

Recolonizing wolves trigger a trophic cascade in Wisconsin (USA)

Ramana Callan^{1*}, Nathan P. Nibbelink², Thomas P. Rooney³, Jane E. Wiedenhoeff⁴ and Adrian P. Wydeven⁴

¹State University of New York College of Environmental Science and Forestry, Box 37, Wanakena, NY 13695, USA;

²Warnell School of Forestry and Natural Resources, The University of Georgia, 180 E. Green Street, Athens, GA 30602, USA; ³Department of Biological Sciences, Wright State University, 3640 Colonel Glenn Hwy, Dayton, OH 45435, USA; and ⁴Wisconsin Department of Natural Resources, 875 S 4th Street, Park Falls, WI 54552, USA

Summary

1. We tested the hypothesis that wolves are reducing local browse intensity by white-tailed deer, thus indirectly mitigating the biotic impoverishment of understorey plant communities in northern Wisconsin.

2. To assess the potential for such a top-down trophic cascade response, we developed a spatially and temporally explicit model of wolf territory occupancy based on three decades of wolf monitoring data. Using a nested multiscale vegetation survey protocol, we compared the understorey plant communities of northern white cedar wetlands found in high wolf areas with control sites found in low wolf areas.

3. We fit species–area curves for 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.

4. As predicted for a trophic cascade response, forb species richness at local scales (10 m²) was significantly higher in high wolf areas (high wolf areas: 10.7 ± 0.9 , $N = 16$, low wolf areas: 7.5 ± 0.9 , $N = 16$, $P < 0.001$), as was shrub species richness (high wolf areas: 4.4 ± 0.4 , $N = 16$, low wolf areas: 3.2 ± 0.5 , $N = 16$, $P < 0.001$). Also as predicted, percentage cover of ferns was lower in high wolf areas (high wolf areas: 6.2 ± 2.1 , $N = 16$, low wolf areas: 11.6 ± 5.3 , $N = 16$, $P < 0.05$).

5. Beta richness was similar between high and low wolf areas, supporting earlier assumptions that deer herbivory impacts plant species richness primarily at local scales. Sampling at multiple spatial scales revealed that changes in species richness were not consistent across scales nor among vegetation growth forms: forbs showed a stronger response at finer scales (1–100 m²), while shrubs showed a response across relatively broader scales (10–1000 m²).

6. *Synthesis.* Our results are consistent with hypothesized trophic effects on understorey plant communities triggered by a keystone predator recovering from regional extinction. In addition, we identified the response variables and spatial scales appropriate for detecting such differences in plant species composition. This study represents the first published evidence of a trophic cascade triggered by wolf recovery in the Great Lakes region.

Key-words: biodiversity, determinants of plant community diversity and structure, grey wolf (*Canis lupus*), herbivory, Northern White Cedar (*Thuja occidentalis*), species–area relationship, trophic cascades, vegetation dynamics, white-tailed deer (*Odocoileus virginianus*), Wisconsin

Introduction

Indirect interactions between carnivores and plants, mediated by herbivores, are commonly referred to as trophic cascades

(Paine 1980; Carpenter, Kitchell & Hodgson 1985). Such interactions are frequently used to justify carnivore conservation, despite limited experimental evidence of trophic cascades involving large mammalian predators (Ray 2005; Ripple, Rooney & Beschta 2010). Recent attempts to infer top-down effects of predators have drawn on comparisons

*Correspondence author. E-mail: rcallan@esf.edu

across areas with and without predators (Berger *et al.* 2001; Terborgh *et al.* 2006), or correlative studies of vegetation response following predator reintroduction (Ripple & Beschta 2012). One of the most well-known examples of a terrestrial trophic cascade is the wolf (*Canis lupus*)/moose (*Alces alces*)/balsam fir (*Abies balsamea*) system on Isle Royale (McLaren & Peterson 1994). Despite its historical significance, cause and effect in the Isle Royale system remains speculative due to the studies' correlative nature and lack of replication or comparable control sites (Eberhardt 1997; Schmitz, Hamback & Beckerman 2000).

