6-11-2019

Press-pulse odocoileus Virginianus herbivory in relict tsuga canadensis stands in the Western Upper Peninsula of Michigan, USA

Grace Parikh
Michigan Technological University, glparikh@mtu.edu

Christopher R. Webster
Michigan Technological University, cwebster@mtu.edu

Recommended Citation

forests

MDPI

Article

Press-Pulse *Odocoileus Virginianus* Herbivory in Relict *Tsuga Canadensis* Stands in the Western Upper Peninsula of Michigan, USA

Grace L. Parikh * and Christopher R. Webster

Ecosystem Science Center, School of Forest Resources and Environmental Science,
Michigan Technological University, Houghton, MI 49931, USA; cwebster@mtu.edu
* Correspondence glparikh@mtu.edu; Tel.: +1-906-487-3437

check for updates

Abstract: Ungulate herbivory occurring within a forest plant community's natural range of variation may help maintain species diversity. However, acute or chronically elevated levels of herbivory can produce dramatic changes in forest communities. For example, chronically high levels of herbivory by white-tailed deer (*Odocoileus virginianus* Zimmerman) in regions of historically low abundance at northern latitudes have dramatically altered forest community composition. In eastern hemlock (*Tsuga canadensis* L. Carrière) stands where deer aggregate during winter, high deer use has been associated with a shift towards deciduous species (i.e., maples [*Acer* spp.]) dominating the regeneration layer. Especially harsh winters can lead to deer population declines, which could facilitate regeneration of species that have been suppressed by browsing, such as hemlock. To enhance our understanding of how fluctuations in herbivory influence regeneration dynamics, we surveyed regeneration and deer use in 15 relict hemlock stands in the western Upper Peninsula of Michigan in 2007 and again in 2015. With the exception of small seedlings (0.04–0.24 m height), primarily maples whose abundance increased significantly ($p < 0.05$), we observed widespread significant declines ($p < 0.05$) in the abundance of medium ($0.25 \leq 1.4$ m height) and large regeneration (>1.4 m tall ≤ 4 cm diameter at breast height) over the study period. Midway through our study period, the region experienced a high severity winter (i.e., "polar vortex") which resulted in a substantial decline in the white-tailed deer population. Given the dominance of maples and dearth of hemlock in the seedling layer, the decline in the deer population may fail to forestall or possibly hasten the trend towards maple dominance of the regeneration layer as these stands recover from pulses of acute herbivory associated with high-severity winters and the press of chronically high herbivory that precedes them.

Keywords: browse; eastern hemlock; hemlock-northern hardwoods; regeneration; understory; white-tailed deer; winter severity

1. Introduction

The consequences of ungulate herbivory for individual plants and plant populations are not uniform among species, often resulting in clear "winners" and "losers" [1]. The response of a species to browsing is influenced by its relative palatability [2], ability to re-sprout and replace lost tissue [3], initial abundance [4], seasonal abundance in relation to animal movements [4–6], and response to indirect effects of herbivory such as altered nutrient and competitive dynamics [7–10]. Species-specific responses, especially among regenerating trees, can have long lasting consequences that alter historic developmental trajectories [11,12] and "ricochet" across trophic levels [13].

Ungulate herbivory has often been characterized as either chronic or acute depending on the duration of impact relative to some baseline co-evolved level [2]. Herbivory within the natural range of

variation of the baseline may foster plant species diversity, for example, by reducing the abundance of palatable but highly competitive species [14]. This chronic-acute framework conceptually is similar to the press-pulse framework used to describe the influence of climate trends and extreme weather events on biological systems [15]. This framework recognizes that most organisms are adapted to short- and long-term climate variability, but as the underlying trend changes the threshold between survivable events and extinction extremes is crossed more frequently [15]. An advantage of this framework is that it recognizes the coupling of slow and fast drivers of change.

Adapting this terminology to ungulate browsing systems could help to integrate fast and slow drivers of plant community change as well as the shifting nature of the underlying relationship. To this end, the "press" of herbivory would represent the near constant strain on plant communities from consistently elevated ungulate populations (i.e., chronic herbivory). Pulse herbivory events would represent acute periods of intense herbivory, such as those associated with periodic irruptions in ungulate populations following introduction/reintroduction or predator removal [16–20], as well as similarly rapid reproductive or aggregative numerical responses to shifting resource availability [21]. Pulse herbivory can produce dramatic changes in forest vegetation of varying importance and duration, depending on its cause and timing relative to other disturbances [17,18]. The consequences of a pulse event, which might be extended to include sudden reductions in ungulate abundance, are likely influenced by the cumulative effects of the press, as in the press-pulse climate framework, on plant community composition and ecosystem function. It would follow then that the likelihood of species loss or a plant community shifting to an alternate state or trajectory in response to a pulse event would be influenced by the duration and strength of the press of chronic herbivory.

A press-pulse analogy may be particularly suited to ungulate populations that have expanded their ranges in response to climate change, or whose populations and impacts on plant communities may be influenced by increasingly erratic weather patterns under global change [15]. For example, white-tailed deer (*Odocoileus virginianus* Zimmerman) populations in northern latitudes have increased in response to milder winters [22,23] and anthropogenic alterations to historically forested landscapes [24,25]. These populations are often 2–10 times presettlement estimates [26] and have had profound influences on forest regeneration and composition [2,11]. Nevertheless, extreme weather events, especially at higher latitudes, such as "polar vortices," can result in large reductions in population size as a result of starvation and reduced reproductive output by surviving females [27,28].

One consequence of the press of chronically elevated white-tailed deer abundance in the Upper Great Lakes region has been the increasing "mapleization" (i.e., sugar maple [*Acer saccharum* Marshall] and red maple [*Acer rubrum* L.]) of coniferous forest types, especially those historically dominated by eastern hemlock (*Tsuga canadensis* L. Carrière) [11,12,29]. Eastern hemlock, which is considered a foundation species because of its disproportionate influence on plant community composition, ecosystem processes, and wildlife populations [30,31], occurs at less than 1 to 10% of its presettlement abundance across the region largely as a result of unregulated harvesting and slash fires during the "cut-over" of the region during the late 1800s and early 1900s, changes in disturbance regimes, and silvicultural practices that favor more economically valuable species [32]. In deep snow zones, eastern hemlock provides important winter habitat for migratory white-tailed deer [33,34]. Concentrated seasonal use of these stands was first identified as a potential bottleneck for regeneration as regional deer populations began to rebound in the 1930s [16]. Given the regional decline in hemlock abundance and high levels of deer abundance that have persisted for nearly a century, contemporary levels of deer herbivory are likely in excess of the co-evolved baseline for the system. Hemlock regeneration failures have been documented in stands where deer overwinter, due to its high palatability [35], its comparatively poor ability to withstand and recover from herbivory in shaded understories [3], and a myriad of indirect effects, including changes in microsite and nutrient dynamics associated with concentrated seasonal use and increasing abundance of maple species [5,9,12,36–38]. The failure of this species to regenerate is particularly striking since evidence from pollen studies in old-growth forest remnants suggest that eastern hemlock had maintained canopy dominance on those sites since its

post-glacial colonization of the region [39]. Hemlock stands provide localized areas of reduced snow depth, thermal cover, and forage [12,32,33], making them important winter refugia during periods of deep, persistent snowpack. The attrition of hemlock-dominated winter refugia will likely have important implications for white-tailed deer populations in northern Michigan and throughout the Upper Great Lakes region [40].

We sought to examine regeneration in relict eastern hemlock stands in the western Upper Peninsula of Michigan over a nine-year period to further clarify local factors that may contribute to winter deer use and mapleization. During this period, the region experienced a series of high-severity winters, including an extreme "polar vortex" during which temperatures reached $-32.8\ °C$ [41,42] and seasonal snowfall totals reached 513 cm [43], compared to the regional long-term average snowfall of 356 cm year^{-1} [44]. This weather event was followed by a substantial white-tailed deer die-off and reduced reproductive output [45]. We capitalized on these exogenous events to examine how abrupt fluctuations in ungulate abundance influence developmental trajectories of forests. We hypothesize that in contrast to chronic browsing, which has been associated with an increase in maple abundance in the understory [5,11,12], acute browsing associated with reduced deer movement and concentrated use in response to high winter severity [46] would result in reduction of all but the most unpalatable species within reach of foraging deer.

