	ρ = 0.003, p = 0.988
5 (1-2.5cm dbh)	ρ = **-0.382***, p < 0.05	ρ = **0.659***, p < 0.0001	ρ = -0.006, p = 0.972
D) Density of woody stem species moderately impacted by deer browsing			
1 (10-50cm)	ρ = **-0.489***, p < 0.005		ρ = **0.459***, p < 0.005
2 (50-100cm)	ρ = 0.060, p = 0.720	ρ = **0.421***, p <0.01	ρ = **0.635***, p < 0.0001
3 (100-137cm)	ρ = 0.292, p = 0.076	ρ = **0.626***, p < 0.0001	ρ = **0.425***, p < 0.01
4 (0-1cm dbh)	ρ = 0.195, p = 0.241	ρ = **0.738***, p < 0.0001	ρ = 0.256, p = 0.121
5 (1-2.5cm dbh)	ρ = 0.**386***, p < 0.05	ρ = **0.750***, p < 0.0001	ρ = -0.005, p = 0.974
E) Density of woody stems of shrub species (not including speckled alder)			
1 (10-50cm)	ρ = **-0.643***, p < 0.0001		ρ = **0.319***, p = 0.05
2 (50-100cm)	ρ = 0.039, p = 0.815	ρ = 0.250, p = 0.129	ρ =**0.626***, p < 0.0001
3 (100-137cm)	ρ = 0.312, p = 0.057	ρ = **0.452***, p < 0.005	ρ =0.238, p = 0.150
4 (0-1cm dbh)	ρ = 0.204, p = 0.219	ρ = **0.752***, p < 0.0001	ρ = 0.093, p = 0.579
5 (1-2.5cm dbh)	ρ = 0.263, p = 0.111	ρ = **0.694***, p < 0.0001	ρ = -0.138, p = 0.408
F) Density of woody stems of tree species (not including balsam fir or spruce)			
1 (10-50cm)	ρ = -0.078, p = 0.643		ρ = **0.321***, p < 0.05
2 (50-100cm)	ρ = 0.081, p = 0.627	ρ = **0.765***, p < 0.0001	ρ = **0.415***, p < 0.01
3 (100-137cm)	ρ = 0.071, p = 0.670	ρ = **0.759***, p < 0.0001	ρ = **0.325***, p < 0.05
4 (0-1cm dbh)	ρ = 0.280, p = 0.089	ρ = **0.668***, p < 0.0001	ρ = **0.337***, p < 0.05
5 (1-2.5cm dbh)	ρ = **0.439***, p < 0.01	ρ = **0.718***, p < 0.0001	ρ = 0.251, p = 0.129

Table 3.4 Relationship between woody stem density of each tree or shrub species and weighted wolf occupancy duration index (WWODI) at the first two seedling size classes.

Tree spp.	**WWODI (10-50cm)**	**WWODI (50-100cm)**
Abies balsamea	ns	ns
Acer rubrum	ns	ns
Acer saccharum	ns	$\rho = 0.325$, $p < 0.05$
Acer spicatum	$\rho = 0.277$, $p = 0.092$	$\rho = 0.485$, $p < 0.005$
Betula alleghaniensis	ns	$\rho = 0.312$, $p = 0.06$
Betula papyrifera	ns	ns
Fraxinus nigra	$\rho = 0.434$, $p = <0.01$	ns
Larix laricina	ns	ns
Picea spp.	ns	ns
Populus tremuloides	$\rho = -0.371$, $p < 0.05$	ns
Quercus rubra	ns	ns
Sorbus spp.	ns	ns
Thuja occidentalis	ns	ns
Tilia americana	ns	ns
Tsuga canadensis	ns	ns
Ulmus americana	ns	ns
Shrub spp.		
Alnus incana ssp. rugosa	ns	ns
Amelanchier spp.	ns	ns
Cornus stolonifera	$\rho = 0.365$, $p < 0.05$	$\rho = 0.381$, $p < 0.05$
Corylus spp.	ns	$\rho = 0.424$, $p < 0.01$
Ilex mucronata	$\rho = -0.261$, $p = 0.114$	ns
Ilex verticillata	ns	ns
Ledum groenlandicum	ns	ns
Lonicera canadensis	$\rho = 0.422$, $p < 0.01$	$\rho = 0.466$, $p < 0.005$
Lonicera oblongifolia	$\rho = 0.461$, $p < 0.005$	ns
Lonicera villosa	ns	ns
Rhamnus alnifolia	$\rho = 0.514$, $p < 0.001$	$\rho = 0.497$, $p < 0.005$
Ribes spp.	$\rho = 0.343$, $p < 0.05$	$\rho = 0.300$, $p = 0.067$
Rubus idaeus	ns	ns
Vaccinium angustifolium	ns	ns
Vaccinium myrtilloides	$\rho =-0.311$, $p = 0.058$	$\rho = -0.294$, $p = 0.073$
Other	ns	ns

Table 3.5 Spearman rank correlation (ρ) values and associated P-values between weighted wolf occupancy duration index (WWODI) and six commonly used measures of browse intensity. Values in bold with asterisks are considered significant.

Index	WWODI
Deer density DMU $^{-1}$	$n = 38$, $\rho = -0.019$, $p = 0.909$
Red Maple Browse Index	$n = 12$, $\rho = -0.197$, $p = 0.540$
Deer visitation day $^{-1}$	$n = 7$, $\rho = -0.270$, $p = 0.558$
Bluebead lily (*Clintonia borealis*) scape height	$n = 10$, $\rho = 0.378$, $p = 0.279$
Wild sarsaparilla (*Aralia nudicaulis*) ha^{-1}	$n = 38$, $\rho = \mathbf{0.462^{*}}$, $p < 0.005$
Nodding trillium (*Trillium cernuum*) ha^{-1}	$n = 38$, $\rho = \mathbf{0.479^{*}}$, $p < 0.005$

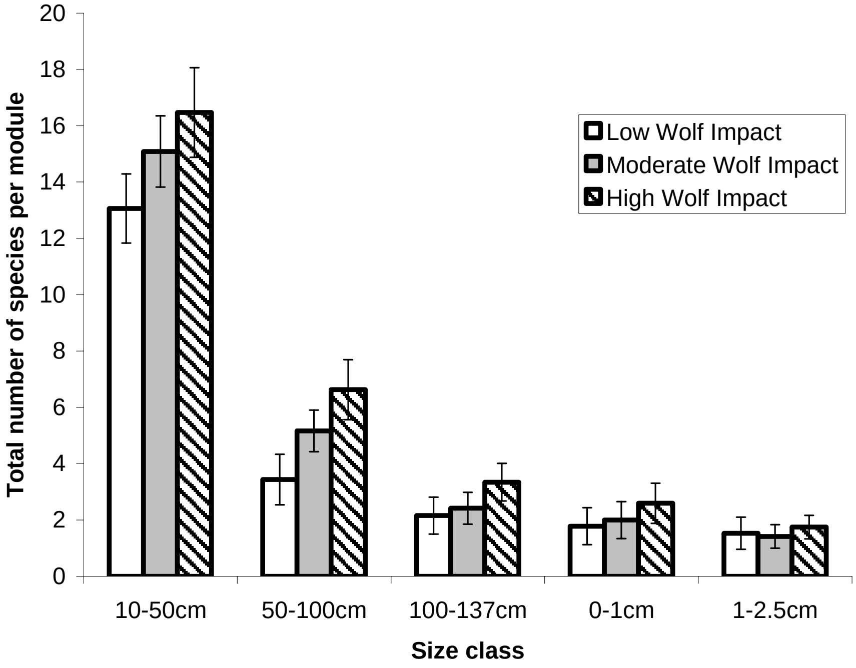


Figure 3.1 Average number of woody stem species for high, moderate and low potential wolf impact plots across 5 size classes representing seedlings and saplings (10-50 cm, 50-100 cm, 100-137 cm, 0-1 cm d.b.h., and 1-2.5 cm d.b.h.) with 95% confidence intervals. Hatched bars represent areas with high potential wolf impact (≥ 8 years of wolf pack occupancy). Asterisks indicate significant differences ($p < 0.05$).

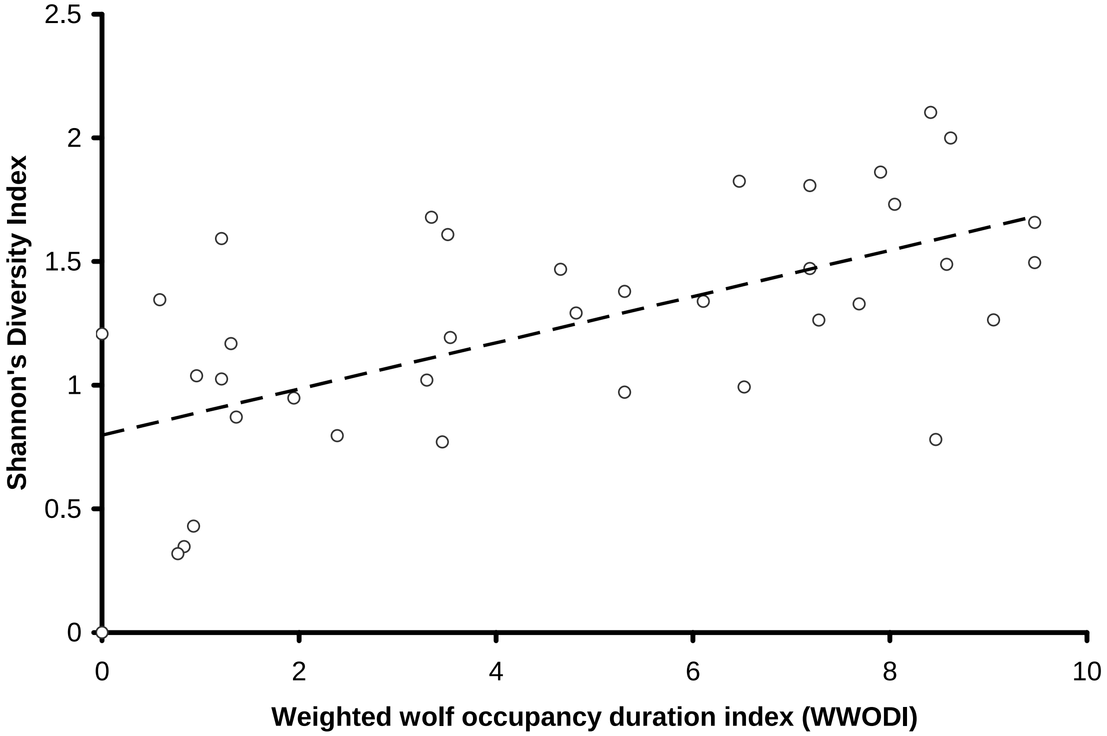


Figure 3.2 Linear relationship ($y = 0.0934x + 0.798$, $r^2 = 0.379$, $p<0.0001$) between weighted wolf occupancy index values and combined species diversity of shrubs and trees 50-100cm in height at the $100m^2$ scale. Wolf occupancy values were weighted to give more strength to recent territory extents (see text).

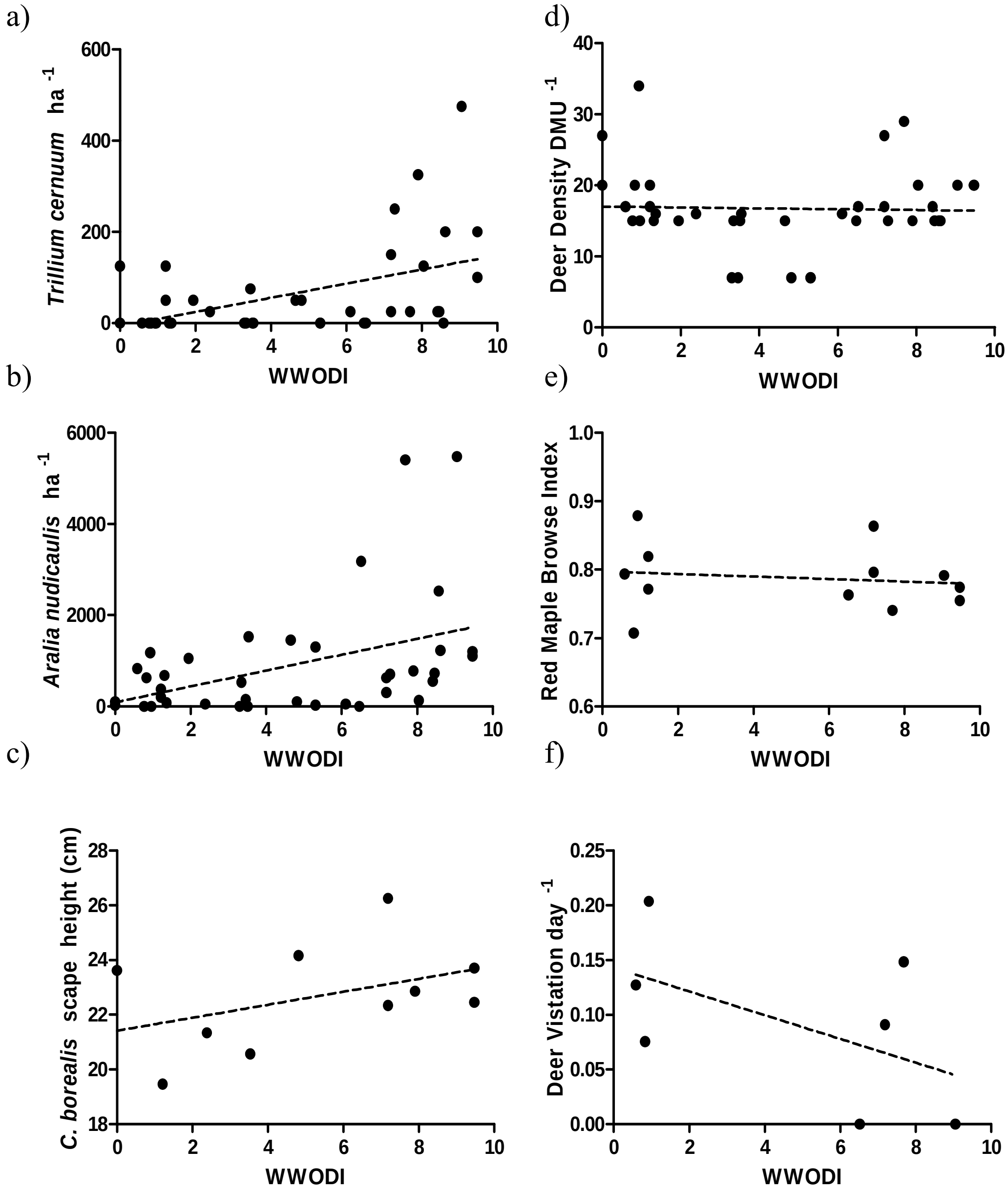
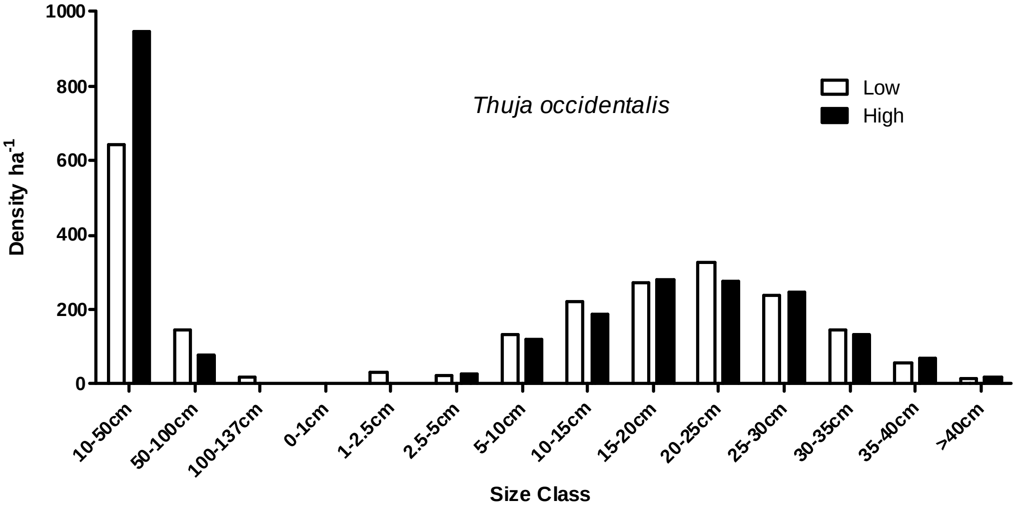
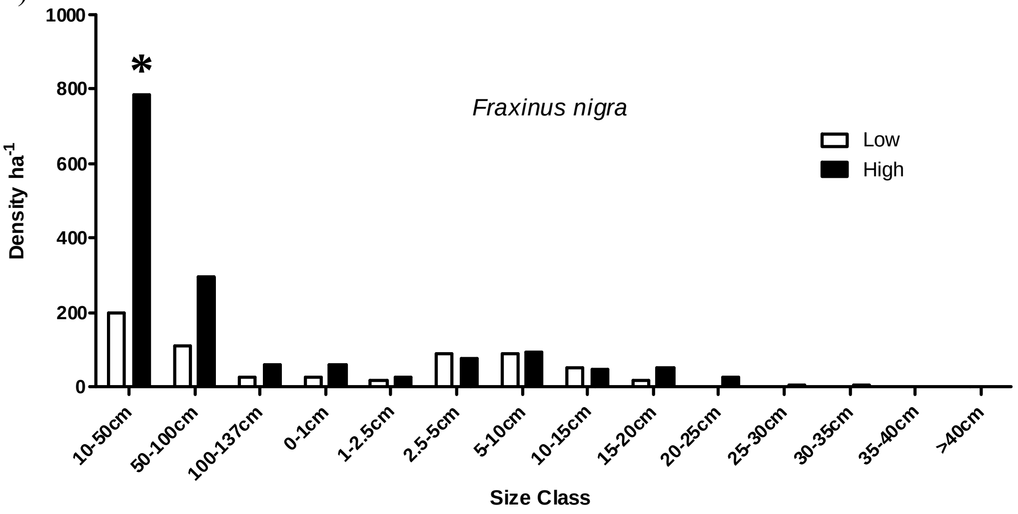