In addition, 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 the productivity of one or occasionally several plant species (McLaren & Peterson 1994; Berger *et al.* 2001; Ripple & Beschta 2012), but failed to test whether predator manipulations affect species composition and diversity of entire plant communities. It has been argued that terrestrial cascades are principally species-level phenomena, due to comparatively nonlinear food-web structure, trophic complexity and effective plant defence mechanisms (Halaj & Wise 2001). However, recent evidence from experimental manipulations of herbivores and carnivores in old field ecosystems suggests that predators in terrestrial systems have much stronger effects on plant species diversity than on plant biomass (Schmitz 2006). Furthermore, it is these changes in plant community composition that influence ecosystem properties.

Ecological processes (including trophic cascades) are likely to manifest differentially over a range of spatial and temporal scales (Levin 1992; Polis 1999; Bowyer & Kie 2006). 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 & 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 & Scheffer 2005). Habitat refugia combined with spatial and temporal variability in species' distributions allow prey to escape predation (Halaj & Wise 2001), potentially creating a mosaic of cascade intensity across the landscape.

The impacts of hyperabundant white-tailed deer (*Odocoileus virginianus*) populations on understorey plant community structure and composition are well-established (Alverson, Waller & Solheim 1988; Tilghman 1989; Peek & Stahl 1997; Crete 1999; Rooney 2001; Rooney & Waller 2003; Horsley, Stout & deCalesta 2003; Rooney *et al.* 2004; Holmes, Curran & Hall 2008). However, few studies have examined how the recovery of wolves might moderate these effects. Recent studies of species interactions in Yellowstone National Park (YNP) suggest that the recovery of wolf populations can naturally ameliorate ungulate-caused ecosystem simplification (White & Garrott 2005; Ripple & Beschta 2012). In this study, we examine whether a similar trophic cascade was

triggered by the recovery of the Great Lakes wolf population in northern Wisconsin. In addition, by assessing community-level responses as opposed to species-level responses and by measuring across several spatial scales of observation, we hope to inform future research by identifying the ideal response variable and spatial scale for detecting effects of top predators in similar terrestrial systems.

Ecological setting

Unlike in Yellowstone, where elk (*Cervus elaphus*) are the primary prey species of grey wolves, wolves in the Great Lakes region prey mainly on white-tailed deer. Wolves were nearly eradicated from the region during the early part of the 20th century. However, the wolf population in neighbouring Minnesota was never fully extirpated and began to recover under the protection of the Endangered Species Act. Dispersing wolves from Minnesota (and possibly Canada) first began to arrive in Wisconsin in the mid-1970s. The Wisconsin population grew slowly for the first few decades and then began to grow almost exponentially (Wydeven, Schultz & Thiel 1995; Wydeven *et al.* 2009). 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 annually mapped all known wolf pack territories in the state since 1979. The high quality of this data set provided the information we needed to examine the spatial and temporal patterns in wolf occupancy throughout the state and thus answer the following question: Is the recovery of wolves releasing some understorey plant communities from over-browsing by white-tailed deer?

Aldo Leopold reported irruptions (abrupt population rise) of deer in Wisconsin as early as 1947 (Leopold, Sows & Spencer 1947). Based on land cover conditions, pre-settlement white-tailed deer densities in northern Wisconsin are thought to have ranged between 4 and 6 km⁻² (McCaffery 1995). The combination of predator extirpation, protective hunting laws and habitat management has contributed to current deer densities ranging between 4 and 15 km⁻² (WiDNR 2010). Densities as low as 1–2 deer km⁻² have been prescribed to improve recruitment of browse-sensitive plant species (Alverson, Waller & Solheim 1988). 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 1989). Hence, the current Wisconsin wolf population, which has grown to *c.* 690 individuals (in winter) since their placement on the endangered species list (Wydeven & Wiedenhoeft 2010), has the capacity to take *c.* 12 000 deer per year. Given the current estimated deer population of 340 000 in the Northern Forests of Wisconsin (WiDNR 2010), region-wide effects of wolf recovery on deer populations are unlikely to manifest in the short term. In addition, whether wolf kills represent primarily compensatory or additive mortality for white-tailed deer is in

part dependent on stochastic environmental variables such as winter severity (Mech & Peterson 2003). However, localized influences of wolf predation on deer populations are more probable, and drastic local herd reductions have been observed in Minnesota (Nelson & Mech 2006).