2. Methods

2.1. Study Sites

Our study system was composed of 15 relict eastern hemlock stands in the western Upper Peninsula of Michigan, USA. These stands are part of a larger network of stands ($n = 39$) which have been used to monitor deer use trends [47], regeneration dynamics [12], cross boundary nitrogen subsidies [38], and resource heterogeneity [5,9]. Vegetation sampling and deer use monitoring via fecal pellet group counts began spring 2006. Our 15 stands were selected based on a stratified random sample by size class to capture the gradient in stand area. Stands ranged in area from 0.4 ha to 46.7 ha, with overstories ranging in basal area from 26.4 m^2 ha^{-1} to 59.6 m^2 ha^{-1} of which the proportion of hemlock ranged from 35.6% to 83.8% (Table 1).

Table 1. Stand attributes for 15 relict *Tsuga canadensis* stands across the western Upper Peninsula of Michigan. Overstory trees were defined as those with a diameter at breast height ≥ 4 cm. All means are reported ± 1 standard error.

Stand Area (ha)	Snow Depth (m) [†]	Basal Area (BA)	Trees ha^{-1}	%Tsuga BA	%*Tsuga* Trees ha^{-1}	Cumulative Deer Harvest km^{-2} [*]	Pellet Groups ha^{-1}		
		(m^2 ha^{-1})		(m^2 ha^{-1})			Mean	Min	Max
34.4	0.43 ± 0.05	40.5	961	53.6%	26.6%	14	126 ± 32	0	431
19.2	0.56 ± 0.03	43.4	1036	37.3%	26.0%	9	79 ± 15	0	179
29.1	0.53 ± 0.04	35.9	1058	36.7%	13.4%	9	1270 ± 167	395	2045
46.7	0.45 ± 0.03	34.3	564	57.1%	35.5%	9	1489 ± 178	323	2296
29.4	0.51 ± 0.04	43.9	475	75.4%	42.1%	9	736 ± 99	323	1364
21.8	0.48 ± 0.04	36.2	706	35.7%	14.2%	9	101 ± 29	0	323
10.6	0.48 ± 0.04	38.4	540	38.8%	11.1%	9	151 ± 29	0	323
6.5	0.41 ± 0.04	26.4	935	40.2%	31.0%	4	210 ± 58	0	538
38.8	0.41 ± 0.04	39.4	578	53.1%	35.1%	4	190 ± 37	162	359
18.3	0.40 ± 0.04	43.9	425	51.3%	35.3%	4	331 ± 88	36	1130
0.5	0.50 ± 0.04	55.6	675	65.6%	48.1%	9	301 ± 83	0	861
0.4	0.44 ± 0.03	42.8	508	79.5%	72.1%	9	280 ± 65	0	646
1.4	0.47 ± 0.04	48.8	342	83.8%	78.1%	4	65 ± 26	0	215
7.4	0.38 ± 0.06	43.4	995	55.3%	22.6%	6	1098 ± 158	323	938
1.7	0.41 ± 0.07	59.6	475	61.0%	64.9%	9	0.00 ± 0.00	0	0
Study-wide mean									
17.7 ± 3.9	0.46 ± 0.01	42.2 ± 2.1	685 ± 64	55.0% ± 4.1	37.1% ± 5.4	7.3 ± 0.7	428 ± 124	104 ± 40	777 ± 176

[†] Average annual snowpack depth derived from SNODAS [48] for the period November 15 to April 15. [*] Cumulative harvest 2005–2018 (all sexes) as reported by the Michigan Department of Natural Resources for the Deer Management Unit (DMU) in which the stand is located.

Latitudes for our subset of stands ranged from 46°10′ to 47°21′ N, and their longitudes ranged from 88°5′ to 90°5′ W. The climate is continental with a strong "lake effect" resulting in greater snowfall closer to Lake Superior [49]. Since study inception, mean winter snow depth (15 Nov–15 Apr) has been 0.46 ± 0.01. Mean winter snow depth at each stand has ranged from a low of 6.9 cm ± 3.9 cm to a high of 78.1 cm ± 20.5 cm [48]. Snowfall totals over the study period ranged from 124.5 to 793 cm year^{-1} [43]. Soils were characterized by medium nutrient, acidic, loamy-sand to sand-loams [50].

In the Upper Great Lakes region, white-tailed deer congregate at high densities in response to deep snow in areas of eastern hemlock or northern white-cedar (*Thuja occidentalis* L.) forests [26,33,40]. Northern white-cedar and eastern hemlock provide high quality forage, thermal cover and interception of snow due to dense foliage. Consequently, locomotion is less energetically expensive [34,51]. Additionally, high densities of animals create a network of deeply incised trails in snow, as well as providing enhanced vigilance [52]. Annual deer use across our study stands ranged from no detectable use to 2296 pellet groups ha^{-1} (Table 1). Land ownership for these stands included the U.S. Forest Service (Ottawa National Forest), Michigan Department of Natural Resources (Porcupine Mountains Wilderness State Park and Copper Country State Forest), and Michigan Technological University (Ford Forest).

2.2. Data Collection

We quantified woody vegetation within each stand on 3–9 randomly located sample plots (total $n = 97$), the number of which was determined based on stand area [12]. These plots were established in 2005 and sampled by Witt and Webster [12] in 2006 for overstory (woody stems ≥ 4 cm diameter at breast height (dbh), 1.37 m) and 2007 for understory (woody stems < 4 cm dbh) vegetation. In 2015, we resampled all of the plots in these stands using the same methodology as the original survey. Each vegetation plot consisted of a circular overstory plot and nested array of regeneration belt transects. Subplot dimensions were as follows: overstory (stems ≥ 4 cm dbh), 400 m^2 circular plot; large saplings (>1.4 m height–4 cm dbh), three 2 × 10 m belt transects; medium saplings (0.25 m–1.4 m height), three 1 × 10 m belt transects; and small saplings/seedlings (0.04–0.24 m height, three 0.1 × 10 m belt transects) [12]. Stems in our small seedling/saplings size class are below the mean winter snow depth observed for any stand over the course of our study (0.38 ± 0.06 to 0.56 ± 0.03 m; Table 1). Saplings in the medium size class are most vulnerable to winter browsing since they are not protected under the snowpack or above the reach of deer (i.e., "molar zone", [25]).

We quantified winter severity using the Wisconsin Department of Natural Resources Winter Severity Index (WSI) [53]. This index is calculated as the sum of the number of days where temperature is below −18 °C and the number of days where snowpack depth exceeds 46 cm. Snow depth data were obtained from the Snow Data Assimilation System [49], and temperature data were obtained from regional weather stations [54–56].

From 2006 to 2015, annual local deer use was estimated based on counts of fecal pellet groups in randomly located 9.29 m^2 circular plots immediately following snow melt (i.e., May). Sampling intensity was determined based on stand area, with either 5, 10, 20, or 30 plots per stand for a total of 280 plots [12]. We also used fall deer harvest data compiled by the Michigan Department of Natural Resources [57–69] as an index of regional deer abundance (by deer management unit, DMU). We calculated the annual deer (all sexes combined) harvest and the cumulative harvest 2005–2018. These data provide an estimate of the availability of deer on the landscape that might use winter yarding complexes in response to deep snow conditions.

2.3. Analytical Methods

To test for differences between sampling periods in the diversity of the seedling and sapling layers, we calculated species richness (S), Shannon's diversity index (H'), and evenness (E) for each size class at each time period [70]. These attributes were compared between time periods, using generalized linear mixed effects models [71], with year as a fixed effect and stand as a random effect, as implemented in the R statistical computing environment [72], using the package nlme [73].