Figure 3.3 Relationships between various potential measures of browsing pressure and the Weighted Wolf Occupancy Duration Index (WWODI). Given a trophic cascade response, variables on the left (a-c) were hypothesized to have a positive relationship with WWODI, while variables on the right (d-f) were hypothesized to have a negative relationship with WWODI.

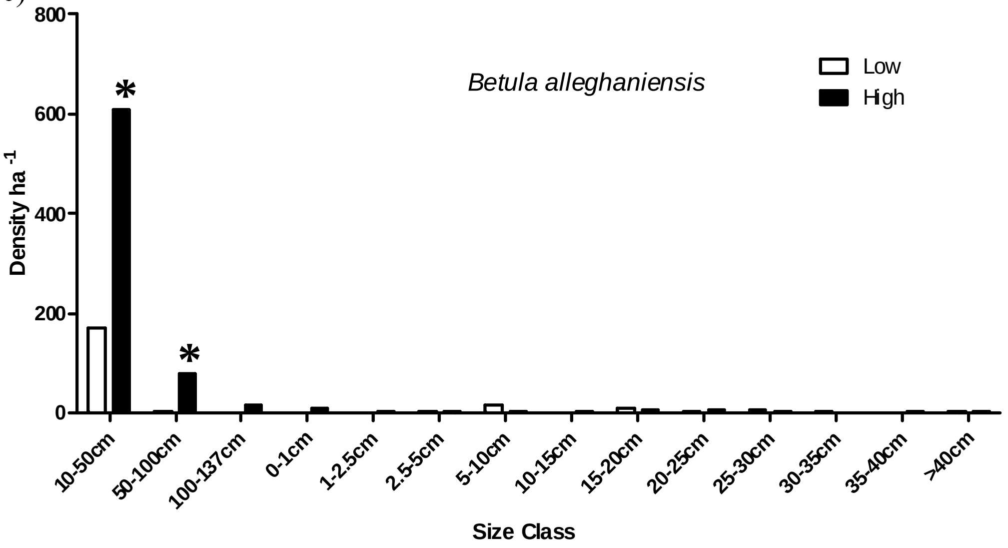
a)


Thuja occidentalis
Low
High
Density ha-1
1000
800
600
400
200
0
10-50cm
50-100cm
100-137cm
0-1cm
1-2.5cm
2.5-5cm
5-10cm
10-15cm
15-20cm
20-25cm
25-30cm
30-35cm
35-40cm
>40cm
Size Class

b)


Fraxinus nigra
Low
High
*
Density ha-1
1000
800
600
400
200
0
10-50cm
50-100cm
100-137cm
0-1cm
1-2.5cm
2.5-5cm
5-10cm
10-15cm
15-20cm
20-25cm
25-30cm
30-35cm
35-40cm
>40cm
Size Class

c)


Betula alleghaniensis
Low
High
*
*
Density ha -1
800
600
400
200
0
10-50cm
50-100cm
100-137cm
0-1cm
1-2.5cm
2.5-5cm
5-10cm
10-15cm
15-20cm
20-25cm
25-30cm
30-35cm
35-40cm
>40cm
Size Class

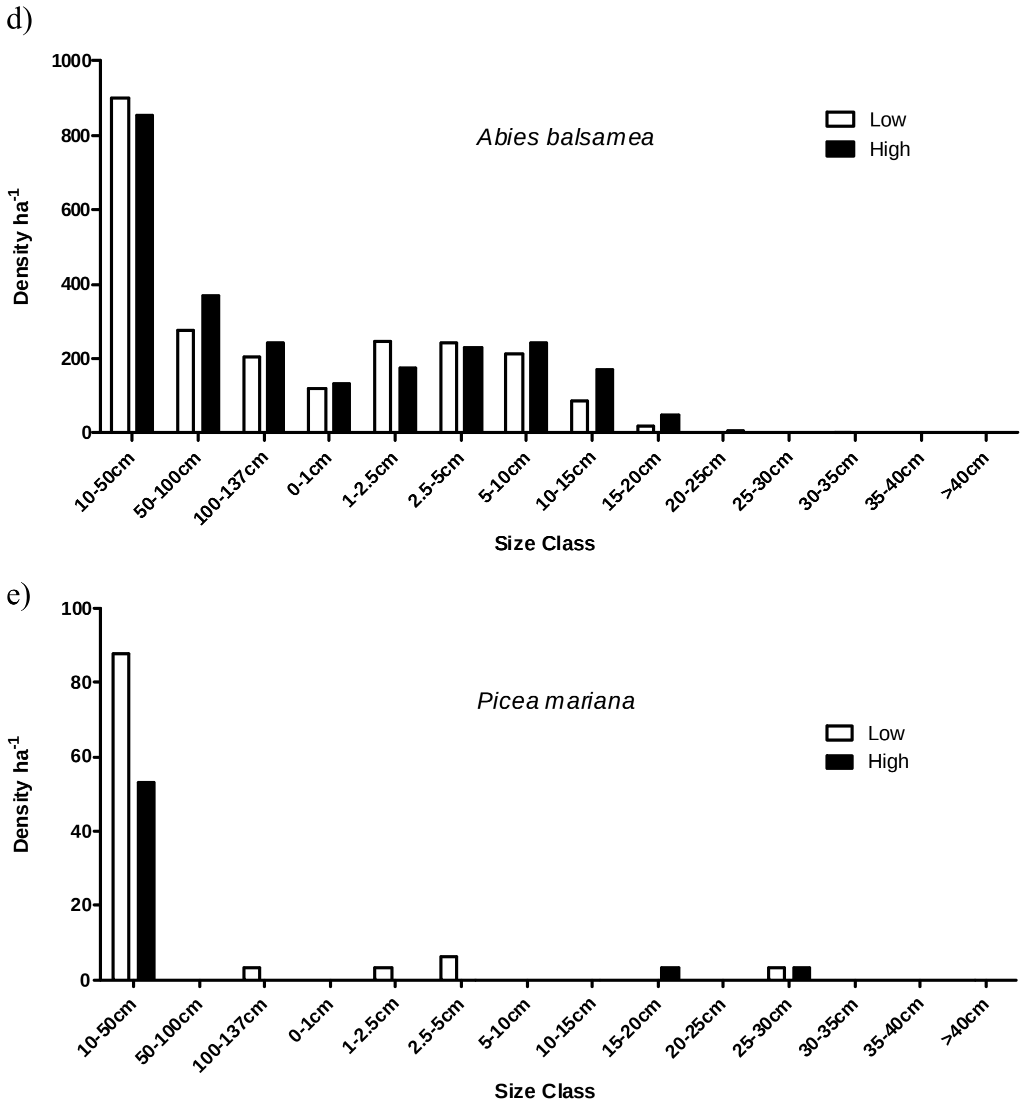


Figure 3.4 Distribution of tree density across all size classes for five canopy species of northern white-cedar wetlands. Low impact wolf sites (n=16) represent areas occupied by wolf packs for 0-3 years and are shown with open bars. High impact wolf sites (n=16) represent areas occupied by wolf packs for at least 8-10 years and are displayed with filled bars. Asterisks indicate significant differences ($p \leq 0.05$).

CHAPTER 4

IS WOLF PACK TENURE AN IMPORTANT VARIABLE WHEN MODELING THE SPECIES RICHNESS OF CHRONICALLY BROWSED UNDERSTORY PLANT COMMUNITIES?[3]

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[2] Callan, R. and N. P. Nibbelink *to be submitted to*

Ecological Applications spring 2011

4.0 Abstract:

Wolf (*Canis lupus*) recovery in the Great Lakes region is anticipated to generate a top-down trophic cascade by altering white-tailed deer (*Odocoileus virginianus*) density, habitat selection, and foraging behavior. Through these direct impacts on white-tailed deer, wolves are predicted to trigger additional indirect impacts on plant communities chronically browsed by white-tailed deer. We conducted vegetation surveys in northern white cedar wetlands to measure species richness of understory plant communities across a gradient of wolf impact. We then tested three possible hypotheses for observed relationships between species richness and wolf impact: (1) a top-down trophic cascade, (2) a bottom-up trophic cascade, and (3) a non-trophic association.

We first calculated a weighted wolf occupancy duration index (WWODI) based on territory mapping data of known wolf packs from 1995-2009. Using local and regional variables, we created multivariate models of species richness of forbs ($S_{\mathbf{forbs}}$), shrubs ($S_{\mathbf{shrubs}}$), seedlings ($S_{\mathbf{seedlings}}$) and ferns ($S_{\mathbf{ferns}}$). We selected the best fit model for each of these vegetation response variables and examined whether inclusion of WWODI improved model fit, thus distinguishing bottom-up from top-down trophic effects. To assess the potential for a non-trophic association we used landscape level variables shown to impact wolf habitat selection to model WWODI. Again we selected the best fit model and tested whether this model of WWODI was able to explain any variability in understory plant species richness ($S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, $S_{\mathbf{seedlings}}$, and $S_{\mathbf{ferns}}$). In this way we sought to account for spurious associations generated by landscape level factors known to benefit both plant diversity and wolf habitat quality, irrespective of a trophic effect.

After accounting for local and landscape level environmental factors (such as litter depth, distance to road, wetness, solar radiation, canopy species richness, precipitation, human

disturbance, mean patch area and proximity of similar patches), WWODI still increased the variability explained by each vegetation response model by 19.0% for $S_{\mathbf{forbs}}$, 10.7% for $S_{\mathbf{shrubs}}$, and 12.2% for $S_{\mathbf{seedlings}}$, but only by 0.5% for $S_{\mathbf{ferns}}$ (based on R^2_{adj} values). This suggests that the positive relationship between WWODI and species richness of forbs, shrubs and seedlings is unlikely to be a result of bottom-up effects propagating up through the food web.

The best fit landscape model of WWODI included the variables mean patch area (forest) and mean distance to paved road (R^2_{adj}= 46.6%, p<0.001). When these variables were used to fit species richness data, the models performed poorly, explaining only 3.8% of variability in $S_{\mathbf{forbs}}$, 2.7% of variability in $S_{\mathbf{shrubs}}$, 0.9% of variability in $S_{\mathbf{seedlings}}$, and 3.3% of variability in $S_{\mathbf{ferns}}$ (based on R^2_{adj} values). These results suggest that a non-trophic association is an unlikely explanation for the strong positive relationship between WWODI and $S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, and $S_{\mathbf{seedlings}}$.

Duration of wolf pack occupancy was a significant predictor of species richness of understory plant species known to respond positively to release from herbivory: forbs, shrubs and seedlings. In contrast, inclusion of WWODI was not supported for models of fern species richness, a plant group unlikely to respond positively to release from herbivory. These results are consistent with a top-down trophic cascade triggering a release from browsing pressure by white-tailed deer in northern white cedar wetlands.

Key Words: trophic cascade, deer browsing intensity, wolf recovery, seedling recruitment, Wisconsin, local and regional variables, AICc, understory plant communities, species richness

4.1. *Introduction*

The gray wolf (*Canis lupus*) is considered a strongly interactive species due to its direct and indirect effects on lower trophic levels (Soulé et al. 2003). Recovery of the gray wolf in the Great Lakes region is thus predicted to generate top-down effects that will contribute to the conservation of regional biodiversity (McShea 2005, Ray 2005). Similar impacts were predicted of wolf recovery in western North America, and documented changes to those ecosystems have exceeded expectations (Ripple et al. 2001, Wilmers et al. 2003, Hebblewhite et al. 2005). Has wolf recovery in the Great Lakes region produced an equally powerful effect?