Hoskinson & Mech (1976) found higher white-tailed deer survival on the edges of wolf territories as compared to their centres. Wolves are less likely to hunt in these buffer zones so as to avoid potentially fatal encounters with neighbouring 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 & Murray 1993). Thus, buffer zones surrounding wolf pack territories may act as refugia for white-tailed deer (Mech 1994). By extension, consistently occupied wolf pack territories may act as refugia for understorey plants that are preferred by white-tailed deer.

Exclosure studies combined with resampling of historic vegetation plots from the 1950s (Curtis 1959) strongly implicate the hyperabundance of white-tailed deer as the causal factor driving local losses in plant species diversity (Rooney & Waller 2003; Rooney *et al.* 2004). This decline in rare and uncommon species is contributing to the biotic homogenization of understorey plant communities in northern Wisconsin (Frelich & Lorimer 1985; Cote *et al.* 2004; Rooney *et al.* 2004; Wiegmann & Waller 2006). Consistent with this pattern, populations of northern white cedar (*Thuja occidentalis*) have suffered region-wide recruitment failure due primarily to decades of over-browsing (Rooney, Solheim & Waller 2002).

White cedar forests are used intensively by white-tailed deer during the winter months, subjecting the highly nutritious and palatable seedlings to excessive herbivory (Habeck 1960; Van Deelen, Pregitzer & Haufler 1996). Historically, these coniferous wetlands have supported extremely diverse plant communities (Curtis 1959; Pregitzer 1990) providing habitat for a variety of rare lilies and orchids (USDA Forest Service 2004). Unique shrub and forb species restricted to conditions found in white cedar wetlands are also susceptible to over-browsing. Without recruitment to the canopy, existing mature stands of white cedar may become increasingly isolated as older stands senesce, accelerating the associated loss of understorey plant species restricted to this unique habitat type (Alverson, Waller & Solheim 1988; Cornett *et al.* 2000) via the process of 'relaxation' described by Diamond (1972).

Given that northern white cedar wetlands are very sensitive to herbivory and are heavily used by white-tailed deer, we anticipated that recovery from over-browsing would be more easily detected in these ecosystems than in other forest cover types. Thus, the tri-trophic cascade that we are testing for is comprised of wolves, white-tailed deer and understorey plant communities of northern white cedar wetlands (Fig. 1). The objective of this study was to develop species-area curves to test whether differences in plant species richness occur between high and low wolf areas (as defined by years of wolf pack occupancy).

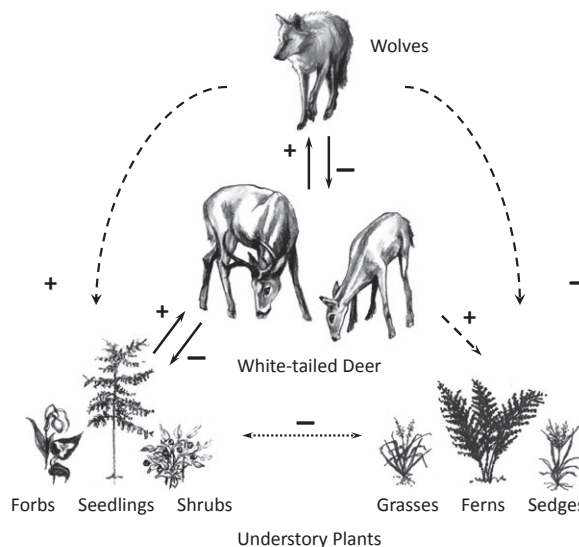


Fig. 1. Diagram of hypothesized tri-trophic interactions in northern Wisconsin forests. Solid arrows represent direct positive and negative interactions. Dashed arrows represent hypothesized indirect interactions. Dotted line represents competitive interactions.