Because stem density (count data) tends to be non-normally distributed and overdispersed [74], we used generalized linear mixed models to examine changes in seedling and sapling abundance between time periods, with year as a fixed effect and stand as a random effect. To identify the proper distribution, we constructed a generalized linear model for each species by size class using a Poisson distribution, and again using a negative binomial distribution [74]. We selected the best model for each species based on the generalized linear model with the lowest Akaike's information criterion (AIC). All models were fit with the *R* package msme [75]. We defined significant results as those with a *p*-value < 0.05.

3. Results

3.1. Deer Use and Abundance

We observed substantial spatiotemporal variation in deer use (Figures 1 and 2). Specifically, evidence of consistent annual deer use (10 out of 10 years) was noted in 5 stands, regular use (7–8 out of 10 years) in 8 stands, and sporadic use (3 out of 10 years) in 1 stand. We found no evidence of use in 1 stand. Mean within-stand deer use ranged from 0 ± 0 to 1489 ± 178 pellet groups ha^{-1} (Table 1).
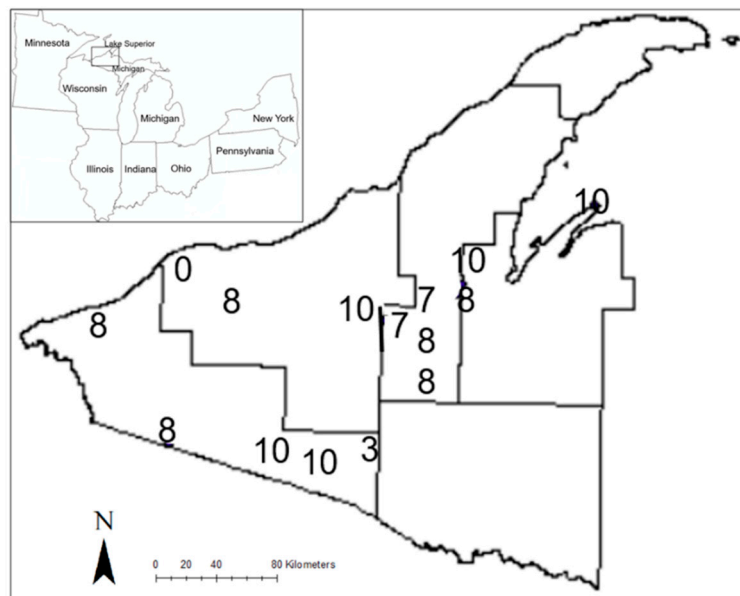

Figure 1. Frequency of use of remnant eastern hemlock (*Tsuga canadensis* L. Carrière) stands by white-tailed deer in the western Upper Peninsula of Michigan over a 10-year period (winter 2005–2006 to 2014–2015). Deer use was estimated by counting fecal pellet groups within networks of 9.29 m^2 plots randomly located within each stand. Numbers illustrate approximate stand location and number of years during which at least one pellet group was found within the plot network.

Our study period experienced periodic high-severity winters, two of which were followed by declines in deer use and hunter harvest (Figures 2 and 3). The polar vortex winter of 2013–2014 displayed the highest WSI and greatest subsequent decline in metrics of deer use and abundance. Prior to the polar vortex, mean use was 453 ± 246 pellet groups ha^{-1}. During the polar vortex, mean use was 433 ± 145 pellet groups ha^{-1}. Following the polar vortex, mean use was 151 ± 92 pellet groups ha^{-1}, and annual deer harvest declined by 76% the subsequent year (Figures 2 and 3). Both deer use and harvest levels have remained low relative to pre-vortex winters encompassed by our study. The period of low evidence of deer abundance following the polar vortex has persisted longer than other lows observed following high severity winters earlier in our chronology. It should also be noted that our index of deer use (pellet groups ha^{-1}) also tended to decline during the most severe winters. This may,

in part, reflect overwinter mortality and lower inputs of pellets as deer carcasses have been observed in these stands following these events (personal observation).
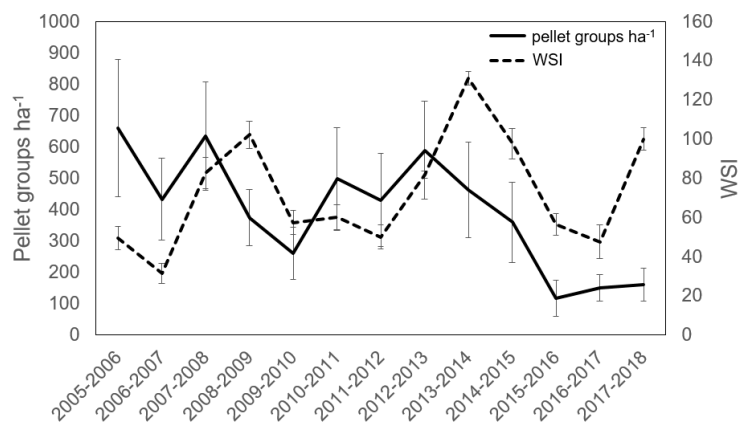

Figure 2. Mean annual deer use (pellet groups ha^{-1}) across 14 relict *Tsuga canadensis* stands where deer use was observed in the western Upper Peninsula of Michigan. Winter severity index (WSI) was calculated by summing the number of days where snow depth exceeded 46 cm and the number of days where temperature was below −18 °C [53].
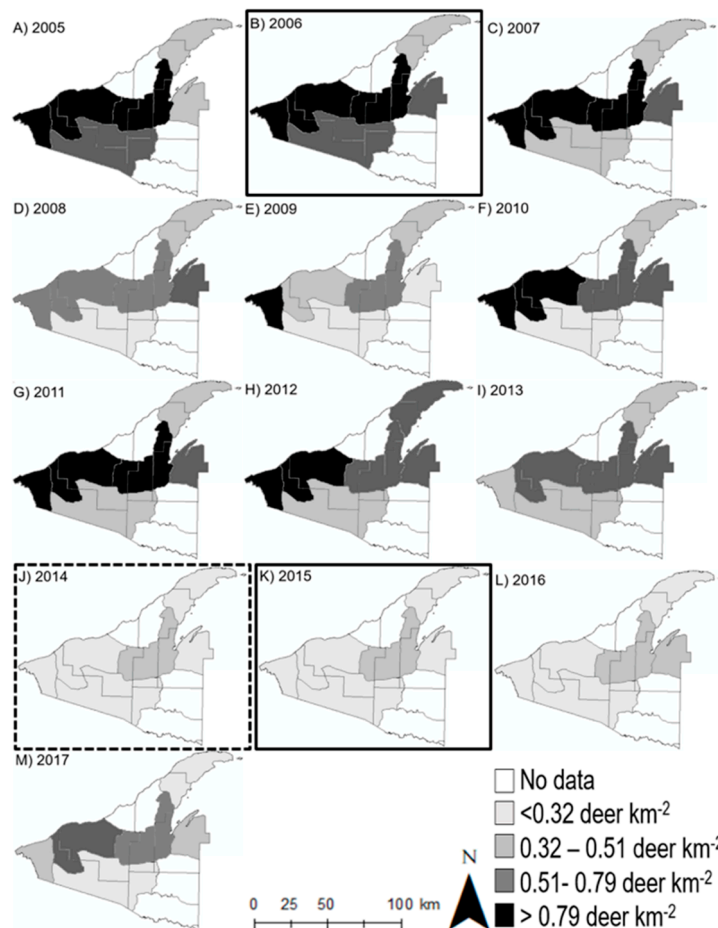

Figure 3. Spatial representation of annual white-tailed deer harvest (all sexes) by deer management unit across the western Upper Peninsula of Michigan. Vegetation sampling was conducted in 2007 and repeated in 2015 (outlined with a solid border). Winter 2013–2014 was marked by a "polar vortex", characterized by deep, persistent snowpack and extreme cold. Panel J, depicting deer harvest in the fall following the winter of the polar vortex, is framed by a dotted line.