Several notable characteristics serve to differentiate the ecological role of wolves in the Great Lakes region, making application of findings from western North America purely speculative (Rooney and Anderson 2009). For example, successful reintroduction of wolves to Yellowstone National Park (YNP) corresponded to a 50% decline in elk (*Cervus elaphus*) density (White and Garrot 2005, Vucetich et al. 2005), however, the main prey species of wolves in the Great Lakes region is white-tailed deer (*Odocoileus virginianus*), and the numerical effect of wolves on white-tailed deer populations is less clear (Nelson and Mech 1986, Messier 1991, Nelson and Mech 2006). Ecosystem recovery in YNP occurred primarily in riparian areas, where high quality elk browse is concentrated (Ripple et al. 2001, Ripple and Bescheta 2003, 2006, 2007, Beyer et al. 2007). In contrast, white-tailed deer forage (forbs and woody plants) is more evenly distributed throughout the landscape, and deer density is related to distance from northern white cedar (*Thuja occidentalis*) wetlands which provide important winter habitat (Millington et al. 2010).

The Great Lakes Region has fewer predator and ungulate species than YNP indicative of a less complex food web (Smith et al. 2003, Kurta 1995), and represents a simplification of the original ecosystems and more diverse ungulate populations that existed in the Great Lakes region prior to European settlement (DelGiudice et al. 2009). Food web complexity has been argued to dampen the indirect effects of trophic cascades (Halaj and Wise 2001), so recovery of wolves in the Great Lakes region may in fact generate stronger impacts on lower trophic levels than those observed in YNP. However, western riparian areas are subject to intense disturbance regimes and show great resilience to disturbance (White and Stromberg *in press*). Understory plant communities of the Midwest experience much lower disturbance intensity and are likely to demonstrate ecological hysteresis (Cote et al. 2004). Diversity of plant communities also plays an important role in ecosystem resilience by contributing to the variety of responses to environmental change ('response diversity' *sensu* Elmqvist et al. 2003). Finally, human density and road density are both considerably higher in the Great Lakes region and are known to influence wolf habitat selection (Mladenoff et al. 1995), white-tailed deer forage availability (Rooney and Anderson 2009), and understory plant diversity (Findlay and Houlahan 1997, Watkins et al. 2003).

The hyper-abundance of white-tailed deer in the Great Lakes region suggests that trait mediated indirect effects may be a more likely mechanism than density mediated direct effects in altering browsing pressure on understory plant communities. The reintroduction of wolves to YNP has shown that foraging prey species alter their spatial use of available habitat in the presence of top predators (Ripple *et al.* 2001, Ripple and Beschta 2003). Ungulates in YNP were also observed to reduce the total amount of time allocated to foraging activities due to increased vigilance (Lima and Dill 1990, Laundré *et al.* 2001). Unfortunately, these behavioral prey responses have not been well documented in the Great Lakes region.

Given these caveats, where should we begin to look for a top-down trophic response to recovery of gray wolves in the Great Lakes region? What response variables should we measure? How can we detect the signal of a top-down trophic response above the ambient noise of ecological variation? Previous research by Anderson *et al.* (unpublished data) showed that the biomass of forb and woody-browse species in northern white cedar wetlands increased toward the center of wolf pack territories. A similar pattern was not observed in other forest-cover types (coniferous forest, deciduous forest and mixed forest), leading Anderson et al. to conclude that trophic cascades in this region are more detectable in browse-sensitive communities with low productivity and high species richness (i.e. cedar wetlands).

Due to differences in life history traits, such as longevity, reproductive rate, dispersal ability and resource allocation to physical and chemical defenses, plant species differ drastically in their response to herbivory. Documented changes over the past 50 years in upland forest stands of northern Wisconsin show an average decline of 18% in the species richness of understory plant communities (Rooney et al. 2004). Species in decline were those known to be sensitive to deer browsing such as palatable forbs and tree seedlings. In contrast, ferns and grasses (generally considered to be either resistant or tolerant of deer browsing) appear to be out-competing more sensitive species (Weigmann and Waller 2006). Thus, we anticipated that understory plants would vary in their response to release from browsing pressure dependent on the vegetation growth form in question (forbs, shrubs, seedlings or ferns). On the Alleghany Plateau, Horsley et al. (2003) found a negative relationship between species richness of seedlings and deer density and a positive relationship between percent cover of ferns and deer density. Based on the concept that species diversity is maximized when disturbance conditions match the historic disturbance regimes under which plant communities developed (Denslow 1985) combined with trophic cascade theory (Schmitz 2006), we hypothesize that species richness of forb, shrub, and seedling species should be higher at high wolf impact areas (since deer browsing pressure should be reduced and closer to historic levels).

The pattern of wolf recolonization has produced a chronosequence of wolf impact across the landscapes of Minnesota, Wisconsin and Michigan. The Wisconsin Department of Natural Resources (WiDNR) has annually mapped wolf pack territory extents since 1979. The high quality of this dataset provides the information needed to explicitly examine the spatial and temporal pattern of wolf occupancy throughout the state (Wiedenhoeft and Wydeven 2005). Some areas have been occupied by wolf packs for more than 15 years, some areas were never successfully recolonized by wolves, and many areas exhibit wolf occupancy duration intermediate between these two extremes. This gradient provides a natural experimental framework with which to measure vegetation response as a function of time since wolf colonization (Rooney and Anderson 2009).

The danger in space-for-time studies is the potential for confounding variables to produce spurious associations. Several factors benefit both plant diversity and wolf habitat quality, irrespective of deer density and any sort of trophic effect. In particular, road density has been shown to be negatively correlated with both plant diversity (Findlay and Houlahan 1997, Rogers et al. 2009) and wolf habitat selection (Mladenoff et al. 1995). Understory vegetation in white cedar stands may also be more influenced by hydrology (drainage rate and variability in depth to water table) and edge effects than by variation in browsing pressure. A bottom-up effect could also result in a positive relationship between plant species richness and wolf impact: areas with high plant biomass and diversity could maintain higher deer densities which in turn support successful wolf pack establishment.

Our objective was to determine the relative importance of wolf occupancy duration in predicting the species richness of understory plant communities of northern white-cedar wetlands. We further sought to rule out potentially confounding factors and to distinguish top-down from bottom-up trophic effects. Our approach was three fold. We first created univariate models of species richness based solely on wolf occupancy duration (top-down model). Second, we modeled species richness of forbs, shrubs, seedlings and ferns based on both local and landscape level variables known to be associated with plant species richness (bottom-up model). We then added wolf occupancy duration to these models to see if the addition of WWODI as a predictor variable improved model accuracy. Our third approach was to model wolf occupancy duration itself based on landscape variables known to influence both wolf habitat selection and plant species richness (non-trophic model). We then tested the accuracy of this model in predicting species richness of plants. Effects attributed to wolf impact based on the top-down model of plant species richness not accounted for by the bottom-up or non-trophic model are thus hypothesized to represent pure top-down trophic effects. This remaining proportion of variability in plant species richness is likely due to release of understory plant communities from over-browsing by white-tailed deer responding to the local establishment and consistent occupancy of wolf pack territories.

4.2. *Methods*

4.2.1 STUDY SITE

Data were collected throughout the Chequamegon-Nicolet National Forest, as well as various state and county forests spanning 7 counties in north-central Wisconsin. The forests of Northern Wisconsin are transitional between deciduous forests to the south and boreal forests to the north (Pastor and Mladenoff 1992, Mladenoff *et al.* 1993). Annual air temperature in northern Wisconsin averages 4º C, and mean annual precipitation ranges between 76 and 86 cm. The freeze free period averages ~80 days, making for a short growing season. Snowfall accumulation frequently exceeds 76 cm and the snow cover provides insulation for ground vegetation (NOAA 1982).

Glaciation strongly influenced the soils and topography of Wisconsin. Soils are derived from sandy loam glacial till, silt covered glacial tills, and sandy outwash. With a maximum elevation of 550 m, there is little topographic relief. The gently rolling terrain is inundated with thousands of lakes and numerous wetlands. Terrestrial landscapes are comprised of 40% deciduous forest types (dominated by sugar maple, *Acer saccharum* and paper birch, *Betula papyrifera*), 9% coniferous, (dominated by white pine, *Pinus resinosa*, red pine, *Pinus strobus*, and balsam fir, *Abies balsamea*), 8% mixed-coniferous-deciduous, and 7% early successional (dominated by aspen, *Populus tremuloides*). Forested and emergent wetland communities cover an additional 26% of the area (dominated by tamarack, *Larix laricina* and black spruce, *Picea mariana*, and Labrador-tea, *Ledum groenlandicum* and leather leaf *Chamaedaphne calyculata*, respectively). Northern-white cedar wetlands occupy less than 5% of the landscape but support a large proportion of the regional biodiversity (WiDNR 1998).

Northern-white cedar wetlands develop on poorly-drained sites with a slight through-flow of groundwater. These conditions elevate the pH and nutrient richness of the soil (Black and Judziewicz 2008). Mature stands of white cedar are densely shaded with nearly closed canopies. The combination of these environmental characteristics produces unique light regimes and soil chemistry required by species restricted to this community type. Co-dominant trees in white cedar wetlands include balsam fir, yellow birch (*Betula alleghaniensis*) and black ash (*Fraxinus* *nigra*). Speckled alder (*Alnus incana* subsp. *rugosa*), hollies (*Ilex mucronata* and *I. verticillata*), hazelnuts (*Corylus* spps.) and honeysuckles (*Lonicera* spps.) are common understory shrubs.

Cedar wetlands are also rich in wildflowers ranging from the common to the extremely rare. Common wildflowers are goldthread (*Coptis trifolia*), starflower (*Trientalis borealis*), wild sarsaparilla (*Aralia nudicaulis*), naked miterwort (*Mitella nuda*), blue-bead lily (*Clintonia borealis*), bunchberry (*Cornus canadensis*), Canada mayflower (*Maianthemum canadense*), and trailing "sub-shrubs" such as creeping snowberry (*Gaultheria hispidula*), dwarf red raspberry (*Rubus pubescens*) and twinflower (*Linnea borealis*). Orchids include yellow lady's slipper (*Cypripedium parviflorum*), heart-leaved twayeblade (*Listera cordata*), lesser rattlesnake plantain (*Goodyera repens*), and blunt-leaved bog orchid (*Platanthera obtusata*).

Fern species found in northern white cedar stands include cinnamon fern (*Osmunda claytoniana*), American royal fern (*Osmunda regalis* var. *spectabilis*), interrupted fern (*Osmunda claytoniana*), wood ferns (*Dryopteris* spps.), lady fern (*Athyrium filix-femina* var. *angustum*), common oak fern (*Gymnocarpium dryopteris*), sensitive fern (*Onoclea sensibilis*), narrow beech fern (*Phegopteris connectilis*), rattlesnake fern (*Botrychium virginianum*) and occasionally bracken fern (*Pteridium aquilinum* var. *latiusculum*). See appendix A for a complete species list.

Wolves have been recolonizing northern Wisconsin since the early 1970s, but wolf distribution remained very limited until the 1990s (Wydeven et al. 1995, Wydeven et al. 2009). Depending on pack size and prey density, wolf territories in the Great Lakes Region can range in size but recently averaged approximately 136 km^2 (Wydeven et al. 2009). Hoskinson and Mech (1976) reported that deer survival is higher on the edges of wolf territories as compared to their centers. Wolves are less likely to hunt in these buffer zones so as to avoid potentially fatal encounters with neighboring wolf packs (Mech 1977). At local scales, the distribution of deer in northeastern Minnesota was found to be negatively correlated with wolf territory extents, and deer were found primarily in buffer zones (Lewis and Murray 1993). Thus buffer zones surrounding wolf pack territories may act as refugia for white-tailed deer (Mech 1994).

In the Great Lakes region, deer winter home ranges vary between 730 and 1859 ha (Van Deelen et al. 1998). Early studies in Wisconsin indicated that mature white-tailed deer consume between two and nine kilograms of quality browse per deer per day (Taylor 1956). Predator extirpation, when combined with protective hunting laws and habitat management, has contributed to current deer densities ranging between 4 and 15/km^2 (Wi DNR 2008). Alverson *et al.* (1988) prescribed densities as low as 1-2 deer/km^2 to improve recruitment of sensitive plant species.

Wolves require 15-18 deer ‘equivalents’ per wolf per year (Fuller 1995). Hence the current Wisconsin wolf population, which has grown to ~690 individuals (Wydeven and Wiedenhoeft 2010), has the capacity to take ~12,000 deer per year. Given that there are an estimated 390,000 deer in the Northern Forests of Wisconsin (posthunt), region-wide effects of wolf recovery on deer populations are unlikely to manifest in the short term (Pers. comm. Keith McCaffery 2008). In addition, whether wolf kills represent primarily compensatory or additive mortality for white-tailed deer is in part dependent on stochastic environmental variables (Mech and Peterson 2003). However, localized influences on deer populations are more probable, and drastic local reductions have been observed in Minnesota (Nelson and Mech 2006).

4.2.2 DATA COLLECTION

WiDNR population estimates of wolves were ascertained by live-trapping and radio tracking (Mech 1974, Fuller and Snow 1988), howl surveys (Harrington and Mech 1982), and winter track surveys (Thiel and Welch 1981, Wydeven *et al.* 1995). Territory extents are delineated using minimum convex polygons based on radiolocations of collared wolves and other wolf sign (Wydeven *et al.* 1995). Using ArcGIS 9.3, we overlaid current wolf territories with historic territory extents back to 1995. Only sites within the Chequamegon-Nicolet National Forest or state and county forest boundaries were selected. Although wolves have established territories outside of public lands, these territories are often located in agricultural or industrial forest landscapes and anthropogenic sources of landscape change are likely to obscure any potential trophic effects of wolf recolonization.

White-tailed deer density data (WiDNR 2009) was obtained for each deer management unit (DMU) for the 15 years prior to vegetation data collection. WiDNR calculates initial deer density estimates using the sex-age-kill method and then corrects for the proportion of the DMU that is considered deer habitat (Millspaugh *et al*. 2006). Wisconsin DMUs are vastly larger in area than the cedar stands and wolf pack territories they contain. Since a deer density estimate for a given DMU is a single value intended to represent an average across a very large heterogeneous area, it is unlikely that these values represent the site specific deer density influencing the understory of isolated cedar stands. However, this was the only historical data available for our entire study area.

We used the Combined Data Systems (CDS) data for the Chequamegon-Nicolet National Forest (USDA 2001) and various state and county forest datasets to select stands characterized as northern white cedar wetlands. Hawth's Analysis Tools add-on for ArcGIS (Beyer 2004) was used to randomly place one vegetation plot within each pre-selected white cedar stand. We surveyed a total of 38 cedar stands across a gradient of wolf impact. Fourteen plots were completed in 2008 and 24 plots were completed in 2009. Vegetation surveys followed the

Carolina Vegetation Survey (CVS) protocol developed by Peet *et al.* (1998). Plots consisted of 4 modules (10 X 10 meters) in a 2 X 2 configuration. Two corners in each module were sampled for presence of vascular plant species (trees, shrubs, seedlings, ferns, forbs) using a series of nested quadrats (increasing incrementally in size from 0.01 m^2 to 10 m^2).

Species richness of forbs, shrubs and ferns was determined for the 10 m^2 scale for each of eight subsamples and then averaged to produce a single richness estimate for each vegetation plot (n=38). Understory seedling species richness was determined by averaging species richness at the 100m^2 scale based on only two subsamples per plot (two 10 X 10 m modules per plot). Identification of forbs conforms to Black and Judziewicz (2008), other plant species names conform to Gleason and Cronquist (1991).