We anticipated that understorey plants would vary in their response to release from browsing pressure dependent on the vegetation growth form in question. For example, tree seedlings, shrubs and forbs are highly preferred by white-tailed deer and collectively 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, because they are released from competition with preferred species (Stromayer & Warren 1997; Cooke & Farrell 2001; Boucher, Crête & Ouellet 2004).

Based on previous studies of deer influence on terrestrial plant communities (Frelich & Lorimer 1985; Stromayer & Warren 1997; Cooke & Farrell 2001; Rooney & Waller 2003; Boucher, Crête & Ouellet 2004; Cote *et al.* 2004; Wiegmann & Waller 2006), we predicted that high wolf areas would be subject to reduced browse pressure and thus be characterized by an increased percentage cover of forbs, shrubs and seedlings. We further expected that ferns, grasses and sedges would demonstrate the opposite response to wolf recovery (decreased percentage cover in high wolf areas). The relationship between disturbance and species diversity described by Denslow (1985) predicts that species richness of seedling, shrub and forb species should be higher at high wolf areas (since browsing pressure should be lower and closer to historic levels).

As noted previously, the spatial scale at which species respond to ecological processes is determined by the life-history traits of each species and thus likely to vary significantly. To address this issue, we measured species richness across a range of spatial scales (0.01, 1.0, 10, 100, 400 and 1000 m²). In this manner, we sought to identify the appropriate scale of measurement for detecting responses to release from

herbivory (as measured by changes in species richness) for each vegetation growth form.

Materials and methods

STUDY SITE

Data were collected throughout the Chequamegon-Nicolet National Forest, as well as from various state and county forests spanning seven counties in north-central Wisconsin (Fig. 2). The forests of northern Wisconsin are transitional between deciduous forests to the south and boreal forests to the north (Pastor & 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 & Judzewicz 2008). Mature stands of white cedar are densely shaded with nearly closed canopies. The combination of these characteristics provides 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* spp.) and honeysuckles (*Lonicera* spp.) are common understorey shrubs. Cedar wetlands are rich in sedges (e.g. *Carex disperma*, *C. trisperma*), ferns (e.g. *Dryopteris* and *Gymnocarpium* spp.) 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 'subshrubs' such as creeping snowberry (*Gaultheria hispidula*), dwarf red raspberry (*Rubus pubescens*) and twinflower (*Linnaea borealis*). Orchids include yellow lady's slipper (*Cypripedium parviflorum*), heart-leaved twayblade (*Listera cordata*), lesser rattlesnake plantain (*Goodyera repens*) and blunt-leaved bog orchid (*Platanthera obtusata*).

RESEARCH DESIGN

Wolf packs establish and occupy territories that are patchily distributed across the landscape (Mladenoff, Sickley & Wydeven 1999). The effect of wolves on deer abundance and foraging behaviour 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 radiotracking, howl surveys and winter track surveys (Wydeven, Schultz & Thiel 1995). Territory extents were delineated using minimum convex polygons based on radiolocations of collared wolves and other wolf sign (Wiedenhoef & Wydeven 2005).

Using ArcGIS, we overlaid current wolf territories with historic territory extents to delineate areas that have been continuously occupied for *c.* 10 years (high wolf areas) and areas that have essentially remained unoccupied since wolf recolonization of the region (low wolf areas). Only sites within the Chequamegon-Nicolet National Forest, state forest or county forest boundaries were selected. We used the Combined Data Systems (CDS) data for the Chequamegon-Nicolet National Forest (USDA 2001) and various state and county forest data sets 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 areas (8–10 years of recent wolf occupancy) or low wolf areas (0–3 years of recent wolf occupancy). To control for spatial autocorrelation and limit the potential for confounding variables to produce false associations, we paired high wolf sites with low wolf sites within a few kilometres (Fig. 3).