3.2. Overstory Structure

Sample stands exhibited variability in mean overstory basal area and composition (Table 1). Eastern hemlock comprised on average 55.0 ± 4.1% of the basal area of trees ≥ 4 cm dbh, with a range from 35.7% to 83.8% (Table 1). Diameter distributions for trees ≥ 4 cm dbh showed hemlock most abundant in larger size classes, with prominent infill in smaller size classes by maples and other species (Figure 4). On average, hemlock comprised 37.1 ± 5.4% of the trees in these stands, with a range from 11.1% to 78.0% (Table 1).

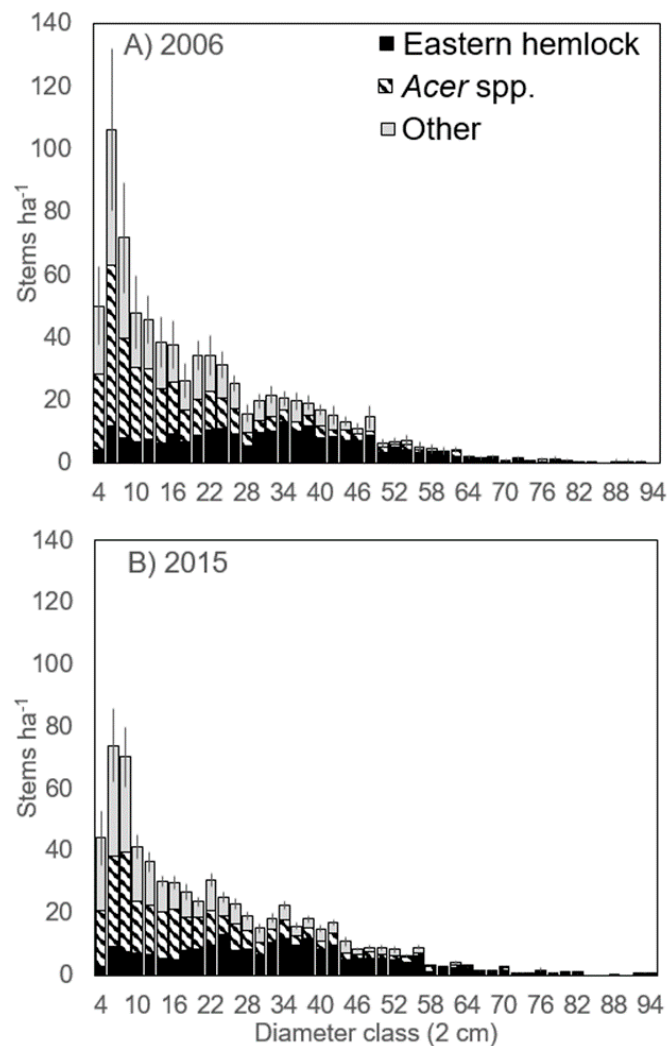**Figure 4.** Composite overstory diameter distributions for 15 relict *Tsuga canadensis* stands across the western Upper Peninsula of Michigan in (**A**) 2006 and (**B**) 2015. Error bars represent ± 1 standard error for mean total stems ha^{-1}.

3.3. Small Seedling/Saplings (0.04–0.24 m height)

The H′ and E of our smallest size class of regeneration were significantly lower in 2015 than 2007 ($p > 0.05$; Figure 5). Species richness of this size class did not vary significantly between sample periods ($p > 0.05$). Within individual stands, small regeneration of most species other than maples was less abundant during the 2015 survey, but study-wide this was offset by large increases in a few stands (Figure 6, Table 2). Consequently, on average across the 15 study stands, most species, with the exception of eastern hemlock, exhibited modest to non-significant increases in abundance (Table 2). The abundance of both small sugar and red maple, on the other hand, increased significantly between surveys ($p < 0.05$, Table 2), and was nearly uniform among stands (Figure 7).
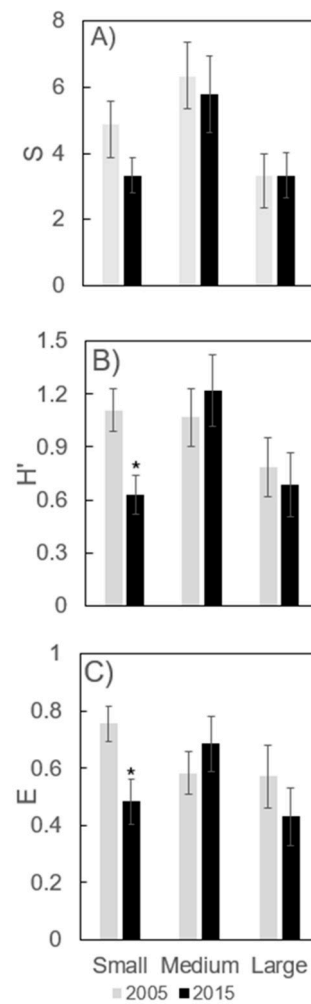
Figure 5. Comparisons of diversity indices ((**A**) species richness, S; (**B**) Shannon's diversity index, H′; (**C**) evenness, E) between 2007 and 2015 for 15 relict *Tsuga canadensis* in the western Upper Peninsula of Michigan by size class of regeneration (small: 0.04–0.24 m height; medium: 0.25–1.4 m height; large: > 1.4 m height–4 cm diameter at breast height). An asterisk (*) above a bar denotes a significant difference (α = 0.05) between time periods within a size class.
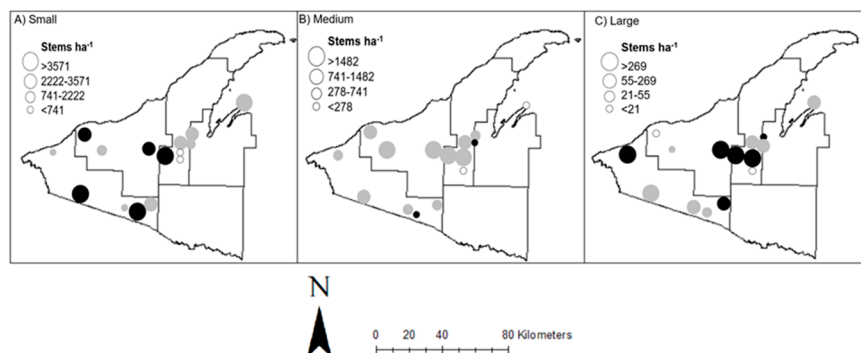

Figure 6. Spatial representation of changes in density of total regeneration (excluding maples (*Acer* spp. L.)) in 15 *Tsuga canadensis* stands from 2007 to 2015 in the western Upper Peninsula of Michigan. Black circles denote an increase in absolute density, and gray circles denote a decrease in absolute density, while an open circle denotes no change in absolute density. Regeneration size classes are as follows (**A**) small: 0.04–0.24 m height; (**B**) medium: 0.25–1.4 m height; (**C**) large: >1.4 m height–4 cm diameter at breast height.

Table 2. Absolute densities of woody regeneration in 15 *Tsuga canadensis* stands in the western Upper Peninsula of Michigan. Densities were compared using a generalized linear mixed model framework. Negative binomial distributions were used for all analyses.