4.2.3 WEIGHTED WOLF OCCUPANCY DURATION INDEX AND DEER DENSITY

Wolf packs establish and occupy territories that are patchily distributed across the landscape (Mladenoff *et al.* 1999). The effect of wolves on deer abundance and foraging behavior is likely to be limited to locations continuously occupied by wolf packs. Presumably, the impact of wolves increases with the number of years the territory has been consistently occupied. Since pack size and territory extent vary from year to year, this creates a mosaic of potential impact intensity across the landscape.

Weighted wolf occupancy duration Index (WWODI) values were calculated by summing the most recent 15 years of DNR wolf territory extent data (1993-2007 for vegetation plots surveyed in 2008 and 1994-2008 for plots surveyed in 2009). Recent years were weighted more strongly given the assumption that wolf occupancy in the distant past would have a weaker impact on current browse intensity and therefore a weaker indirect effect on understory plant communities. The most recent year of wolf occupancy (presence/absence of a wolf pack at each location) was divided by 1, the next most recent year was divided by 1.1, and so on. Thus:

$$\mathbf{WWODI = Y_t/1 + Y_{t-1}/1.1 + Y_{t-2}/1.2 + \ldots\ldots\ldots Y_{t-15}/2.4}$$

where $\mathbf{Y_t}$ is the current year of wolf occupancy and $\mathbf{Y_{t-15}}$ is the wolf occupancy 15 years ago. Although we had hoped to calculate wolf density by dividing territory area by the number of wolves in each pack, pack size data was not consistently collected for all years and all packs.

A similar process was used to calculate a 15 year weighted index for deer density DMU^{-1}. To calculate the 15 year weighted index for deer density, we divided the current year by one, the next most recent year by 1.1, then by 1.2 and so on until 15 years before data collection. Again, these values were summed to provide a weighted index of deer density.

4.2.4 LOCAL AND LANDSCAPE VARIABLES

Remnant northern white cedar stands are often embedded within an early successional forest matrix representing isolated islands of speciose plant communities (Cornett et al. 2000). Cedar wetlands of various shapes and sizes are patchily distributed throughout the landscape. In such a patchy environment, species establishment of forbs and shrubs will depend on their ability to disperse into the stand and persist long enough to successfully reproduce. Assuming that our focal wetlands are drawing from the same regional species pool, species richness represents the outcome of the combined suite of restraints influencing both dispersal and persistence. Dispersal is determined by landscape level variables influenced by the configuration of habitat types and level of fragmentation. Persistence is determined by local biotic and abiotic factors. Biotic factors impacting understory plant survival are competition with other plant species, seed predators, pathogens, symbiotic relationships with mycorrhizae, and herbivory by white-tailed deer.

Local environmental factors shown to influence plant survival and reproductive success (Table 4.1a) are canopy cover (Brosofske et al. 1999), litter depth (Xiong and Nilsson 1999), slope (Honnay et al. 1999, Kumar et al. 2006, Marini et al. 2008), elevation (Kumar et al. 2006, Marini et al. 2008), Canopy *S* (Brosofske et al. 1999), patch area (Findlay and Houlahan 1996, Marini et al. 2008, Rogers et al. 2009), patch age (Matthews et al. 2009), wetness (Wright et al. 2003, Matthews et al. 2009), solar radiation (Marini et al. 2008), precipitation (Marini et al. 2008, Matthews et al. 2009), distance to road (Brosofske et al. 1999, Watkins et al. 2003), and proportion of sand in the soil (Kumar et al. 2006).

We measured canopy cover with a densiometer, averaging readings from the center of each 100m^2 module facing the four cardinal directions. Litter depth was measured to the nearest centimeter per module. The “Wetness” variable was based on a visual estimate of the percentage of each module that was covered by standing water. Species richness of canopy trees (Canopy *S*) is simply the number of canopy species per module. All variables measured in the field were averaged across four modules to produce a single value per vegetation plot.

Patch area and patch age were obtained from stand level data from the Chequamegon Nicolet National Forest CDS data and various state and county datasets. Elevation was acquired from 30m Digital Elevation Models (DEMs) of the study area. Slope and solar radiation were derived from the same DEM dataset using the slope and solar radiation tools in ArcGIS 9.2. Solar radiation represents the cumulative radiation for the month of May, 2009 in kWH/m^2 (similar to Marini et al. 2008). Precipitation represents the cumulative precipitation (in mm) for May, June, July, August, and September, 2008 (similar to Marini et al. 2008) based on data from

NOAA (2008). We measured distance to the nearest road (all road types) based on Tiger line files for Wisconsin roads (US Census Bureau 2000). The proportion of sand in the surficial deposits layer (which directly affects permeability and drainage rate) was obtained from the Groundwater Contamination Susceptibility Model (1:500,000 scale) developed by WiDNR et al. (1997).

Landscape level factors thought to influence dispersal success of understory plant species (Table 4.1b) are mean patch area (Honnay et al. 2003, Kumar et al. 2006), edge density (Honnay et al. 2003, Kumar et al. 2006, Marini et al. 2008), proportion of disturbed land (Honnay et al. 2003, Marini et al. 2008, Matthews et al. 2009, Rogers et al. 2009), proportion of forested land (Honnay et al. 1999, Honnay et al. 2003, Marini et al. 2008, Rogers et al. 2009), proportion of open water (Matthews et al. 2009), Shannon’s Diversity Index of the landscape (Honnay et al. 2003), paved road density (Findlay and Houlahan 1996, Rogers et al. 2009), proximity of similar patches (Rogers et al. 2009), and aggregation/interspersion of similar patches (Kumar et al. 2006).

Although most authors use paved road density as a landscape variable, we used mean distance to paved road. We chose to use the aggregation index because He et al. (2000) found that this index out performs other measures of juxtaposition/interspersion (contagion index, shape index, probability of adjacency of the same class) because it is class specific. For landscape variables requiring a patch type such as total edge density, proximity index and aggregation index we used a combined patch type we called ‘coniferous forest’. We combined the GAP Land Cover vegetation types ‘white spruce’ and ‘alkaline conifer’ to represent ‘coniferous forest’ because the algorithm GAP used to assign vegetation classes did not seem to successfully differentiate between these two vegetation types (most of our cedar stands were categorized as white spruce and should have been categorized as alkaline conifer).

In southeastern Ontario wetlands, Findlay and Houlahan (1997) found the critical distance in plant species richness response to landscape variables to lie between 1000 and 2000 m. Based on this previous study, we calculated our landscape variables within a 1,000 m buffer of each vegetation plot using GAP Land Cover data (USGS 2010). We also calculated mean distance to paved roads within 1000 m buffer using Tiger line files for Wisconsin roads (US Census Bureau 2000). ArcGIS 9.2 (ESRI) and FRAGSTATS (McGarigal et al. 2002) were used to extract and summarize the variables. All data were projected using the HARN Wisconsin TM (NAD 83) coordinate system.

4.2.5 MODEL SELECTION

We used ordinary least squares regression (OLS) to examine relationships between our predictor and response variables. Variables displaying OLS regression coefficients with $p < 0.10$ were retained in the global models for each response variable (Millington et al. 2010). Once global models were formulated, we applied a model-selection approach (Burnham and Anderson 2002) using Akaike's information criterion (AICc) to determine the best-fitting model from among the candidate set of models (all possible variable combinations).

We also used model selection to compare our competing hypotheses for explaining observed relationships between WWODI and $S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, $S_{\mathbf{seedlings}}$, and $S_{\mathbf{ferns}}$: (1) the top-down hypothesis, (2) the bottom-up hypothesis, and (3) the non-trophic hypothesis. To evaluate the evidence in support of a bottom-up trophic cascade, we selected the best models for predicting species richness of forbs, shrubs, seedlings and ferns, based on local and landscape level factors, and examined whether the addition of wolf impact (WWODI) improved model fit (similar to Beyer et al. 2007). We also observed the difference in $R^2_{\mathbf{adj}}$ values between competing models with and without WWODI.

To evaluate the evidence in support of the non-trophic association hypothesis, we applied the best fitting model for WWODI ($\mathrm{WWODI}_{\mathbf{model}}$) to our vegetation response variables ($S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, $S_{\mathbf{seedlings}}$, and $S_{\mathbf{ferns}}$) to determine the amount of variability in species richness explained by these landscape variables thought to influence both wolf habitat selection and plant species richness. We further compared model performance using $R^2_{\mathbf{adj}}$ values by subtracting the variability in plant species richness accounted for by landscape level variables associated with wolf habitat selection ($\mathrm{WWODI}_{\mathbf{model}}$) from the variability initially attributed to top-down effects (WWODI). All statistical analyses were performed using SAS 9.1 software (Cary, NC, USA).

4.3. ***Results***

4.3.1 UNIVARIATE MODELS

Table 4.2 shows descriptive statistics for the response variables ($S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, $S_{\mathbf{seedlings}}$, and $S_{\mathbf{ferns}}$). All vegetation response variables were normally distributed according to Anderson-Darling normality tests. The weighted wolf occupancy duration index ranged from 0.00 – 9.47 with an average value of 4.66 ± 0.51 (SE). Figure 1 shows linear relationships between WWODI and the four vegetation response variables ($S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, $S_{\mathbf{seedlings}}$, and $S_{\mathbf{ferns}}$) (n=38). The strong positive relationships between WWODI and $S_{\mathbf{forbs}}$ ($R^2 = 30.2\%$, $p < 0.001$) and WWODI and $S_{\mathbf{shrubs}}$ ($R^2 = 21.2\%$, $p < 0.005$) are consistent with an indirect trophic response to wolf recovery (Table 4.3). The relationship between WWODI and $S_{\mathbf{seedlings}}$ ($R^{2 =}$ 11.4%, $p < 0.05$) is not as strong as expected but still significant and positive. We did not anticipate a positive response of $S_{\mathbf{ferns}}$ to release from deer browsing since ferns are generally unpalatable and tend to display competitive release under high browsing pressure. However, our data suggest a weak and non-significant but positive relationship between WWODI and $S_{\mathbf{ferns}}$ ($R^2 = 5.3\%$, p= 0.166).

Current year deer density DMU^{-1} estimates ranged from 2.64 km^{-2} to 13.12 km^{-2} with an average value of 6.44 ± 0.33 km^{-2}. This variable was unrelated to any of the vegetation response variables and was not used in further analyses. The fifteen year weighted deer density DMU^{-1} index ranged from 44.25 to 126.66 with an average value of 71.10 ± 2.45. This variable was also unrelated to $S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, $S_{\mathbf{seedlings}}$ or $S_{\mathbf{ferns}}$ (Table 4.3). Percent cover of ferns showed no significant relationship with deer density but was negatively related to WWODI ($R^2 = 11.8\%$, $p < 0.05$). Deer density at this scale was unrelated to WWODI ($R^2 = 0.5\%$, p = 0.68).

Table 4.4 shows the descriptive statistics for independent local and landscape level variables used in the model selection process. To avoid multicollinearity, predictor variables with Pearson correlation coefficients above a threshold of 0.49 were removed (Moore and McCabe 1993). Elevation was highly correlated with wetness ($r = -0.625$, $p < 0.001$) and precipitation ($r = -0.739$, $p < 0.001$) and was removed. Proportion of forested land was negatively correlated with Shannon Diversity Index of the landscape ($r = -0.843$, $p < 0.001$) and with the proportion of sand in the surficial deposits layer (0.650, $p < 0.001$) and was removed. Aggregation index was positively correlated with the proximity index (0.510, $p < 0.001$) and was removed. Cedar stand area was positively correlated with mean patch area (coniferous forest) (0.537, $p < 0.001$) and was removed. Retained variables had stronger relationships with response variables in all cases.

Variables were further reduced by removing those that failed to demonstrate a univariate relationship with the response variables (variables displaying OLS regression coefficients with $p \geq 0.10$). Slope, SDI of the landscape and patch age showed weak or nonexistent relationships with $S_{\textbf{forbs}}$, $S_{\textbf{shrubs}}$, $S_{\textbf{seedlings}}$, $S_{\textbf{ferns}}$ or WWODI and were thus removed from the global models. Figures 2-6 show the univariate relationships between $S_{\textbf{forbs}}$, $S_{\textbf{shrubs}}$, $S_{\textbf{seedlings}}$, $S_{\textbf{ferns}}$ and their respective retained independent variables.

4.3.2 MODEL-SELECTION

Variables retained in the global models of each response variable are shown in Table 4.5. The global model for $S_{\textbf{forbs}}$ consisted of litter depth, percent standing water, distance to road, proportion disturbed, and proportion open water. The global model for $S_{\textbf{shrubs}}$ consisted of proportion disturbed, canopy cover and canopy species richness (*S*). The global model for $S_{\textbf{seedlings}}$ consisted of mean patch area of forest, canopy species richness (*S*) and proportion sand. The global model for $S_{\textbf{ferns}}$ consisted of proximity index (for coniferous forest), solar radiation, precipitation, and litter depth.

The highest ranking models (based on 95% Akaike weights ($\boldsymbol{w_i}$)) for our vegetation response variables ($S_{\textbf{forbs}}$, $S_{\textbf{shrubs}}$, $S_{\textbf{seedlings}}$, $S_{\textbf{ferns}}$) are presented in Table 4.6.

Among the candidate model set, the model with the most support for $S_{\textbf{forbs}}$ indicated that species richness of forbs is negatively related to litter depth ($\beta = -0.7629 \pm 0.3139$ [mean ± SE]), negatively related to proportion disturbed ($\beta = -59.93 \pm 18.12$), and positively related to wetness ($\beta = 0.5466 \pm 0.2203$). The model with the most support for $S_{\textbf{shrubs}}$ indicated that species richness of shrubs is negatively related to proportion disturbed ($\beta = -13.242 \pm 7.847$), and negatively related to canopy *S* ($\beta = 0.2999 \pm 0.1396$). The model with the most support for $S_{\textbf{seedlings}}$ indicated that species richness of seedlings is positively related to canopy *S* ($\beta = 0.4910 \pm 0.2047$), and positively related to proportion of sand in the surficial deposits layer ($\beta = 1.6558 \pm 0.001719$). The model with the most support for $S_{\textbf{ferns}}$ indicated that species richness of ferns is positively related to the proximity index (coniferous forest) (β = 0.003839 ± 0.2047), positively related to precipitation (β = 0.02390 ± 0.01398) and negatively related to litter depth (β = -0.2642 ± 0.1317).

4.3.3 EVIDENCE FOR COMPETING HYPOTHESES

We tested three possible hypotheses for observed relationships between species richness and wolf impact: (1) a top-down trophic cascade, (2) a bottom-up trophic cascade and (3) a non-trophic association. There was strong support for the top-down trophic cascade model for species richness of forbs, shrubs and seedlings, but not for ferns (Figure 1 and Table 4.3).