VEGETATION SURVEYS

We randomly placed 1 vegetation plot within each pre-selected white cedar stand and surveyed a total of 32 cedar stands (16 in low and 16 in high wolf areas). Fourteen plots were completed in 2008, and 18

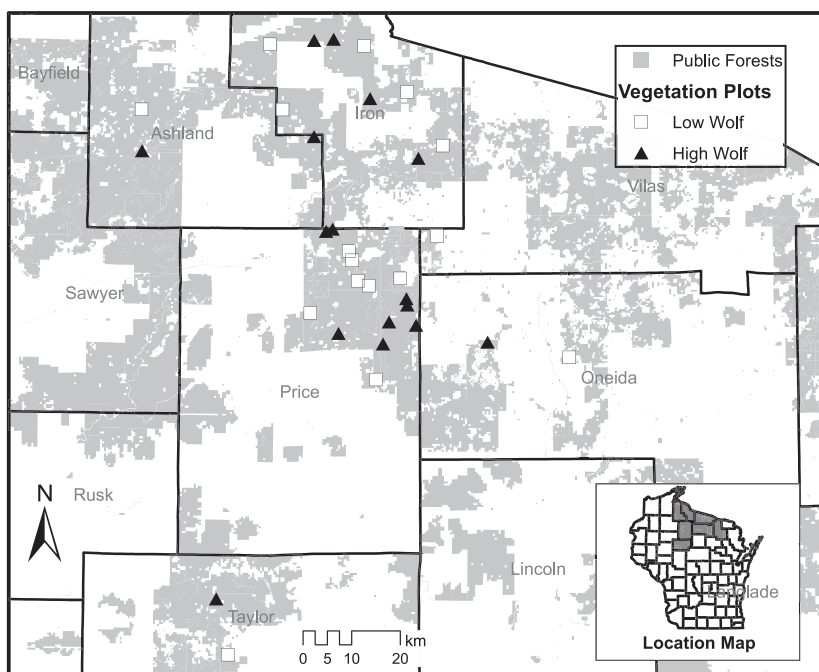


Fig. 2. Study areas in northern Wisconsin. Black triangles indicate vegetation plots located in high wolf areas. White triangles represent vegetation plots in low wolf areas.

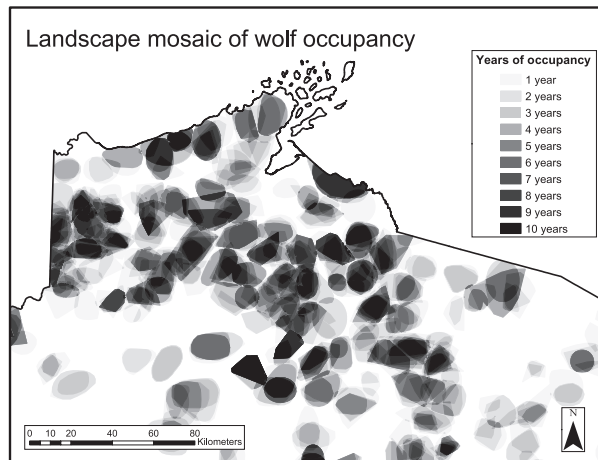


Fig. 3. Intensity of wolf impact based on 10 years (1998–2008) of wolf pack territory data (WiDNR). Years of occupancy represent the duration of wolf pack tenure. High wolf areas = 8–10 years of occupancy, low wolf areas = 0–3 years of occupancy.

plots were completed in 2009. Vegetation surveys followed the Carolina Vegetation Survey (CVS) protocol developed by Peet, Wentworth & White (1998). Plots consisted of 10 modules (10×10 m) in a 2×5 array (1000 m^2 in total). Four of the 10 modules were sampled intensively, while the remaining plots were surveyed for additional species occurrences only. Two corners in each of the intensive modules were sampled for the 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 to 10 m^2). Percentage cover data were 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 & Judziewicz (2008). All other plant species names conform to Gleason & Cronquist (1991). Due to extensive time requirements, species identification of grasses and sedges was discontinued for the second field season.

DATA ANALYSIS

Percentage 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. Student's *t*-tests were used to compare percentage plant cover between high and low wolf areas across all vegetation growth forms.