Scientific Name	Common Name	Stems ha^{-1} 2007	Stems ha^{-1} 2015	% Change	*p*-Value
Small regeneration (0.04–0.24 m height)					
Abies balsamea L.	Balsam fir	632 ± 323	1088 ± 439	72%	0.07
Acer rubrum L.	Red maple	4989 ± 691	20527 ± 5721	311%	<0.001
Acer saccharum Marshall	Sugar maple	4768 ± 712	27534 ± 9851	477%	0.007
Betula alleghaniensis Britton	Yellow birch	286 ± 140	455 ± 262	59%	0.60
Tsuga canadensis L. Carrière	Eastern hemlock	1163 ± 486	924 ± 440	−21%	0.06
	Other hardwood*	1358 ± 634	2868 ± 1828	111%	0.04
	Other conifer†	49 ± 34	291 ± 192	490%	0.04
	Total (no maple)	3488 ± 989	5626 ± 1889	61%	0.03
Medium regeneration (0.25 m–1.4 m height)					
Abies balsamea L.	Balsam fir	436 ± 130	105 ± 34	−68%	<0.001
Acer rubrum L.	Red maple	438 ± 166	248 ± 116	−43%	0.08
Acer saccharum Marshall	Sugar maple	2648 ± 1291	290 ± 144	−79%	<0.001
Betula alleghaniensis Britton	Yellow birch	255 ± 205	92 ± 39	−55%	0.63
Tsuga canadensis L. Carrière	Eastern hemlock	371 ± 122	195 ± 58	−44%	0.006
	Other hardwood	1258 ± 590	556 ± 213	−56%	<0.001
	Other conifer	89 ± 37	74 ± 19	−17%	0.53
	Total (no maple)	2409 ± 767	898 ± 277	−63%	0.005
Large regeneration (>1.4 m height–4 cm dbh)					
Abies balsamea L.	Balsam fir	181 ± 100	104 ± 44	−42%	0.02
Acer rubrum L.	Red maple	43 ± 14	68 ± 29	58%	0.22
Acer saccharum Marshall	Sugar maple	209 ± 75	172 ± 110	−18%	0.05
Betula alleghaniensis Britton	Yellow birch	77 ± 46	44 ± 20	−42%	0.06
Tsuga canadensis L. Carrière	Eastern hemlock	88 ± 63	55 ± 32	−38%	0.15
	Other hardwood	97 ± 65	180 ± 122	86%	<0.001
	Other conifer	7 ± 4	17 ± 11	133%	0.08
	Total (no maple)	450 ± 210	401 ± 150	−11%	0.55

Note: means are reported ± 1 standard error. * Species in the "other hardwood" category were *Betula papyrifera* Marshall, *Fraxinus americana* L., *Fraxinus nigra* Marshall, *Ostrya virginiana* (Mill.) K. Koch, *Populus grandidentata* L., *Populus tremuloides* L., *Prunus spp.* L., *Quercus rubra* L., *Salix spp.* L., *Tilia americana* L., and *Ulmus americana* L. † Species in the "other conifer" category were *Picea glauca* (Moench) Voss, *Picea mariana* (Mill.), *Pinus strobus* L., and *Thuja occidentalis* L.
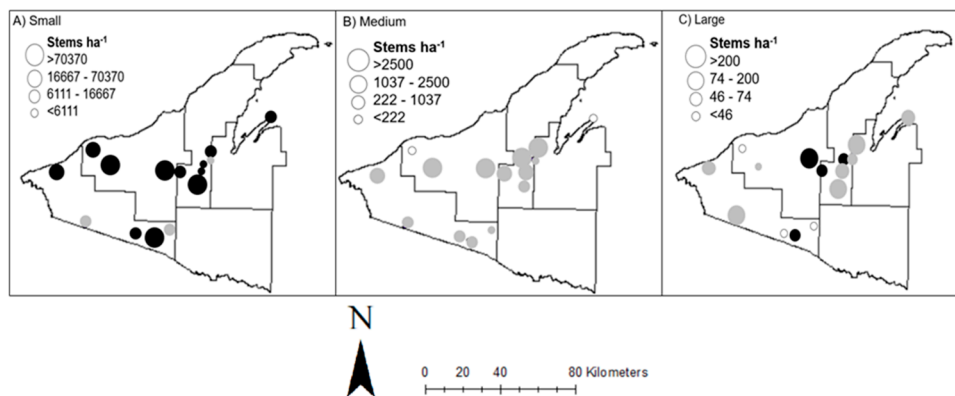
Figure 7. Spatial representation of changes in density of maple regeneration (*Acer saccharum* and *A. rubrum*) from 2007 to 2015 in 15 *Tsuga canadensis* stands from 2007 to 2015 in the western Upper Peninsula of Michigan. Black circles denote an increase in absolute density, and gray circles denote a decrease in absolute density while open circles denote no change in absolute density. Regeneration size classes are as follows (**A**) small: 0.04–0.24 m height; (**B**) medium: 0.25–1.4 m height; (**C**) large: >1.4 m height–4 cm diameter at breast height.

3.4. Medium Saplings (0.25–1.4 m height)

While there were no significant changes in the diversity indices for medium sized regeneration ($p > 0.05$; Figure 5), all species exhibited declines in abundance between sample periods, most of which were statistically significant ($p < 0.05$; Table 2). These declines in abundance were widespread across the study region for non-maples, and nearly ubiquitous for red and sugar maple (Figures 6 and 7). The greatest decline in abundance was experienced by sugar maple (79%, Table 2).

3.5. Large Saplings (>1.4 m height to 4 cm dbh)

In aggregate, diversity indices and abundance of large regeneration changed little between 2007 and 2015 (Figure 5, Table 2). Nevertheless, at the individual stand level, modest declines for most non-maple species were observed in 7 out of the 15 sample stands, which were offset by large increases in minor hardwood species in a few stands (Figure 6, Table 2). Study-wide, there was no significant change in red maple abundance ($p = 0.22$), and a marginally significant decrease in sugar maple abundance (Table 2, $p = 0.05$). At the individual stand level, fewer large sapling maples were observed in 8 of the 15 sample stands in 2015 compared to 2007 (Figure 7).

3.6. Eastern Hemlock Regeneration

The abundance of eastern hemlock regeneration in the small and medium size classes was 1–2 orders of magnitude lower than either maple species during the initial survey in 2007 (Table 2). In the 2015 survey, this disparity remained in the small size class, but was greatly reduced in the medium size class where the greatest decline in maples was observed. In the large size class, abundances of eastern hemlock and red maple were of similar magnitude in 2015 (55 ± 32 vs. 68 ± 29 stems ha^{-1}), which were both an order of magnitude less than that of sugar maple (Table 2).

4. Discussion

Our results suggest that the trend towards increasing maple dominance associated with the press of chronic herbivory in hemlock northern hardwood stands may be disrupted at least temporarily by pulses of acute herbivory. These pulses, however, may prime the system for a more rapid transition, since declines in medium-sized maple regeneration were associated with large increases in maple abundance in the small seedling/sapling layer.

Press herbivory has been associated with the differential response of the main shade-tolerant tree species in this system to browsing [3,29,37]. This is illustrated in our data by the infill of maple in the

understories of forest stands where the upper canopy layers are dominated by shade-tolerant eastern hemlock [37]. Diameter distributions clearly suggest that without intervention, demographic inertia will result in transition to hardwood dominance in stands where deer overwinter. This observation is in contrast with historic developmental trajectories [39], but consistent with contemporary observations and predictions [12,37]. For example, Salk et al. [11] estimated that hemlock stands in Sylvania Wilderness Area, Ottawa National Forest would likely transition to hardwood in 500 years barring active management, including control of hardwood reproduction. Because winter migration in response to deep snow is a learned behavior by white-tailed deer [76,77], an abrupt loss of hemlock overstory due to disturbance or arrival by the non-native hemlock woolly adelgid (*Adelges tsugae*) to northern latitudes, which is a likely consequence of climate change [78], could have important implications for migratory deer populations.

Historically, a number of mechanisms helped to maintain hemlock dominance on sites where it successfully established [39], but given the paucity of conspecific regeneration, those developmental pathways appear decreasingly viable. In particular, trends toward a warmer, drier climate have created conditions that limit hemlock seedling establishment [79]. Additionally, the logging boom of the 1800s and associated slash fires led to a proliferation of second-growth aspen (*Populus spp.* L.) and maple forest [80]. Slash fires eliminated large volumes of coarse woody debris, which altered germination microsites for hemlock. These conditions furthered regeneration of hardwood species, which produce a matted, nitrogen-rich litter layer which is more suitable to their own regeneration than that of hemlock [32]. These changes in composition, which have been perpetuated by contemporary forest management, may have far reaching implications since shifts in forest composition in response to a changing climate will in part be driven by local biotic conditions, including the availability of propagules and understory competition [81].