When we took the predictor variables from the best-fit model for each vegetation response variable and added WWODI to the variables used in the candidate model set (all possible combinations of variables), models for $S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, and $S_{\mathbf{seedlings}}$ containing WWODI consistently outperformed models without WWODI (Table 4.7). The top models of $S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, and $S_{\mathbf{seedlings}}$ (representing 98%, 91% and 86% of Akaike weights, respectively) contained WWODI as a predictor variable. Models containing WWODI were 264 times, 12 times, and 11 times more likely to be true than the best-fit models without WWODI for $S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, and $S_{\mathbf{seedlings}}$, respectively. In contrast, the top models for $S_{\mathbf{ferns}}$ did not contain WWODI (representing 42% of Akaike weights) and the original best-fit model containing only local and landscape variables had 2.3 times more support than the same model with WWODI. The parameter estimates for the model averaged model for each response variable, when candidate models included WWODI, are provided in Table 4.8.

After accounting for environmental effects on species richness, WWODI still increased the variability explained by each model by 19.0% for $S_{\mathbf{forbs}}$, 10.7% for $S_{\mathbf{shrubs}}$, and 12.2% for S

$_{\textbf{seedlings}}$, but only by 0.5% for $S_{\textbf{ferns}}$ (based on $R^2_{\textbf{adj}}$, Table 4.9). This suggests that while local and landscape level factors have a major impact on plant species richness, the positive relationship between WWODI and species richness of forbs, shrubs and seedlings is more likely due to a top-down trophic cascade triggering a release from herbivory than to bottom-up effects propagating up through the food web.

The best fit landscape model of WWODI (again based on lower AICc values and higher Akaike weights ($\boldsymbol{w_i}$)) included the variables mean patch area (forest) and mean distance to paved road ($R^2_{\textbf{adj}}$= 46.6%, $p<0.001$). When the variables for this WWODI model were used to fit species richness data it performed poorly, explaining only 3.8% [$R^2_{\textbf{adj}}$] of variability in $S_{\textbf{forbs}}$, 2.7% of variability in $S_{\textbf{shrubs}}$, 0.9% of variability in $S_{\textbf{seedlings}}$, and 3.3% of variability in $S_{\textbf{ferns}}$ (Table 4.10). Since our best-fit model only accounts for 46.6% of the variability in wolf occupancy, it is possible that the independent variables responsible for the unexplained variance in WWODI are more strongly associated with species richness. However, based on the landscape level variables we assessed, a non-trophic association is an unlikely explanation for the strong positive relationship between WWODI and $S_{\textbf{forbs}}$, $S_{\textbf{shrubs}}$, and $S_{\textbf{seedlings}}$.

4.4. *Discussion*

After we accounted for local and landscape factors, the duration of wolf pack occupancy was a significant predictor of species richness of understory plant species known to respond positively to release from herbivory: forbs, shrubs and seedlings. In contrast, species richness of ferns showed a possible weak positive relationship with WWODI, but this relationship was more likely due to non-trophic associations. In addition, inclusion of WWODI was not supported for models of fern species richness. These results are consistent with a top-down trophic cascade triggering a release from browsing pressure by white-tailed deer.

Evidence from the Allegheny Plateau, predicts that ferns represent aspects of understory plant communities that will not respond to release from browsing pressure (Horsley and Marquis 1983), indicative of an alternate stable state (Friedel 1991, Laycock 1991, Stromayer and Warren 1997). While our data do not indicate an effect of wolf occupancy (and by extension release from browsing pressure) on species richness of ferns, we did find a negative relationship between wolf occupancy and percent cover of ferns. However, a reduction in percent cover could indicate either that individual fern plants do not grow as large due to over-shading by shrubs, or that some fern plants are being out-competed by shrubs which could eventually lead to a decline in local species richness of ferns.

We found little evidence to support that species richness of understory plant communities are associated with white-tailed deer density at the scale of deer management units. However, as stated earlier, deer density estimates representing entire DMUs are unlikely to characterize the site specific deer density influencing the understory of isolated cedar stands. A better estimate of local browse pressure is clearly needed (e.g. density of *Aralia nudicaulis*, see Chapter 3). The lack of association between deer density DMU^{-1} and WWODI is not surprising given the inappropriate scale of the deer density data (most DMUs in our study area had both high and low wolf impact areas). Given the low density of wolves, however, numerical effects on deer populations may be unlikely. Our objective was not to model effects of wolves on white-tailed deer population growth, and a more comprehensive approach is needed to test these assumptions (see Van Deelen et al. *in review*). Regardless of numerical effects, the consistent presence of a wolf pack is predicted to alter: (1) local habitat selection by white tailed deer (i.e. buffer zones between adjacent packs act as refugia), and/or (2) foraging behavior by white-tailed deer (i.e. deer increase vigilance and movement).

Initial evidence from YNP indicated trait mediated indirect effects of wolves on aspen, cottonwood and willow recruitment (Ripple et al. 2001, Ripple and Beschta 2003, 2004, 2007, Beyer et al. 2007). However, several recent studies question the scientific validity of these earlier works. For example, Creel and Christianson (2009) found that elk consumption of willow actually increased when wolves were present. They cite eight years of low snow accumulation (causing elk to reduce browsing in favor of grazing) and declines in elk density as the proximate causes for willow recovery. When Kaufmann et al. (2010) used an a priori measure of predation risk based on actual predation events, incorporated abiotic factors, and conducted a multi-year manipulative experiment, they found no evidence for a behaviorally mediated trophic cascade (BMTC) triggering recovery of aspen. They argue that the reduction in elk numbers (due at least in part to wolf predation) will have reduced browsing pressure by ~40%, and that this numerical effect is responsible for the patchy recovery of aspens, cottonwoods and willows in areas with high productivity.

Since our abiotic environmental models were only able to explain some of the variability in species richness of forbs (39.1%), shrubs (19.6%), seedlings (21.3%), and ferns (31.7%), it is possible that we missed some important factors influencing species richness of understory plant communities in northern white cedar swamps. For example, several studies have found significant relationships between species richness and soil properties such as total soil nitrogen, organic carbon, pH and reduction potential (Kumar et al. 2006, Matthews et al 2009). However, Weiher et al. (2003) found the total effect of soils on species richness in Wisconsin oak savannahs to be negligible as the effects of different components canceled each other out (some were positive and some negative). Regardless, it is doubtful that wolf occupancy is correlated with soil properties, so inclusion of these variables would be unlikely to weaken support for a top-down trophic effect.

Fawn predation by black bears (*Ursus americanus*) is considered an important mortality factor for white-tailed deer, and black bear numbers have been relatively high in Wisconsin in recent years (Rolley and Worland 2009). Since adult deer are not preyed upon by bears, fawn predation alone is likely to have relatively weak effects on population growth of white-tailed deer. However, some evidence suggests that the regional coexistence of wolves and bears may limit population irruptions of moose (*Alces alces*) (Gassaway et al. 1992, Messier 1994). Whether this same pattern will be observed for white-tailed deer in the Great Lakes region is of significant management interest. The possible synergistic effects of wolf and bear predation may have exaggerated the variability in plant species richness that we attributed to top-down effects of wolf recovery.

4.5. *Conclusion*

Most previous studies of top-down trophic effects of wolves used wolf presence and/or predation risk by wolves as a dichotomous variable in either space or time (Ripple et al. 2001, Ripple and Beschta 2003, Ripple and Beschta 2004, Hebblewhite et al. 2005, Ripple and Beschta 2006, Beschta and Ripple 2007, Beyer et al. 2007). Here we provide wolf impact as a gradient representing the historic spatial extents of wolf pack territories through time since colonization. Plant species are thought to recover slowly from disturbance (Foster 1992, Pearson et al. 1998), so current vegetation conditions will reflect historic disturbance patterns, making a gradient in space and time a more appropriate variable for measuring top-down trophic effects.

We also incorporated local and landscape level factors thought to impact our vegetation response variables and employed model selection using an information theoretic approach. Through this process, we showed a lack of evidence for competing explanations for the positive relationship we found between wolf occupancy duration and plant species richness of forbs, shrubs and seedlings at local scales (10 -100m^2). Our data indicate that wolf recovery in the Great Lakes region is associated with local recovery of understory plant communities in northern white cedar wetlands.

Future research should explicitly examine whether the response of deer to wolf recovery is behavioral or numerical. If deer response to wolf recovery is purely behavioral, it is possible that the presence of wolves simply alters the pattern of browsing intensity experienced by plant communities across the landscape. By increasing browsing pressure in the buffer zones between packs and reducing browsing pressure within pack territory extents, wolves may have an overall neutral impact on regional biodiversity. Alternatively, by providing refugia from deer, wolves may prevent local extinctions of rare and browse sensitive plant species.

Recovery of wolves presents an opportunity to observe how top predators influence biodiversity of lower trophic levels and ecosystem properties. The high quality dataset of historic wolf pack territory extents, collected and maintained by Wisconsin's DNR, provided the experimental framework we needed to explicitly examine impacts of wolf occupancy duration. The continued funding of this and similar long term studies is essential for a more mechanistic understanding of trophic interactions and the ecological recovery of chronically over-browsed ecosystems (Carpenter 1998).

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Table 4.1 Variables hypothesized to affect species richness and diversity of the understory plant communities of Northern white cedar stands. Landscape variable descriptions are modified from the FRAGSTATS manual.

Variable	Quantification
A) Local variables	
Canopy cover	The average percentage of closed canopy above each module, as measured with the use of a densiometer.
Litter depth	The depth of the leaf litter
Slope	The slope in degrees
Elevation	In meters from DEM
Canopy *S*	Average number of canopy species per 100m^2 module
Patch area	Area of cedar stand based on CDS data
Patch age	Age of cedar stand in years based on CDS data
Wetness	Average percent of standing water per 100m^2 module
Solar Radiation	Cumulative radiation for the month of May, 2009 (kWH/m^2)
Precipitation	Cumulative precipitation (in mm) for May, June, July, August, and September, 2008
Distance to road	Distance to nearest road (m)
Sand	Proportion of surficial deposition that is sand (0, 0.5 or 1)
B) Landscape variables (1000m)	
Mean patch area (forest)	the sum, across all patches of the corresponding patch type, of the corresponding patch metric values, divided by the number of patches of the same type. $MN = \frac{\sum_{j=1}^{n} x_{ij}}{n_i}$
Mean patch area (coniferous forest)	the sum, across all patches of the corresponding patch type, of the corresponding patch metric values, divided by the number of patches of the same type. $MN = \frac{\sum_{j=1}^{n} x_{ij}}{n_i}$
Edge density (coniferous forest)	the sum of the lengths (m) of all edge segments involving the corresponding patch type, divided by the total landscape area (m^2), multiplied by 10,000 (to convert to hectares). $ED = \frac{\sum_{k=1}^{m} e_{ik}}{A}(10{,}000)$
Proportion disturbed	the proportion of the landscape comprised of cultivated cropland, pasture/hay, or developed land

Proportion forested	the proportion of the landscape comprised of forest
Proportion open water	the proportion of the landscape comprised of open water
SDI of landscape	the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion. $SHDI = -\sum_{i=1}^{m} (P_i * \ln P_i)$ P_i = proportion of the landscape occupied by patch type (class) i.
Mean paved road	Averaged distance to a major road in meters
Proximity index (coniferous forest)	the sum of patch area (m^2) divided by the nearest edge-to-edge distance squared (m^2) between the focal patch and all other patches of the corresponding patch type whose edges are within 1000 (m) of the focal patch. $PROX = \sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^2}$ a_{ijs} = area (m^2) of patch ijs within 1,000 (m) of patch ij. h_{ijs} = distance (m) between patch ijs and patch ijs, based on patch edge-to-edge distance, computed from cell center to cell center.
Aggregation index (coniferous forest)	the number of like adjacencies involving the corresponding class, divided by the maximum possible number of like adjacencies involving the corresponding class, which is achieved when the class is maximally clumped into a single, compact patch, multiplied by the proportion of the landscape comprised of the corresponding class, summed over all classes and multiplied by 100 (to convert to a percentage). $AI = \left[\sum_{i=1}^{m} \left(\frac{g_{ii}}{\max \rightarrow g_{ii}} \right) P_i \right] (100)$ g_{ii} = number of like adjacencies (joins) between pixels of patch type (class) i based on the *single-count* method. max-g_{ii} = maximum number of like adjacencies (joins) between pixels of patch type (class) i (see below) based on the *single-count* method. P_i = proportion of landscape comprised of patch type (class) i.

Table 4.2 Descriptive statistics for response variables: species richness and diversity of understory plant communities in Northern white-cedar stands.

Variable	MEAN	SE	MIN	MAX
Species richness of forbs at the 10m^2 scale ($S_{\mathbf{forbs}}$)	9.145	0.395	5.000	15.125
Species richness of shrubs at the 10m^2 scale ($S_{\mathbf{shrubs}}$)	3.860	0.173	1.571	5.625
Species richness of seedlings at the 100m^2 scale ($S_{\mathbf{seedlings}}$)	6.947	0.271	3.500	10.000
Species richness of ferns at the 10m^2 scale ($S_{\mathbf{ferns}}$)	2.546	0.150	0.333	4.625

Table 4.3 Top-down trophic models of species richness for four vegetation growth forms (S_{forbs}, S_{shrubs}, $S_{\text{seedlings}}$, and S_{ferns}). The predictor variables are the weighted wolf occupancy duration index (*WWODI*) and weighted deer density DMU^{-1}. Models significant at $p < 0.05$ are shown in bold. Models use data with n = 38.

Response	Predictor variable	β ± SE	P	R^2	R^2_{adj}
$S_{\textbf{forbs}}$	*WWODI*	**0.424 ± 0.107**	**0.001**	**30.2%**	**28.3%**
	Weighted deer density DMU^{-1}	0.0368 ± 0.0261	0.168	5.2%	2.6%
$S_{\textbf{shrubs}}$	*WWODI*	**0.156 ± 0.050**	**0.004**	**21.2%**	**19.0%**
	Weighted deer density DMU^{-1}	0.00499 ± 0.01177	0.678	0.5%	0.0%
$S_{\textbf{seedlings}}$	*WWODI*	**0.178 ± 0.083**	**0.038**	**11.4%**	**8.9%**
	Weighted deer density DMU^{-1}	0.00761 ± 0.01834	0.681	0.5%	0.0%
$S_{\textbf{ferns}}$	*WWODI*	0.0672 ± 0.0475	0.166	5.3%	2.6%
	Weighted deer density DMU^{-1}	0.01435 ± 0.009908	0.156	5.5%	2.9%

Table 4.4 Descriptive statistics for variables hypothesized to affect species richness and diversity of the understory plant communities of northern white cedar stands.