Species richness at each scale (0.01, 1.0, 10, 100, 400 and 1000 m^2) was calculated for each plot by averaging subsamples. The number of subsamples varied depending on the scale sampled ($0.01\text{--}10 \text{ m}^2$, $n = 8$, 100 m^2 , $n = 4$, and $400\text{--}1000 \text{ m}^2$, $n = 1$). Again, Student's *t*-tests were used to compare species richness between high and low wolf areas and across all vegetation growth forms and spatial scales. The multiscale nested structure of the CVS protocol also facilitates the construction of species–area curves. Species–area curves describe the rate at which species richness increases as the total area sampled increases (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 & Stohlgren 2003). The power model has an equation of the form:

$$S = cA^z \quad \text{eqn 1}$$

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:

$$\log(S) = z\log(A) + \log(c) \quad \text{eqn 2}$$

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), allows us to predict the direction and magnitude of differences in species richness. We grouped species–area curves for low and high wolf 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.

Results

PERCENTAGE COVER BY STRATA

We identified a total of 199 vascular plant species: 23 trees, 31 shrubs, 98 forbs, 12 ferns, 5 fern allies, 16 sedges, 7 grasses, 2 vines, 1 rush and 4 non-native species (see Callan 2010 for a complete list). In general, sites with high wolf occupancy had a diverse understorey community with complex vertical structure (Fig. 4a). In contrast, low wolf occupancy sites were characterized by a very limited herbaceous layer and almost no woody-browse (Fig. 4b). Some low wolf sites were characterized by an understorey dominated by ferns but still lacking in forbs, shrubs and tree seedlings.

Percentage cover of forbs was higher in high wolf areas (high wolf areas: $15.0 \pm 4.4\%$, $N = 16$, low wolf areas: $8.8 \pm 2.5\%$, $N = 16$, $P < 0.05$) as were shrub and tree seedling cover combined (high wolf areas: $11.2 \pm 4.3\%$, $N = 16$, low wolf areas: $6.1 \pm 2.1\%$, $N = 16$, $P < 0.05$), while cover of ferns was lower (high wolf areas: $6.2 \pm 2.1\%$, $N = 16$, low wolf areas: $11.6 \pm 5.3\%$, $N = 16$, $P < 0.05$) (Fig. 5). Percentage cover of grasses was equivalent in low and high wolf areas (high wolf areas: $0.50 \pm 0.22\%$, $N = 16$, low wolf areas: $0.59 \pm 0.50\%$, $N = 16$, $P = 0.32$), and sedge cover did not differ significantly (high wolf areas: 7.4 ± 4.0 , $N = 16$, low wolf areas: 4.5 ± 1.8 , $N = 16$, $P = 0.10$). Percentage tree cover was very similar between high and low wolf areas (high wolf areas: $69.9 \pm 5.7\%$, $N = 16$, low wolf areas: $71.2 \pm 7.4\%$, $N = 16$, $P = 0.39$).

SPECIES–AREA RELATIONSHIPS

When all species were included in the analysis, species–area curves in high wolf areas tended towards higher alpha richness (*c*) for all species combined (Table 1), but this difference was not significant ($P = 0.10$). Beta richness (*z*) ranged from 0.27–0.35 across all sites, but was similar between low



Fig. 4. Photo pair of understory vegetation within the Chequamegon-Nicolet National Forest, WI. (a) Shows a high wolf area (within the Bootjack Lake pack territory) and (b) shows the paired low wolf area (in the buffer zone between the Bootjack Lake pack and the Miles Lake pack).