The influence of winter severity on white-tailed deer movement and population dynamics at northern latitudes are well-documented in the literature [33,40,46,47]. Regional declines in deer abundance following severe winters result from starvation and reduced reproductive output among surviving adult females [22,23,27,76]. Our deer pellet survey data, in conjunction with Michigan Department of Natural Resources deer harvest data, suggest two such declines occurred during our study period, one following the winter 2008–2009 and a more substantial and persistent decline following the polar vortex winter of 2013–2014. At the individual stand scale, deer pellet counts appear to track WSI during low-to moderate-severity winters; however, pellet counts during both high-severity winters were lower than the previous year. This is likely a result of lower pellet inputs due to overwinter deer mortality. Following these high-severity winters, especially the polar vortex, deer carcasses were commonly observed during spring pellet surveys. Other likely contributors to this discontinuity between pellet counts and WSI are that some stands may become less suitable habitat during extreme weather conditions, and as deer reduce their movement in an effort to conserve energy, [34] the likelihood of them encountering our plots declines.

High-severity winters, such as the polar vortex, likely result in local pulses of intense herbivory as deer restrict their travel to conserve energy. It seems likely that such a pulse occurred since work in these and other relict hemlock stands in the region had documented a positive association between deer use and deciduous sapling abundance as recently as the summer of 2008 [5,12]. Consequently, the broad reduction in the abundance of medium-sized saplings coupled with the significant increase in the abundance of small seedling/saplings are likely associated with changes in deer use patterns in response to high-severity winters. Small seedling/saplings are unavailable to overwintering deer during most winters because they are below the snowpack (mean snowpack during study period, 0.46 ± 0.01 m). High-severity winters may offer additional protection to this layer. For example, the mean snowpack depth during the polar vortex was 0.62 ± 0.08 m, which was 58% higher than the long-term average for these stands.

Regeneration dynamics following these pulsed events will depend on the rate and nature of recovery of the deer population and their interaction with climate. A rapid rebound in deer abundance

combined with moderate to high winter severity would likely prevent this cohort of seedling/sapling maples from recruiting into larger size classes. However, if deer abundance remains low and/or winter severity is not high enough to stimulate migration, then this cohort may advance unimpeded. Regardless, rather than favoring browse sensitive eastern hemlock, both scenarios may actually accelerate the transition to maple by either maintaining a suppressed maple seedling bank or relieving pressure on medium sized regeneration and releasing the suppressed seedling layer. The failure of this system to return to its previous trajectory, even when the primary stressor has been relieved, suggests it has moved toward an alternate state [4,10].

Both climate change and changes in land use have altered ecosystem disturbance regimes. In particular, shifts in intensity and frequency have altered forest successional pathways [82]. For instance, European settlement in New Zealand introduced anthropogenic fire into a previously fireless system to clear forested land for grazing. This practice eliminated topsoil, a material legacy and facilitated invasion by fire-adapted plants. Loss of legacies after a novel disturbance can erode ecological memory, and affect ecosystem resilience. As a response, novel systems are created when an ecosystem does not return to its pre-disturbance state [83].

In conclusion, our results build on a growing body of literature that suggests key foundation species, such as eastern hemlock, are increasingly imperiled by the aggregate effects of changes in abiotic and biotic stressors [30]. In many of the stands we examined, overstory hemlocks represent relicts of past trajectories as their understories become increasingly dominated by hardwood reproduction. While this shift is likely in part associated with changes in regional climate and a paucity of suitable microsites for reproduction [32,81], it has clearly been exacerbated by the press and pulse of novel levels of deer herbivory [12,37,84,85]. This trend is especially pronounced in stands with high overwintering populations of white-tailed deer [12].

5. Conclusions Management Implications

As white-tailed deer migratory traditions evolve in response to changes in winter severity and frequency of extreme events, opportunities may arise to create refugia for hemlock reproduction, especially following declines in deer abundance or changes in patterns of winter habitat use (e.g., habitat abandonment [76]). To create viable refugia, management should focus on slowing the transition to hardwood dominance in the understory, as well as discouraging deer from overwintering in stands where hemlock regeneration is currently abundant or actively being promoted. For example, mechanical control and/or scarification may be used to reduce the understory maple component and provide a better seedbed for hemlock establishment [86,87]. Harvesting should be timed to avoid providing tree tops as a food subsidy and attractant to overwintering deer. Finally, timing, location, and sex of deer harvest may also be adjusted to modify winter habitat selection and use. Without active management, this shift towards hardwoods in relict hemlock stands in the Upper Great Lakes region will likely continue to gain momentum.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Wiegmann, S.M.; Waller, D.M. Fifty years of change in northern upland forest understories: Identity and traits of "winner" and "loser" plant species. *Biol. Conserv.* **2006**, *129*, 109–123. [CrossRef]
2. Bradshaw, L.; Waller, D.M. Impacts of white-tailed deer on regional patterns of forest tree recruitment. *For. Ecol. Manag.* **2016**, *375*, 1–11. [CrossRef]
3. Anderson, R.C.; Katz, A.J. Recovery of browse-sensitive tree species following release from white-tailed deer *Odocoileus virginianus* Zimmerman browsing pressure. *Biol. Conserv.* **1993**, *63*, 203–208. [CrossRef]
4. Augustine, D.J.; Frelich, L.E.; Jordan, P.A. Evidence for two alternate stable states in an ungulate grazing system. *Ecol. Appl.* **1998**, *8*, 1260–1269. [CrossRef]
5. Jensen, N.R.; Webster, C.R.; Witt, J.C.; Grant, J.B. Ungulate winter habitat selection as a driver of herbaceous-layer heterogeneity in northern temperate forests. *Ecosphere* **2011**, *2*, 1–16. [CrossRef]
6. Walters, M.B.; Farinosi, E.J.; Willis, J.L.; Gottschalk, K.W. Managing for diversity: Harvest gap size drives complex light, vegetation and deer herbivory impacts on tree seedlings. *Ecosphere* **2016**, *7*, e01397. [CrossRef]
7. Augustine, D.; McNaughton, S. Ungulate Effects on the Functional Species Composition of Plant Communities: Herbivore Selectivity and Plant Tolerance. *J. Wildl. Manag.* **1998**, *62*, 1165–1183. [CrossRef]
8. Rooney, T.P.; Waller, D.M. Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manag.* **2003**, *181*, 165–176. [CrossRef]
9. Murray, B.D.; Webster, C.R.; Bump, J.K. Broadening the ecological context of ungulate–ecosystem interactions: The importance of space, seasonality, and nitrogen. *Ecology* **2013**, *94*, 1317–1326. [CrossRef] [PubMed]
10. Webster, C.R.; Dickinson, Y.L.; Burton, J.L.; Frelich, L.E.; Jenkins, M.A.; Kern, C.C.; Raymond, P.; Saunders, M.R.; Walters, M.B.; Willis, J.L. Promoting and maintaining diversity in contemporary hardwood forests: Confronting contemporary drivers of change and the loss of ecological memory. *For. Ecol. Manag.* **2018**, *421*, 98–108. [CrossRef]
11. Salk, T.T.; Frelich, L.E.; Sugita, S.; Calcote, R.; Ferrari, J.B.; Montgomery, R.A. Poor recruitment is changing the structure and species composition of an old growth hemlock hardwood forest. *For. Ecol. Manag.* **2011**, *261*, 1998–2006. [CrossRef]
12. Witt, J.C.; Webster, C.R. Regeneration dynamics in remnant *Tsuga canadensis* stands in the northern Lake States: Potential direct and indirect effects of herbivory. *For. Ecol. Manag.* **2010**, *260*, 519–525. [CrossRef]
13. Nuttle, T.; Yerger, E.H.; Stoleson, S.H.; Ristau, T.E. Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. *Ecosphere* **2011**, *2*, 1–11. [CrossRef]
14. Royo, A.A.; Collins, R.; Adams, M.B.; Kirschbaum, C.; Carson, W.P. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* **2010**, *91*, 93–105. [CrossRef] [PubMed]
15. Harris, R.M.B.; Beaumont, L.J.; Vance, T.R.; Tozer, C.R.; Remenyi, T.A.; Perkins-Kirkpatrick, S.E.; Mitchell, P.J.; Nicotra, A.B.; McGregor, S.; Andrew, N.R.; et al. Biological responses to the press and pulse of climate trends and extreme events. *Nat. Clim. Chang.* **2018**, *8*, 579–587. [CrossRef]
16. Leopold, A.; Sowls, L.; Spencer, D.A. Survey of Over-Populated Deer Ranges in the United States. *J. Wildl. Manag.* **1947**, *11*, 162–177. [CrossRef]
17. Husheer, S.W.; Coomes, D.A.; Robertson, A.W. Long-term influences of introduced deer on the composition and structure of New Zealand Nothofagus forests. *For. Ecol. Manag.* **2003**, *181*, 99–117. [CrossRef]
18. Binkley, D.; Moore, M.M.; Romme, W.H.; Brown, P.M. Was Aldo Leopold right about the Kaibab Deer Herd? *Ecosystems* **2006**, *9*, 227–241. [CrossRef]
19. Forsyth, D.M.; Caley, P. Testing the irruptive paradigm of large herbivore dynamics. *Ecology* **2006**, *87*, 297–303. [CrossRef]
20. Starns, H.D.; Weckerly, F.W.; Ricca, M.A.; Duarte, A. Vegetation changes associated with a population irruption by Roosevelt elk. *Ecol. Evol.* **2014**, *5*, 109–120. [CrossRef]
21. Takimoto, G.; Spiller, D.A.; Post, D.M. Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. *Ecology* **2008**, *89*, 3001–3007. [CrossRef]
22. Fuller, T.K. Dynamics of a declining white-tailed deer population in northern central Minnesota. *Wildl. Monogr.* **1990**, *110*, 3–37.