Variable	MEAN	SE	MIN	MAX	Units	Hypothesized effect
A) Local variables						
Canopy cover	0.910	0.0073	0.811	0.982	proportion	negative
Litter depth	2.373	0.189	1.000	6.000	cm	negative
Slope	1.427	0.201	0.000	5.808	degrees	
Elevation	476.42	3.48	404.00	511.00	meters	negative
Canopy *S*	3.224	0.193	1.500	5.500	# of species	positive
Patch area	27.44	4.21	2.94	94.61	ha	positive
Patch age	120.36	4.25	55.00	195.00	years	negative
Wetness	0.754	0.248	0.000	8.250	proportion	positive
Solar radiation	172.30	0.184	168.85	175.00	kWH m^{-2}	positive
Precipitation	497.87	1.65	473.48	520.75	mm	positive
Distance to road	315.0	32.3	49.2	884.8	meters	positive
Sand	0.7368	0.0646	0.0000	1.0000	proportion	positive
B) Landscape variables (1000m)						
Mean patch area (forest)	56.3	11.7	3.5	280.4	ha	positive
Mean patch area (coniferous forest)	2.318	0.284	0.549	9.034	ha	positive
Edge density (conifer forest)	152.22	5.69	84.29	225.19	m m^{-2}	negative
Disturbed land	0.027	0.003	0.000	0.095	proportion	negative
Forested land	0.644	0.021	0.380	0.839	proportion	positive
Open Water	0.021	0.006	0.000	0.167	proportion	negative
SDI of landscape	1.548	0.039	0.981	2.084	Index	positive
Mean distance to paved road	3994	396	459	8860	meters	positive
Proximity index (conifer forest)	59.0	11.9	5.1	404.5	index	positive
Aggregation index (conifer forest)	64.88	1.38	41.14	82.06	index	positive

Table 4.5 Univariate ordinary least squares regression models of species richness for four vegetation growth forms (forbs, shrubs, seedlings and ferns). Variables significant at $p < 0.05$ are shown in bold. Models use data with n = 38 except for *litter depth* which has only n=35.

Response	Predictor variable	$\beta \pm SE$	P	R^2	R^2_{adj}
S_{forbs}					
	Litter depth	**-0.851 ± 0.360**	**0.024**	**14.5%**	**11.9%**
	Wetness	**0.688 ± 0.239**	**0.007**	**18.7%**	**16.4%**
	Distance to road	0.004 ± 0.002	0.083	8.1%	5.6%
	Proportion disturbed	**-42.3 ± 17.8**	**0.023**	**13.6%**	**11.2%**
	Proportion open water	**-20.8 ± 9.82**	**0.041**	**11.1%**	**8.6%**
S_{shrubs}					
	Proportion disturbed	**-18.8 ± 7.78**	**0.021**	**13.9%**	**11.5%**
	Canopy cover	-0.0664 ± 0.0380	0.089	7.8%	5.2%
	Canopy S	**-0.377 ± 0.135**	**0.008**	**17.8%**	**15.5%**
$S_{seedlings}$					
	Mean patch area (forest)	0.00693 ± 0.00368	0.068	9.0%	6.4%
	Canopy S	0.443 ± 0.221	0.052	10.1%	7.6%
	Sand	**1.52 ± 0.650**	**0.024**	**13.3%**	**10.9%**
S_{ferns}					
	Proximity Index (conifer forest)	0.00362 ± 0.00201	0.081	8.2%	5.7%
	Solar radiation	-0.257 ± 0.129	0.054	9.9%	7.4%
	Precipitation	**0.0342 ± 0.0140**	**0.020**	**14.2%**	**11.8%**
	Litter depth	**-0.392 ± 0.124**	**0.003**	**23.2%**	**20.9%**

Table 4.6 Results of top regression models (representing 95% of Akaike weights) for species richness of forbs ($S_{\textbf{forbs}}$), shrubs ($S_{\textbf{shrubs}}$), seedlings ($S_{\textbf{seedlings}}$) and ferns ($S_{\textbf{ferns}}$).

Model description	R^2_{adj}	AIC_c	$\Delta\text{AIC}_\text{c}$	w_i
$S_{\textbf{forbs}}$				
Litter depth, wetness, proportion disturbed	*39.1%*	154.007	0.0000	0.36482
Litter depth, wetness, proportion disturbed, proportion open water	*40.6%*	155.078	1.0710	0.21356
Litter depth, wetness, distance to road, proportion disturbed	*39.6%*	155.686	1.6790	0.15758
Litter depth, wetness, distance to road, proportion disturbed, proportion open water	*40.5%*	157.313	3.3052	0.06988
Litter depth, proportion disturbed	*29.3%*	157.501	3.4940	0.06359
Litter depth, proportion disturbed, proportion open water	*32.0%*	157.908	3.9005	0.05189
Litter depth, distance to road, proportion disturbed	*30.1%*	158.843	4.8358	0.03251
$S_{\textbf{shrubs}}$				
Proportion disturbed, canopy S	*19.6%*	110.672	0.0000	0.29956
Canopy S	*15.5%*	111.068	0.3960	0.24575
Proportion disturbed, canopy cover	*17.0%*	111.873	1.2019	0.16425
Proportion disturbed	*11.5%*	112.800	2.1282	0.10336
Proportion disturbed, canopy cover, canopy S	*18.1%*	113.056	2.3847	0.09092
Canopy cover, canopy S	*13.1%*	113.631	2.9591	0.06822
$S_{\textbf{seedlings}}$				
Canopy S, sand	*21.3%*	143.807	0.0000	0.46271
Mean patch area (forest), canopy S, sand	*21.8%*	145.241	1.4336	0.22595
Sand	*10.9%*	147.013	3.2062	0.09313
Mean patch area (forest), canopy S	*13.8%*	147.272	3.4644	0.08185
Mean patch area (forest), sand	*11.9%*	148.106	4.2993	0.05392
Canopy S	*7.6%*	148.427	4.6202	0.04592
$S_{\textbf{ferns}}$				
Proximity index, precipitation, litter depth	31.7%	87.216	0.0000	0.24921
Proximity index, litter depth	27.6%	87.522	0.3062	0.21383
Proximity index, solar radiation, litter depth	29.9%	88.091	0.8752	0.16089
Proximity index, solar radiation, precipitation, litter depth	32.2%	88.851	1.6351	0.11003
Litter depth	20.9%	89.037	1.8207	0.10028
Precipitation, litter depth	23.3%	89.589	2.3730	0.07608
Solar radiation, litter depth	22.0%	90.105	2.8887	0.05879

Table 4.7 Results of top regression models (representing 95% of Akaike weights) for species richness of forbs ($S_{\mathbf{forbs}}$), shrubs ($S_{\mathbf{shrubs}}$), seedlings ($S_{\mathbf{seedlings}}$) and ferns ($S_{\mathbf{ferns}}$) with the weighted wolf occupancy duration index (WWODI) included.

Model description	$R^2_{\mathbf{adj}}$	AIC_c	ΔAIC_c	w_i
$S_{\mathbf{forbs}}$				
Litter depth, wetness, proportion disturbed, WWODI	58.1%	142.853	0.0000	0.82958
Litter depth, wetness, WWODI	50.0%	147.096	4.2428	0.09943
Litter depth, proportion disturbed, WWODI	48.2%	148.363	5.5093	0.05279
$S_{\mathbf{shrubs}}$				
Canopy S, WWODI	29.4%	105.715	0.0000	0.47028
Proportion disturbed, Canopy S, WWODI	30.3%	106.894	1.1790	0.26082
Proportion disturbed, WWODI	23.9%	108.599	2.8843	0.11118
WWODI	19.0%	109.460	3.7450	0.07230
Proportion disturbed, canopy S	19.6%	110.672	4.9569	0.03944
$S_{\mathbf{seedlings}}$				
Canopy S, sand, WWODI	33.5%	139.057	0.0000	0.78313
Canopy S, WWODI	21.6%	143.652	4.5945	0.07873
Canopy S, sand	18.1%	143.807	4.7497	0.07285
Sand, WWODI	10.9%	145.343	6.2858	0.03380
$S_{\mathbf{ferns}}$				
Proximity index, precipitation, litter depth	31.7%	87.216	0.0000	0.22846
Proximity index, litter depth	27.6%	87.522	0.3062	0.19603
Litter depth, WWODI	25.5%	88.500	1.2834	0.12026
Precipitation, litter depth, WWODI	28.4%	88.832	1.6159	0.10184
Proximity, precipitation, litter depth, WWODI	32.2%	88.869	1.6533	0.09996
Litter depth	20.9%	89.037	1.8207	0.09193
Proximity index, litter depth, WWODI	28.0%	89.060	1.8434	0.09089
Precipitation, litter depth	23.2%	89.589	2.3730	0.06975

Table 4.8 Coefficients table for the model averaged model for four vegetation growth forms (forbs, shrubs, seedlings and ferns) when the weighted wolf occupancy duration index is included in the global model.

Response	Predictor variable	β ± SE	Upper 95%	Lower 95%	Parameter Importance
$S_{\textbf{forbs}}$					
	Litter depth	-0.7564 ± 0.2694	-0.2284	-1.2844	0.99938
	Wetness	0.5267 ± 0.1848	0.8888	0.1645	0.93283
	Proportion disturbed	-41.6173 ± 15.9057	-10.4421	-72.7926	0.88649
	WWODI	0.3599 ± 0.0942	0.5445	0.1753	0.99622
$S_{\textbf{shrubs}}$					
	Proportion disturbed	-10.9245 ± 7.93597	4.63005	-26.4790	0.42506
	Canopy S	-0.3022 ± 0.13075	-0.04595	-0.5585	0.80291
	WWODI	0.1324 ± 0.04893	0.22833	0.0365	0.91459
$S_{\textbf{seedlings}}$					
	Canopy S	0.56616 ± 0.19507	0.94848	0.18383	0.94195
	Sand	1.53012 ± 0.57438	2.65590	0.40434	0.90445
	WWODI	0.19651 ± 0.07346	0.34049	0.05254	0.90525
$S_{\textbf{ferns}}$					
	Proximity index	0.00345 ± 0.00182	0.0070	-0.0001	0.61589
	Precipitation	0.02300 ± 0.01419	0.0508	-0.0048	0.50080
	Litter depth	-0.33033 ± 0.13765	-0.0605	-0.6001	0.99912
	WWODI	0.06215 ± 0.04448	0.1493	-0.0250	0.41328

Table 4.9 Best-fit linear regression models for vegetation response variables $S_{\mathbf{forbs}}$, $S_{\mathbf{shrubs}}$, $S_{\mathbf{seedlings}}$, $S_{\mathbf{ferns}}$ with and without weighted wolf occupancy duration index (WWODI) as a predictor variable. 'Top-down trophic' represents $R^2_{\mathbf{adj}}$ of the best-fit model without WWODI subtracted from the $R^2_{\mathbf{adj}}$ of the same model with WWODI included.

Model description	P	$R^2_{\mathbf{adj}}$
$S_{\mathbf{forbs}}$		
Litter depth, wetness, proportion disturbed	<0.001	39.1%
Litter depth, wetness, proportion disturbed, WWODI	<0.001	58.1%
Top-down trophic		**19.0%**
$S_{\mathbf{shrubs}}$		
Proportion disturbed, canopy S	0.008	19.6%
Proportion disturbed, canopy S, WWODI	0.002	30.3%
Top-down trophic		**10.7%**
$S_{\mathbf{seedlings}}$		
Canopy S, sand	0.006	21.3%
Canopy S, sand, WWODI	0.001	33.5%
Top-down trophic		**12.2%**
$S_{\mathbf{ferns}}$		
Proximity index, precipitation, litter depth	0.002	31.7%
Proximity index, precipitation, litter depth, WWODI	0.003	32.2%
Top-down trophic		**0.5%**

Table 4.10 Top regression model for weighted wolf occupancy duration index (WWODI) applied to vegetation response variables $S_{\textbf{forbs}}$, $S_{\textbf{shrubs}}$, $S_{\textbf{seedlings}}$, $S_{\textbf{ferns}}$.

Model description	P	$R^2_{\textbf{adj}}$
Mean distance to paved road, mean patch area (coniferous forest)		
$S_{\textbf{forbs}}$	0.19	3.8%
$S_{\textbf{shrubs}}$	0.24	2.7%
$S_{\textbf{seedlings}}$	0.32	0.9%
$S_{\textbf{ferns}}$	0.21	3.3%

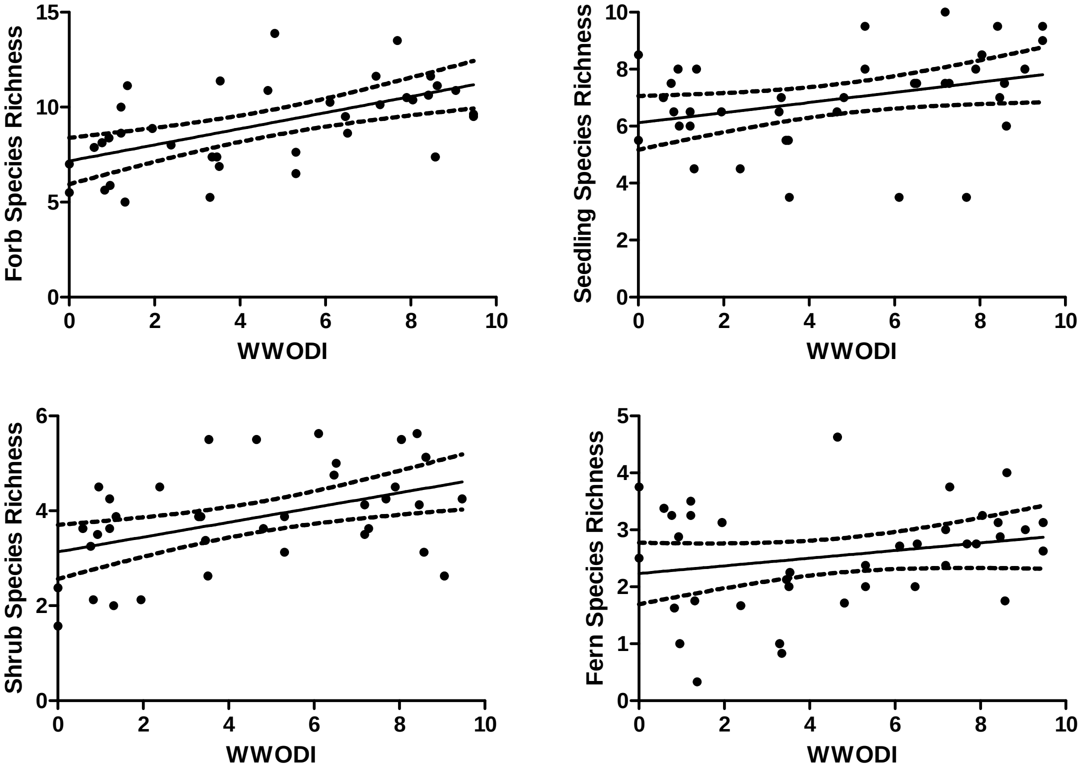

Figure 4.1 Univariate relationships between *S* of forbs, shrubs, seedlings, ferns and the weighted wolf occupancy duration index (WWODI). Ordinary least squares regression lines and confidence bands (95%) are shown for all variables.