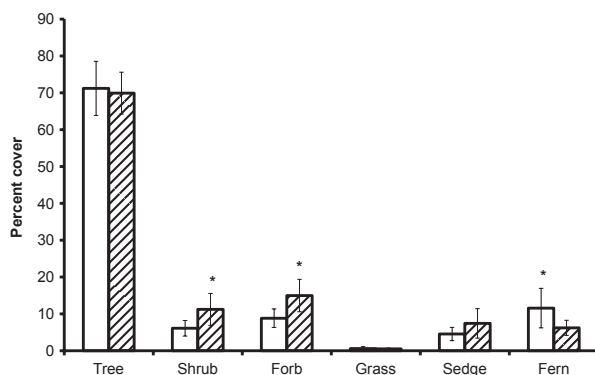


Fig. 5. Average percentage cover of high and low wolf area plots across 6 vegetation growth forms (forbs, shrubs, trees, ferns, grasses and sedges) with 95% confidence intervals. Values are averaged geometric means of cover classes (0–1%, 1–2%, 2–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–95%, 95–100%). Hatched bars represent high wolf areas. Asterisks indicate significant differences ($P < 0.05$).

and high wolf 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 areas were more pronounced (Table 1). Alpha richness of forbs was much higher in high wolf 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 areas ($P < 0.05$), and alpha richness of sedges tended to be higher in high wolf areas, but this differ-

ence was not significant ($P < 0.10$). Again, beta richness was equivalent between high and low wolf areas across all vegetation growth forms.

As predicted for a trophic response, forb species richness at local scales (10 m^2) was significantly higher in high wolf areas (high wolf areas: 10.7 ± 0.9 N, low wolf areas: 7.5 ± 0.9 , $N = 16$, $P < 0.0001$), as was shrub species richness [high wolf areas: 4.4 ± 0.4 , low wolf areas: 3.2 ± 0.5 , $N = 16$, $P < 0.001$ (Fig. 6)]. Contrary to our expectations, species richness of ferns was higher at the 10-m^2 scale (high wolf areas: 2.99 ± 0.3 , low wolf areas: 2.08 ± 0.47 , $N = 16$, $P < 0.01$). Species richness of sedges was higher in high wolf areas at the smallest spatial scale measured, 0.01 m^2 (high wolf areas: 0.47 ± 0.16 , low wolf areas: 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 areas across all scales.

Discussion

As predicted, percentage cover of forbs was 70% higher on average in high wolf areas, and species richness of forbs was 43% higher (at the 10-m^2 scale). Shrubs showed a similar pattern with 84% higher percentage cover for seedlings and shrubs grouped and 39% higher species richness for shrubs alone. Percentage cover of ferns was 47% lower in high wolf areas. Although we expected greater species richness of tree seedlings in high wolf/low deer impact sites (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 less related to browsing pressure. The nearly equivalent percentage tree cover between high and low wolf areas eliminates the possibility that differences in light availability are responsible for the observed differences in percentage cover of the lower strata.

The similarity in percentage cover of grasses in high and low wolf 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 percentage cover of grass species. Almost all visual estimates of grass cover fell in the same cover class: 0–1%. This area represents *c.* 1 m^2 of a 100-m^2 module. Percentage cover of grasses and sedges may need to be estimated at finer scales than at the 100-m^2 module. Evidence does suggest that sedges may actually be more abundant in high wolf areas. It is possible that sedge species in northern white cedar swamps respond negatively to white-tailed deer grazing even though *Carex* spp. collectively have been shown to respond positively in other vegetation types (Wiegmann & Waller 2006).

The similarity in z values (beta richness) between high and low wolf areas 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

Table 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 wolf occupancy. Values in parentheses represent 95% confidence intervals

	Low wolf areas			High wolf areas		
	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