23. Patterson, B.R.; Power, V.A. Contribution of forage competition, harvest and climate fluctuation to changes in population growth of northern white-tailed deer. *Oecologia* **2002**, *130*, 62–71. [CrossRef] [PubMed]

24. Alverson, W.S.; Waller, D.M.; Solheim, S.L. Forests too deer: Edge effects in northern Wisconsin. *Conserv. Biol.* **1988**, *2*, 348–358. [CrossRef]

25. Waller, D.M. Effects of deer on forest herb layers. In *The Herbaceous Layer in Forests of Eastern North America*; Gilliam, F.S., Ed.; Oxford University Press: New York, NY, USA, 2014; pp. 369–399.

26. Doepker, R.V.; Beyer, D.E.; Donovan, M.L. *Deer Population Trends in Michigan's Upper Peninsula*; Michigan Department of Natural Resources, Wildlife Division: Lansing, MI, USA, 1994.

27. Pekins, P.J.; Smith, K.S.; Mautz, W.W. The energy cost of gestation in white-tailed deer. *Can. J. Zool.* **1998**, *76*, 1091–1097. [CrossRef]

28. Albon, S.D.; Irvine, R.J.; Halvorsen, O.; Langvatn, R.; Loe, E.; Ropstad, E.; Veiberg, V.; van der Wal, R.; Bjørkvoll, E.M.; Duff, E.I.; et al. Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Glob. Chang. Biol.* **2017**, *23*, 1374–1389. [CrossRef]

29. Anderson, R.C.; Loucks, O.L. White-tailed deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. *J. Appl. Ecol.* **1979**, *16*, 855–861. [CrossRef]

30. Ellison, A.M.; Bank, M.S.; Clinton, B.D.; Colburn, E.A.; Elliott, K.; Ford, C.R.; Foster, D.R.; Kloeppel, B.D.; Knoepp, J.D.; Lovett, G.M.; et al. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* **2005**, *3*, 479–486. [CrossRef]

31. Martin, K.L.; Goebel, P.C. The foundation species influence of eastern hemlock (*Tsuga canadensis*) on biodiversity and ecosystem function on the Unglaciated Allegheny Plateau. *For. Ecol. Manag.* **2013**, *289*, 143–152. [CrossRef]

32. Mladenoff, D.J.; Stearns, F. Eastern hemlock regeneration and deer browsing in the northern Great Lakes region: A re-examination and model simulation. *Conserv. Biol.* **1993**, *7*, 889–900. [CrossRef]

33. Verme, L.J. 1973 Movements of white-tailed deer in Upper Michigan. *J. Wildl. Manag.* **1973**, *37*, 545–552. [CrossRef]

34. Morrison, S.F.; Forbes, G.J.; Young, G.J.; Lusk, S. Within-yard habitat use by white-tailed deer at varying winter severity. *For. Ecol. Manag.* **2003**, *172*, 173–182. [CrossRef]

35. Beals, E.W.; Cottam, G.; Vogl, R.J. Influence of Deer on Vegetation of the Apostle Islands, Wisconsin. *J. Wildl. Manag.* **1960**, *24*, 68–80. [CrossRef]

36. Rooney, T.P.; Waller, D.M. Local and regional variation in hemlock seedling establishment in forests of the Upper Great Lakes region. *For. Ecol. Manag.* **1998**, *111*, 211–224. [CrossRef]

37. Rooney, T.P.; McCormick, R.J.; Solheim, S.L.; Waller, D.M. Regional variation in recruitment of hemlock seedlings and saplings in the Upper Great Lakes, USA. *Ecol. Appl.* **2000**, *10*, 1119–1132. [CrossRef]

38. Murray, B.D.; Webster, C.R.; Bump, J.K. A migratory ungulate facilitates cross-boundary nitrogen transport in forested landscapes. *Ecosystems* **2014**, *17*, 1002–1013. [CrossRef]

39. Frelich, L.E.; Calcote, R.R.; Davis, M.B.; Pastor, J. Patch Formation and Maintenance in an Old-Growth Hemlock-Hardwood Forest. *Ecology* **1993**, *74*, 513–527. [CrossRef]

40. Van Deelen, T.R.; Campa, H.; Hamady, M.; Haufler, J.B. Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan. *J. Wildl. Manag.* **1998**, *62*, 205–213. [CrossRef]

41. National Data Buoy Center. Historical Data and Climatic Summaries, 1 Jan–15 April in 2014. 2014. Available online: https://www.ndbc.noaa.gov/station_page.php?station=sxhw3 (accessed on 11 March 2019).

42. National Data Buoy Center. Historical Data and Climatic Summaries, 1 Jan–15 April in 2014. 2014. Available online: http://www.ndbc.noaa.gov/station_history.php?station=pclm4 (accessed on 11 March 2019).

43. National Weather Service National Weather Service, Marquette, Michigan. 2019. Available online: https://www.weather.gov/mqt/seasonsnowfallmaps (accessed on 18 February 2019).

44. Mroz, G.D.; Gale, M.R.; Jurgensen, M.F.; Frederick, D.J.; Clark, A. Composition, structure and aboveground biomass of two old-growth northern hardwood stands in Upper Michigan. *Can. J. For. Res.* **1985**, *15*, 78–82. [CrossRef]

45. Wisconsin Department of Natural Resources. *Wisconsin Deer Research Studies Annual Report 2013–2014*; Bureau of Sciences Services, Wildlife and Forestry Research Section: Madison, WI, USA, 2014.

46. Sabine, D.L.; Forbes, G.; Ballard, W.B.; Bowman, J.; Whitlaw, H. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. *J. Wildl. Manag.* **2002**, *66*, 718–728. [CrossRef]

47. Witt, J.C.; Webster, C.R.; Froese, R.E.; Vucetich, J.A. Scale-dependent drivers of ungulate patch use along a temporal and spatial gradient of snow depth. *Can. J. Zool.* **2012**, *90*, 972–983. [CrossRef]

48. National Operational Hydrologic Remote Sensing Center. *Snow Data Assimilation System (SNODAS) Data Products at NSIDC, November 15–April 15 in 2005–2018*; National Snow and Ice Data Center: Boulder, CO, USA, 2004.