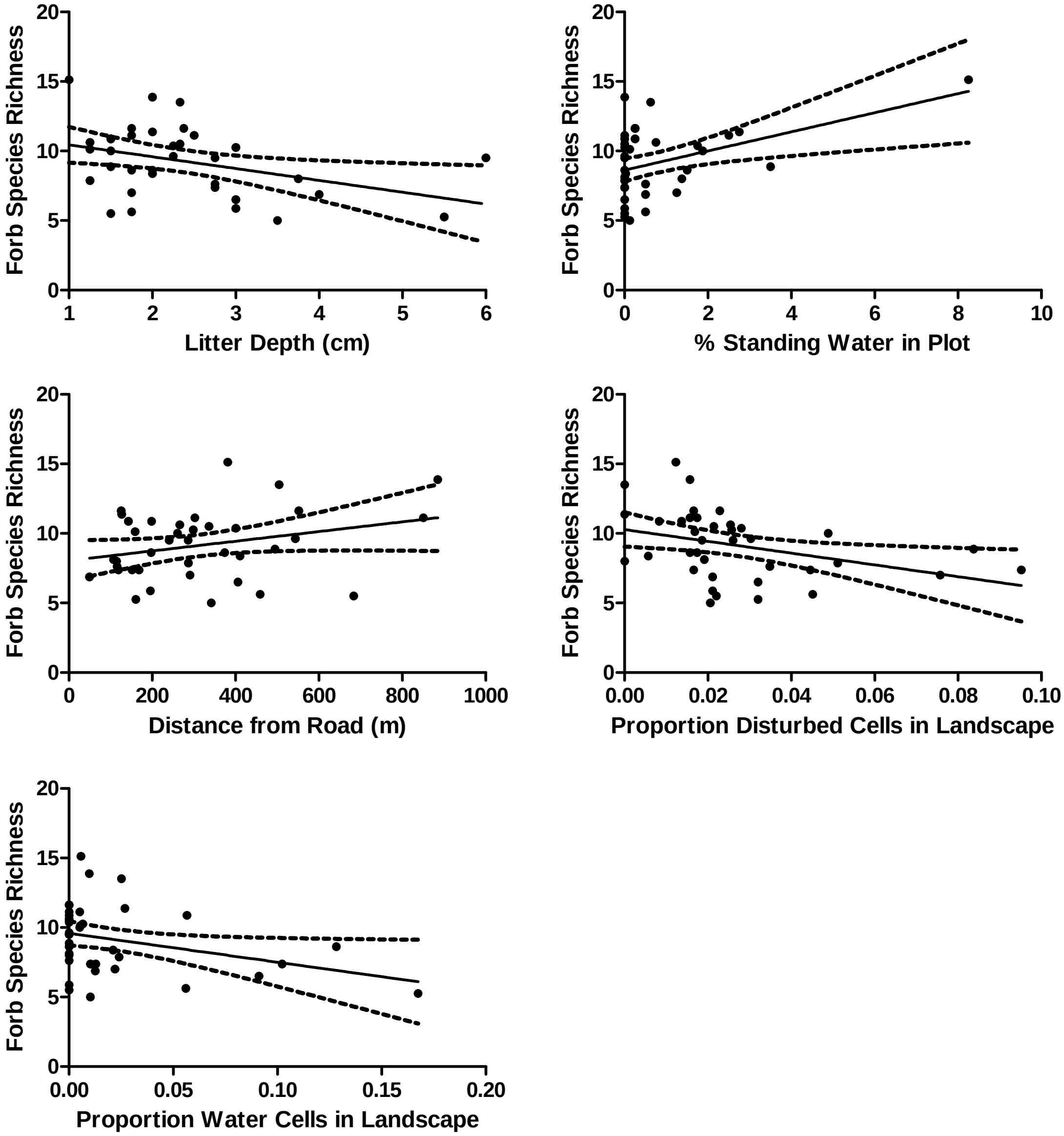

Figure 4.2 Univariate relationships between *S* of forbs at the $10m^2$ scale and independent variables with $P < 0.10$. Ordinary least squares regression lines and confidence bands (95%) are shown for all variables.

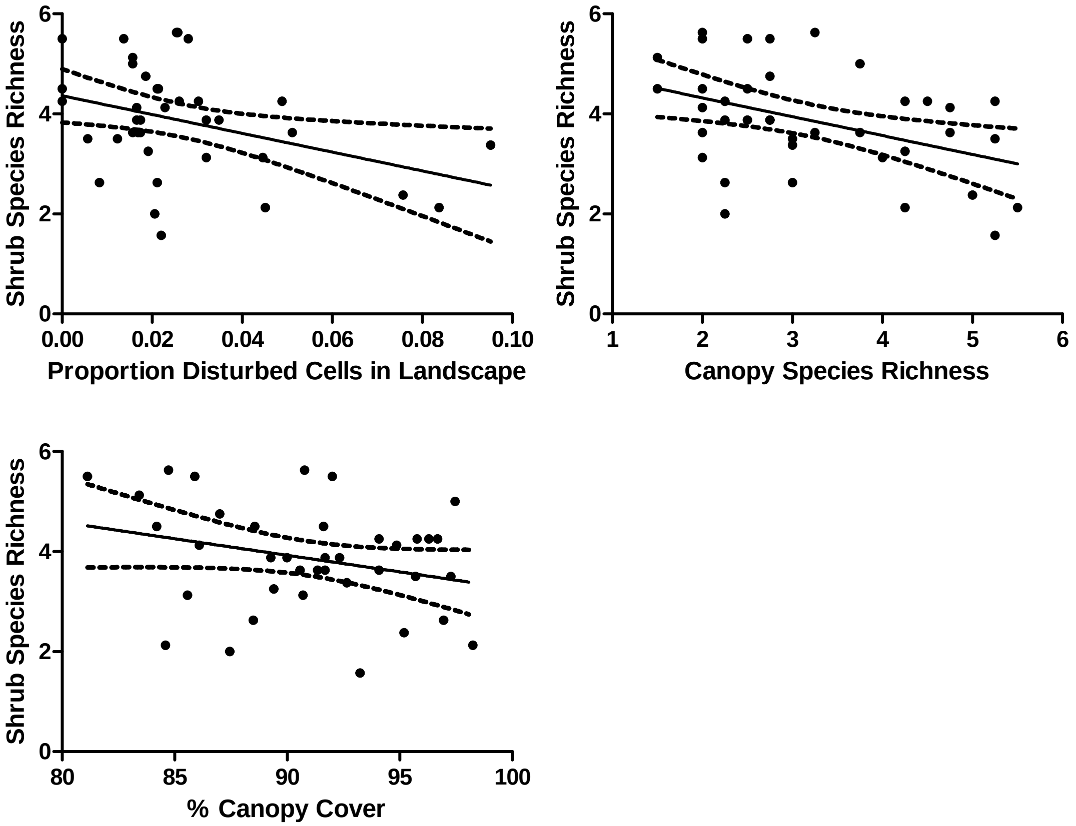

Figure 4.3 Univariate relationships between shrub *S* at the 10 m^2 scale and independent variables with $P < 0.10$. Ordinary least squares regression lines and confidence bands (95%) are shown for all variables.

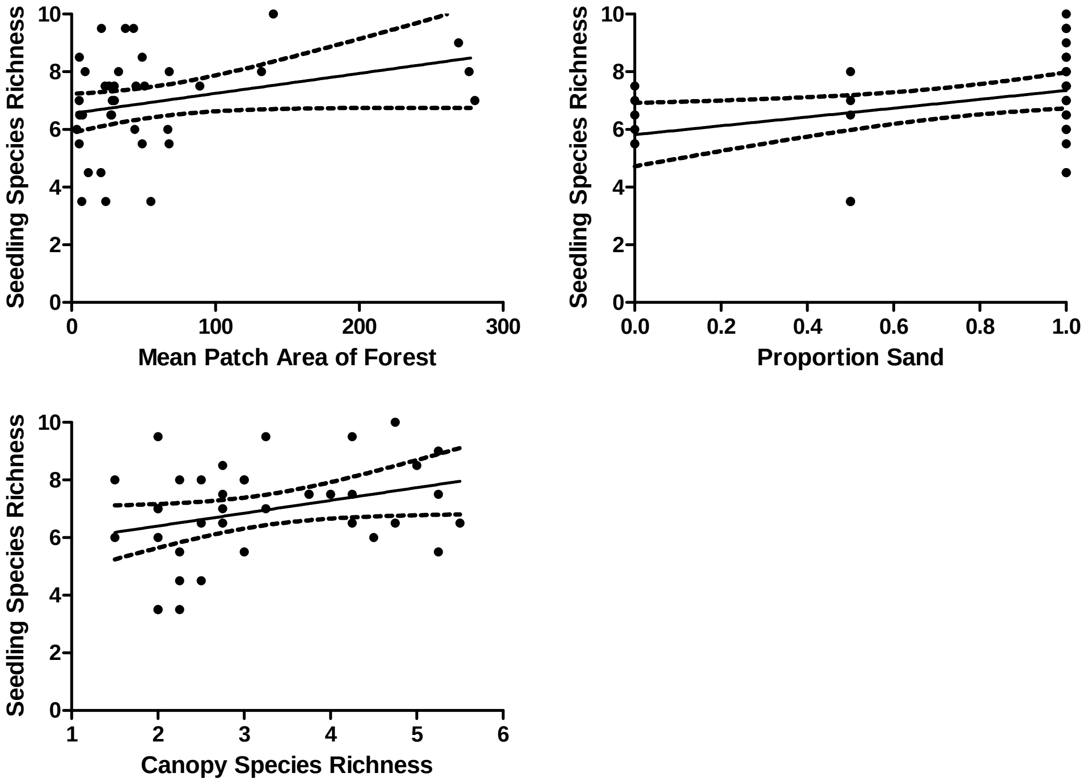

Figure 4.4 Univariate relationships between seedling *S* at the 100m^2 scale and independent variables with P < 0.10. Ordinary least squares regression lines and confidence bands (95%) are shown for all variables.

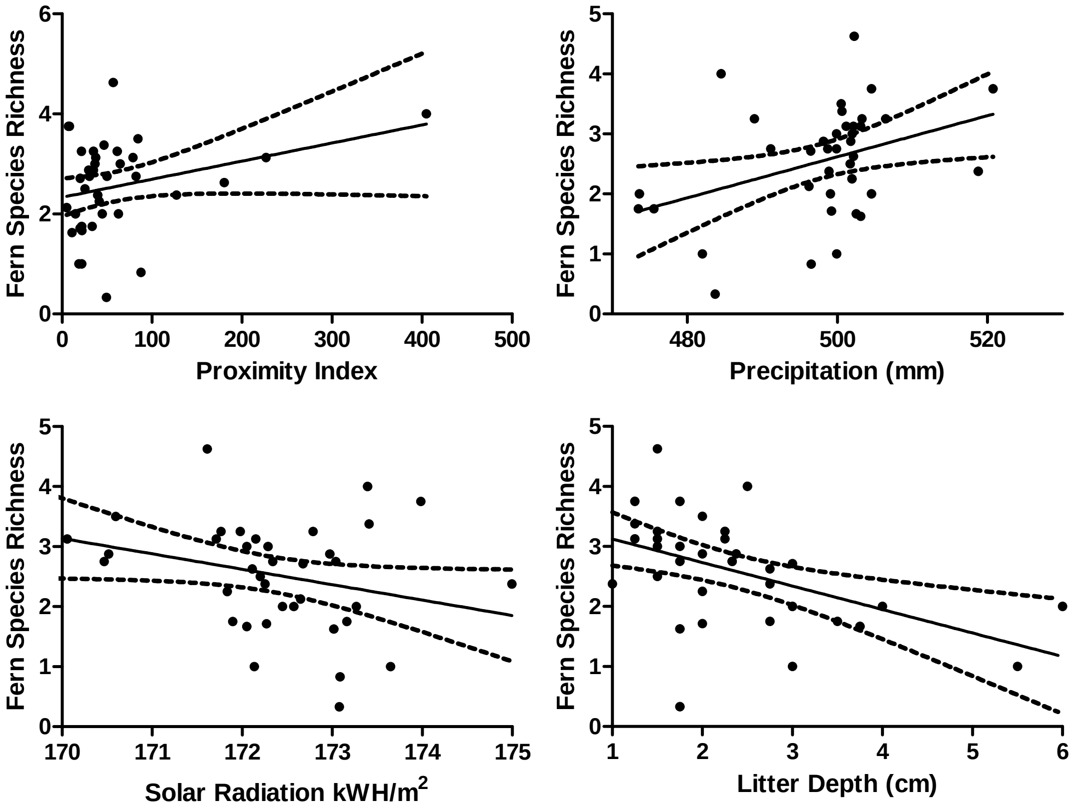

Figure 4.5 Univariate relationships between fern *S* at the $10m^2$ scale and independent variables with $P < 0.10$. Ordinary least squares regression lines and confidence bands (95%) are shown for all variables.

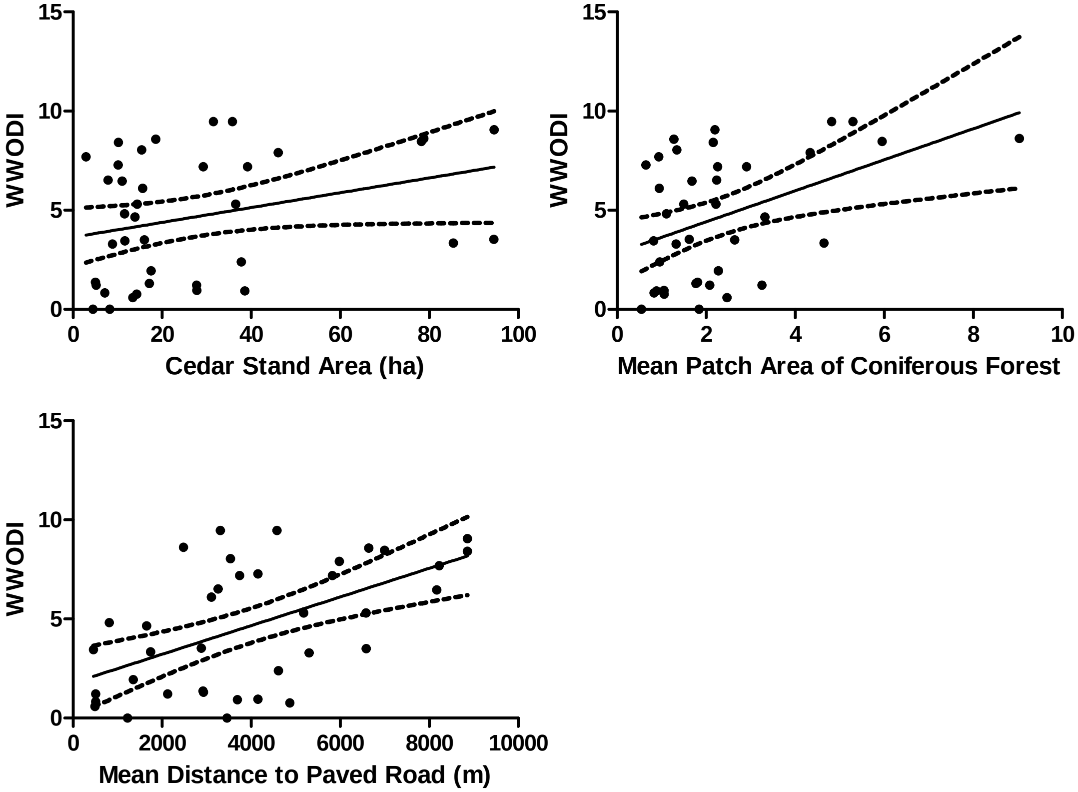

Figure 4.6 Univariate relationships between WWODI and independent variables with P < 0.10. Ordinary least squares regression lines and confidence bands (95%) are shown for all variables.