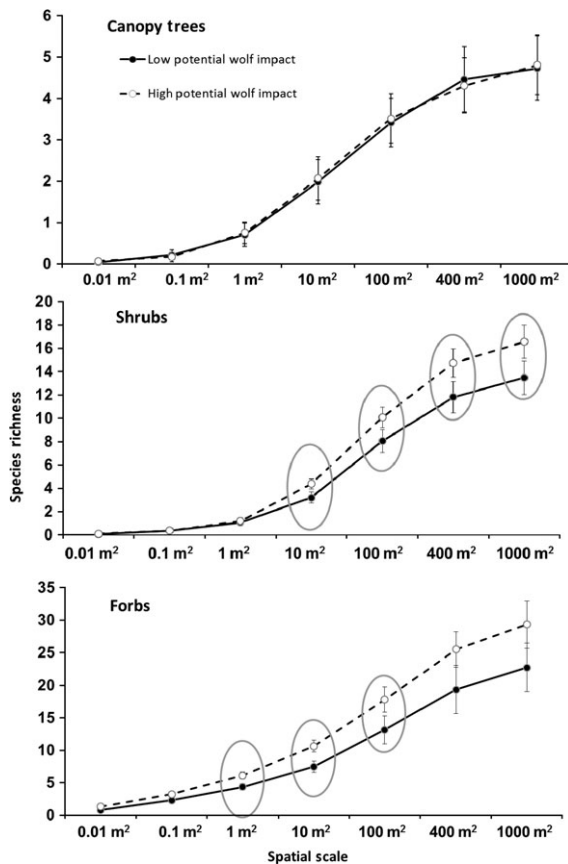


Fig. 6. Species–area curves for high and low wolf areas displayed across seven spatial scales for canopy trees, forbs and shrubs. High wolf area data points are represented by open circles and dashed lines. Data points are the mean number of species at each scale from each plot. Scales on the y-axis (number of plant species) vary depending on maximum species richness for each vegetation growth form. X-axis intervals are not to scale.

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 & White 1997; Hubbell 2001; Schnitzer & Carson 2001).

Plant species richness is determined by linked processes that act differentially across small, intermediate and large spatial scales (Schmid & Wilson 1985). Species richness at small scales ($< 1 \text{ m}^2$) is a consequence of direct competition and niche relations (variability in resource utilization and allocation). At intermediate scales ($1\text{--}100 \text{ m}^2$), species richness is more a consequence of microhabitat heterogeneity promoting the coexistence of species with different habitat requirements. At scales beyond 100 m^2 , species richness is more likely determined by immigration of seeds from source habitats ('mass effect' dynamics, Schmid & 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). Had we surveyed at scales $< 1000 \text{ m}^2$, we might expect a point at which species richness between high and low wolf areas would converge. However, patch occupancy of cedar stands and metapopulation dynamics 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 areas.

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 finer scales ($1\text{--}100 \text{ m}^2$), while shrubs show a response across broader scales ($10\text{--}1000 \text{ m}^2$). 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 1 m^2 , which is likely to miss significant differences in shrub species richness. Whether these scales are appropriate for community types other than 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 similar regardless of forest cover type.

Unfortunately, reciprocal relationships between trophic levels, like those found by McLaren & Peterson (1994) between wolves, moose and balsam fir on Isle Royale, are lacking in Wisconsin. At present, deer data are available for the past several decades, but only at the very coarse scale of deer management blocks (WiDNR 2010). Since most low and high wolf areas in our study were within the same deer man-

agement unit, we considered existing deer data to be unsuitable for the scale of this study. Future research should focus on monitoring deer abundance and/or foraging behaviour 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 pattern that we documented. In particular, road density has been shown to be negatively correlated with both plant diversity (Findlay & Houlihan 1997; Watkins *et al.* 2003) and wolf habitat selection (Mladenoff *et al.* 1995). In addition, understorey vegetation in white cedar stands may be more influenced by hydrology and edge effects than by trophic effects. Landscape-level connectivity between cedar stands is likely to influence mass effects. A bottom-up effect could also be responsible for observed patterns. Areas with high plant 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 and bottom-up effects is needed.

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 control sites ($n = 16$). We also identified species richness of forbs and shrubs in northern white cedar wetlands as ideal community-level responses for detecting trophic cascades involving wolves and white-tailed deer in the boreal forests of the Great Lakes region.

The spatially hierarchical sampling design we developed to analyse 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.

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. Our results indicate that wolf recovery in other regions of North America (such as the northeastern United States) could be vital to maintaining the ecological integrity of northern white cedar wetlands (and potentially other temperate and boreal forest systems as well). Whether efforts should be focused on reintroducing wolves or on increasing the connectivity between existing wolf populations and unoccupied wolf habitat should be carefully considered.

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