49. Norton, D.C.; Bolsenga, S.J. Spatiotemporal Trends in Lake Effect and Continental Snowfall in the Laurentian Great Lakes, 1951–1980. *J. Clim.* **1993**, *6*, 1943–1956. [CrossRef]

50. Albert, D.A. *Regional Landscape Ecosystems of Michigan, Minnesota, and Wisconsin: A Working Map and Classification*; General Technical Report NC-178; U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: St. Paul, MN, USA, 1995.

51. Reay, R.S. Management of eastern hemlock for deer wintering areas. In *Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America*; McManus, K.A., Shields, K.S., Souto, D.R., Eds.; U.S. Forest Service: Newtown Square, PA, USA, 1999; pp. 144–147.

52. Nelson, M.E.; Mech, L.D. Wolf predation risk associated with white-tailed deer movements. *Can. J. Zool.* **1991**, *69*, 2696–2699. [CrossRef]

53. Wisconsin Department of Natural Resources. *Management Workbook for White-Tailed Deer*; Bureau of Wildlife Management and Bureau of Integrated Science Services: Madison, WI, USA, 2001.

54. Michigan Technological University Keweenaw Research Center. Weather History. 2019. Available online: http://blizzard.mtukrc.org/~{}weather/00_KRC_Weather_History.xls (accessed on 20 May 2019).

55. National Data Buoy Center. Historical Data and Climatic Summaries, Nov 15–April 15 in 2009–2018. Available online: https://www.ndbc.noaa.gov/station_page.php?station=sxhw3 (accessed on 11 March 2019).

56. National Data Buoy Center. Historical Data and Climatic Summaries, Nov 15–April 15 in 2009–2018. Available online: http://www.ndbc.noaa.gov/station_history.php?station=pclm4 (accessed on 11 March 2019).

57. Frawley, B.J. *Michigan Deer Harvest Survey Report 2005 Seasons*; Wildlife Report No. 3454; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

58. Frawley, B.J. *Michigan Deer Harvest Survey Report 2006 Seasons*; Wildlife Report No. 3467; Michigan Department of Natural Resources: Lansing, MI, USA, 2007.

59. Frawley, B.J. *Michigan Deer Harvest Survey Report 2007 Seasons*; Wildlife Report No. 3499; Michigan Department of Natural Resources: Lansing, MI, USA, 2008.

60. Frawley, B.J. *Michigan Deer Harvest Survey Report 2008 Seasons*; Wildlife Report No. 3513; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

61. Frawley, B.J. *Michigan Deer Harvest Survey Report 2009 Seasons*; Wildlife Report No. 3513; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

62. Frawley, B.J. *Michigan Deer Harvest Survey Report 2010 Seasons*; Wildlife Report No. 3526; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

63. Frawley, B.J. *Michigan Deer Harvest Survey Report 2011 Seasons*; Wildlife Report No. 3548; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

64. Frawley, B.J. *Michigan Deer Harvest Survey Report 2012 Seasons*; Wildlife Report No. 3566; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

65. Frawley, B.J. *Michigan Deer Harvest Survey Report 2013 Seasons*; Wildlife Report No. 3585; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

66. Frawley, B.J.; Boon, C.E. *Michigan Deer Harvest Survey Report 2014 Seasons*; Wildlife Report No. 3609; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

67. Frawley, B.J.; Boon, C.E. *Michigan Deer Harvest Survey Report 2015 Seasons*; Wildlife Report No. 3621; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

68. Frawley, B.J. *Michigan Deer Harvest Survey Report 2016 Seasons*; Wildlife Report No. 3639; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

69. Frawley, B.J. *Michigan Deer Harvest Survey Report 2017 Seasons*; Wildlife Report No. 3656; Michigan Department of Natural Resources: Lansing, MI, USA, 2006.

70. McCune, B.; Grace, J.B. *Analysis of Ecological Communities*; mJm Software Design: Gleneden Beach, OR, USA, 2002; pp. 25–34.

71. Zuur, A.F.; Ieno, E.N.; Walker, N.J.; Saveliev, A.A.; Smith, G.M. *Mixed Effects Models and Extensions in Ecology with R*; Springer Science and Business Media: New York, NY, USA, 2009.

72. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2019; Available online: https://www.R-project.org (accessed on 26 March 2019).

73. Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, D.; R Core Team. nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-131. 2017. Available online: https://CRAN.R-project.org/package=nlme (accessed on 6 December 2018).

74. Hilbe, J.M.; Robinson, A.P. *Methods of Statistical Model Estimation*; CRC Press: Boca Raton, FL, USA, 2013.

75. Hilbe, J.; Robinson, A. msme: Functions and Datasets for "Methods of Statistical Model Estimation". R Package Version 0.5.3. 2018. Available online: https://CRAN.Rproject.org/package=msme (accessed on 6 December 2018).

76. Nelson, M.E.; Mech, L.D. A three-decade dearth of deer (*Odocoileus virginianus)* in a wolf (Canis lupus) dominated ecosystem. *Am. Midl. Nat.* **2006**, *155*, 373–382. [CrossRef]

77. Hurst, J.E.; Porter, W.F. Evaluation of shifts in white-tailed deer winter yards in the Adirondack region of New York. *J. Wildl. Manag.* **2008**, *72*, 367–375. [CrossRef]

78. Dukes, J.S.; Pontius, J.; Orwig, D.; Garnas, J.R.; Rodgers, V.L.; Brazee, N.; Cooke, B.; Theoharides, K.A.; Stange, E.E.; Harrington, R.; et al. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Can. J. For. Res.* **2009**, *39*, 231–248. [CrossRef]

79. Waller, D.M. Local and regional factors influencing the regeneration of hemlock. In *Hemlock Ecology and Management*; Mroz, G., Martin, J., Eds.; University of Wisconsin Press: Madison, WI, USA, 1995; pp. 73–90.

80. Schulte, L.A.; Mladenoff, D.J.; Crow, T.R.; Merrick, L.C.; Cleland, D.T. Homogenization of northern U.S. Great Lakes forests due to land use. *Landsc. Ecol.* **2007**, *22*, 1089–1103. [CrossRef]

81. Fisichelli, N.A.; Frelich, L.E.; Reich, P.B. Climate and interrelated tree regeneration drivers in mixed temperate–boreal forests. *Landsc. Ecol.* **2013**, *28*, 149–159. [CrossRef]

82. Frelich, L.E.; Reich, P.B. Minireviews: Neighborhood effects, disturbance severity, and community stability in forests. *Ecosystems* **1999**, *2*, 151–166. [CrossRef]

83. Jõgiste, K.; Korjus, H.; Stanturf, J.A.; Frelich, L.E.; Baders, E.; Donis, J.; Jansons, A.; Kangur, A.; Köster, K.; Laarmann, D.; et al. Hemiboreal forest: Natural disturbances and the importance of ecosystem legacies to management. *Ecosphere* **2017**, *8*, e01706. [CrossRef]

84. Mladenoff, D.J. The role of eastern hemlock across scales in the northern lake states. In *Hemlock Ecology and Management*; Mroz, G., Martin, J., Eds.; University of Wisconsin Press: Madison, WI, USA, 1995; pp. 29–42.

85. Frelich, L.E.; Lorimer, C.G. Current and Predicted Long-term Effects of Deer Browsing in Hemlock Forests in Michigan, USA. *Biol. Conserv.* **1985**, *34*, 99–120. [CrossRef]

86. Lancaster, K.F. *Managing Eastern Hemlock: A Preliminary Guide*; USDA Forest Service, Northeastern Area: Broomall, PA, USA, 1985.

87. Lorimer, C.G. Dynamics and structural characteristics of eastern hemlock stands. In *Hemlock Ecology and Management*; Mroz, G., Martin, J., Eds.; University of Wisconsin—Madison: Madison, WI, USA, 1995; pp. 43–60.