CHAPTER 5

CONCLUSION

Wolf recovery in the Great Lakes region presents an opportunity to observe how top predators influence biodiversity of lower trophic levels and ecosystem properties. There has been limited experimental evidence of trophic cascades initiated by vertebrate predators in temperate terrestrial ecosystems, partly due to the difficulty in administering and monitoring such large scale manipulations (Shurin et al. 2002). Recent attempts to infer top-down effects of predators have drawn on comparisons across areas with and without predators (Berger et al. 2001), or correlative studies of vegetation response following predator restoration (Ripple et al. 2001, Ripple and Beschta 2003).

Most of these previous studies of top-down trophic effects of wolves used wolf presence and/or predation risk by wolves as a dichotomous variable in either space or time (Ripple et al. 2001, Ripple and Beschta 2003, Ripple and Beschta 2004, Hebblewhite et al. 2005, Ripple and Beschta 2006, Beschta and Ripple 2007, Beyer et al. 2007). Here we provide wolf impact as a gradient representing the historic spatial extents of wolf pack territories through time since colonization. Plant species are thought to recover slowly from disturbance (Foster 1992, Pearson et al. 1998), so current vegetation conditions will reflect historic disturbance patterns, making a gradient in space and time a more appropriate variable for measuring top-down trophic effects. By addressing wolf impact at the scale of wolf territory extents, instead of presence/absence of wolves for entire regions, we were able to have both replication of "treatments" and comparable local control sites.

Ecological processes (such as trophic cascades) are likely to manifest differentially over a range of spatial and temporal scales (Levin 1992, Polis 1999, Bowyer and Kie 2006). Levin (2000) argues that we must develop experimental research designs that measure patterns of variability in space and time if we are to understand how ecological processes interact to structure ecosystems and drive community dynamics. By sampling at multiple spatial scales, we revealed that changes in species richness are not consistent across scales nor among vegetation growth forms: forbs show a stronger response at local scales ($1\text{-}10m^2$), while shrubs show a response across broader scales ($10m^2$ - $400m^2$). The design of future research should incorporate the proper scale in order to effectively detect top-down effects

For northern white-cedar wetlands, we found density and species diversity of woody stems 50-100cm tall to be ideal plant response variables with which to measure release from browsing pressure, especially when allowances were made for variability in species specific browsing response. The gap in the size structure of woody stems characteristic of over-browsed understories was less apparent in cedar wetlands with high potential wolf impact. However, regardless of wolf impact, recruitment of cedar in lowland cedar stands in our study area continues to be very limited. Alverson et al. (1988) concluded that deer densities need to be maintained below $1\text{-}2/km^2$ in order to sustain the diversity of native Wisconsin plants. In our study area, maximum deer densities of $13/km^2$ and above are common. It is unlikely that the recovery of the wolf population alone will reduce the deer population to densities recommended by Alverson et al. (1988). However, as the proportion of early successional forests decreases across the Great Lakes Region, reduced forage, when combined with predation by wolves and bears, may cause deer densities to naturally decline.

Top-down and bottom-up forces are both critical for maintaining biodiversity and ecological integrity of ecosystems, but it is not well understood how the relative strengths of these processes vary in space and time. Carnivores may cause herbivores to switch habitats or change their foraging behavior, resulting in net-positive indirect effects on some plant populations and net-negative indirect effects on other plant populations (Polis 1999). In addition, the potential for confounding variables to produce spurious associations can cause serious complications when interpreting the results of space-for-time studies such as this one. To address these issues, we incorporated local and landscape level factors thought to impact our vegetation response variables and employed model selection using an information theoretic approach. Through this process, we showed a lack of evidence for competing explanations (bottom-up and non-trophic) for the positive relationship we found between wolf occupancy duration and plant species richness of forbs, shrubs and seedlings.

Total trophic-level biomass, a sufficient response variable for aquatic systems, may be an inappropriate response variable with which to measure trophic responses in terrestrial systems. Recent evidence suggests that the indirect effects of predators in terrestrial systems are much stronger on plant species diversity than on plant biomass, and that these changes in species composition and evenness have strong effects on ecosystem properties (Schmitz 2006). Thus, we need to rethink how we address trophic cascades in terrestrial systems as opposed to characterizing them as weaker examples of aquatic cascades (*sensu* Strong 1992, Halaj and Wise 2001, Shurin et al. 2002). If we fail to do so, we risk measuring the wrong plant response variables and missing evidence of ecologically important trophic cascades in terrestrial systems.

Our data from northern white cedar wetlands support Schmitz's argument that species diversity, richness and composition are more meaningful measures of trophic level responses in terrestrial systems.

Whether the differences we observed in vegetation patterns are due to direct predation on ungulates (density mediated indirect effects) or to the indirect effect of wolves on deer foraging behavior (trait mediated indirect effects) continues to be hotly debated (Ripple and Beschta 2004, Beyer et al. 2007, Creel and Christianson 2009, Kaufmann et al. 2010) and is beyond the scope of this study. We suspect, however, that density mediated indirect effects may be unlikely given that the current Wisconsin wolf population, which has grown to ~690 individuals (Wydeven and Wiedenhoeft 2010), has the capacity to take only ~12,000 deer per year. There are an estimated 390,000 deer in the Northern Forests of Wisconsin (posthunt), so region-wide effects of wolf recovery on deer populations are unlikely to manifest in the short term. Trait mediated indirect effects may be the more likely mechanism responsible for higher density and diversity of woody stems in high impact wolf areas.

Unfortunately, reciprocal relationships between wolves, deer and vegetation are still lacking. At present, deer data is available for the past several decades, but only at the very coarse scale of deer management blocks (WiDNR 2009). Since most low and high wolf impact areas in our study were within the same deer management unit, existing deer data was not ideal for the scale of this study. Future research should focus on monitoring deer abundance and/or foraging behavior concurrent with wolf occupancy and vegetation response.

Future research should also explicitly examine whether the response of deer to wolf recovery is behavioral or numerical. If deer response to wolf recovery is purely behavioral, it is possible that the presence of wolves simply alters the pattern of browsing intensity experienced by plant communities across the landscape. By increasing browsing pressure in the buffer zones between packs and reducing browsing pressure within pack territory extents, wolves may have an overall neutral impact on regional biodiversity. Alternatively, by providing refugia from deer, wolves may prevent local extinctions of rare and browse sensitive plant species.

The loss of wolves as a keystone predator has contributed to a less desirable state for understory plant communities in northern white-cedar wetlands. Our data suggests that the recovery of wolves in northern Wisconsin can partially reverse this trend, at least in specific community types where wolf packs have been continuously present for at least 8 years. Our results provide compelling correlative evidence of top-down trophic effects generated by the recovery of Wisconsin's wolf population.

The methods employed here can be used to predict long-term, region-wide effects of reintroducing top predators to other terrestrial systems. In addition, the spatially hierarchical sampling design developed to analyze wildlife census data in conjunction with vegetation data provides a template for addressing other broad scale ecological impacts. Regardless of the process in question, multi-scale approaches allow us to determine the scale at which a pattern becomes detectable. The ability to detect such signals above the ambient noise of ecological variation is essential to understanding the relationship between pattern and process.

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Appendix

Species Name	Growth form	
Athyrium filix-femina var. angustum	Fern	
Botrychium virginianum	Fern	
Dryopteris carthusiana	Fern	
Dryopteris cristata	Fern	
Dryopteris intermedia	Fern	
Gymnocarpium dryopteris	Fern	
Onoclea sensibilis	Fern	
Osmunda cinnamomea	Fern	
Osmunda claytoniana	Fern	
Osmunda regalis var. spectabilis	Fern	
Phegopteris connectilis	Fern	
Pteridium aquilinum var. latiusculum	Fern	
Fern Count		12
Equisetum arvense	Fern Ally	
Equisetum sylvaticum	Fern Ally	
Huperzia lucidula	Fern Ally	
Lycopodium annotinum	Fern Ally	
Lycopodium dendroideum	Fern Ally	
Fern Ally Count		5
Actaea rubra	Forb	
Anemone quinquefolia	Forb	
Apocynum androsaemifolium	Forb	
Aralia nudicaulis	Forb	
Aralia racemosa	Forb	
Arisaema triphyllum ssp. triphyllum	Forb	
Aster ciliolatus	Forb	
Aster macrophyllus	Forb	
Caltha palustris	Forb	
Campanula aparinoides	Forb	
Chelone glabra	Forb	
Chrysosplenium americanum	Forb	
Cicuta maculata	Forb	
Circaea alpina subsp. alpina	Forb	
Cirsium muticum	Forb	
Clintonia borealis	Forb	
Comarum palustre	Forb	
Coptis trifolia var. groenlandica	Forb	
Corallorhiza striata	Forb	
Corallorhiza trifida	Forb	
Cornus canadensis	Forb	
Cypripedium acaule	Forb	
Cypripedium candidum	Forb	
Cypripedium parviflorum	Forb	
Doellingeria umbellata	Forb	
Echinocystis lobata	Forb	
Epilobium ciliatum	Forb	
Epilobium coloratum	Forb	
Eupatorium maculatum	Forb	
Fragaria virginiana	Forb	

Species Name	**Growth form**
Galium tinctorium	Forb
Galium trifidum	Forb
Galium triflorum	Forb
Gaultheria hispidula	Forb
Gaultheria procumbens	Forb
Geum rivale	Forb
Goodyera repens	Forb
Impatiens capensis	Forb
Iris versicolor	Forb
Laportea canadensis	Forb
Linnaea borealis	Forb
Listera cordata	Forb
Lycopus americanus	Forb
Lycopus uniflorus	Forb
Lysimachia thyrsiflora	Forb
Maianthemum canadense	Forb
Maianthemum trifolium	Forb
Malaxis monophyllos var. brachypoda	Forb
Menyanthes trifoliata	Forb
Mitchella repens	Forb
Mitella diphylla	Forb
Mitella nuda	Forb
Moneses uniflora subsp. Uniflora	Forb
Monotropa hypopithys	Forb
Monotropa uniflora	Forb
Oxalis montana	Forb
Packera aurea	Forb
Platanthera clavellata	Forb
Platanthera obtusata	Forb
Polygala paucifolia	Forb
Polygonatum biflorum	Forb
Polygonatum pubescens	Forb
Polygonum arifolium	Forb
Polygonum cilinode	Forb
Prenanthes alba	Forb
Prunella vulgaris	Forb
Pyrola asarifolia subsp. asarifolia	Forb
Pyrola secunda	Forb
Ranunculus abortivus	Forb
Ranunculus acris	Forb
Ranunculus hispidus var. nitidus	Forb
Ranunculus recurvatus var. recurvatus	Forb
Rubus pubescens	Forb
Saxifraga pensylvanica	Forb
Scutellaria galericulata	Forb
Scutellaria lateriflora	Forb
Solidago uliginosa	Forb
Streptopus lanceolatus var. longipes	Forb
Symphyotrichum puniceum	Forb
Symplocarpus foetidus	Forb
Thalictrum dioicum	Forb

Species Name	**Growth form**	
Toxicodendron radicans var. negundo	Forb	
Trentalis borealis	Forb	
Trillium cernuum	Forb	
Vaccinium oxycoccos	Forb	
Viola blanda var. palustriformis	Forb	
Viola macloskeyi subsp. pallens	Forb	
Viola renifolia	Forb	
Waldsteinia fragarioides	Forb	
Forb Count		89
Brachyelytrum erectum	Grass	
Cinna latifolia	Grass	
Poa palustris	Grass	
Calamagrostis canadensis	Grass	
Oryzopsis asperifolia	Grass	
Bromus ciliatus L.	Grass	
Elymus hystrix var. hystrix	Grass	
Grass Count		7
Cirsium palustre	Non-native	
Hieracium aurantiacum	Non-native	
Taraxacum officinale	Non-native	
Veronica officinalis	Non-native	
Non-native Count		4
Luzula acuminata var. acuminata	Rush	
Rush Count		1
Carex arctata	Sedge	
Carex brunnescens	Sedge	
Carex communis	Sedge	
Carex crinita	Sedge	
Carex deflexa	Sedge	
Carex disperma	Sedge	
Carex interior	Sedge	
Carex intumescens	Sedge	
Carex leptalea	Sedge	
Carex leptonervia	Sedge	
Carex pedunculata	Sedge	
Carex pennsylvanica	Sedge	
Carex projecta	Sedge	
Carex scoparia	Sedge	
Carex stipata	Sedge	
Carex trisperma	Sedge	
Sedge Count		16
Abies balsamea	Tree	
Acer rubrum	Tree	
Acer saccharum	Tree	
Acer spicatum	Tree	
Betula alleghaniensis	Tree	
Betula papyrifera	Tree	
Fraxinus nigra	Tree	
Fraxinus pennsylvanica	Tree	
Larix laricina	Tree	
Picea glauca	Tree	

Species Name	Growth form	
Picea mariana	Tree	
Pinus strobus	Tree	
Populus tremuloides	Tree	
Prunus virginiana	Tree	
Quercus bicolor	Tree	
Quercus macrocarpa var. macrocarpa	Tree	
Quercus rubra	Tree	
Sorbus americana	Tree	
Sorbus decora	Tree	
Thuja occidentalis	Tree	
Tilia americana var. americana	Tree	
Tsuga canadensis	Tree	
Ulmus americana	Tree	
Tree Count		23
Acer spicatum	Shrub	
Alnus incana ssp. rugosa	Shrub	
Amelanchier sp. 1	Shrub	
Cornus stolonifera	Shrub	
Corylus americana	Shrub	
Corylus cornuta	Shrub	
Diervilla lonicera	Shrub	
Ilex mucronata	Shrub	
Ilex verticillata	Shrub	
Kalmia polifolia	Shrub	
Ledum groenlandicum	Shrub	
Lonicera canadensis	Shrub	
Lonicera oblongifolia	Shrub	
Lonicera villosa	Shrub	
Rhamnus alnifolia	Shrub	
Ribes americanum	Shrub	
Ribes americanum	Shrub	
Ribes cynosbati	Shrub	
Ribes glandulosum	Shrub	
Ribes hirtellum	Shrub	
Ribes hudsonianum	Shrub	
Ribes hudsonianum	Shrub	
Ribes lacustre	Shrub	
Ribes triste	Shrub	
Rubus idaeus	Shrub	
Sambucus sp. 1	Shrub	
Vaccinium angustifolium	Shrub	
Vaccinium myrtilloides	Shrub	
Vaccinium myrtilloides	Shrub	
Vaccinium oxycoccos	Shrub	
Viburnum opulus	Shrub	
Shrub Count		31
Parthenocissus quinquefolia	Vine	
Toxicodendron radicans subsp. negundo	Vine	
Vine Count		2
Grand Count		190