Deer-mediated changes in environment compound the direct impacts of herbivory on understorey plant communities

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Summary

1. In forests of eastern North America, white-tailed deer (*Odocoileus virginianus*) can directly affect, via herbivory, the presence, abundance and reproductive success of many plant species. In addition, deer indirectly influence understorey communities by altering environmental conditions.

2. To examine how deer indirectly influence understorey plants via environmental modification, we sampled vegetation and environmental variables in- and outside deer exclosures (10–20 years old) located in temperate forests in northern Wisconsin and the Upper Peninsula of Michigan, USA. We assessed how excluding deer affected understorey community composition and structure, the soil and light environment, and relationships between direct and indirect effects, using non-metric multi-dimensional scaling (NMDS), mixed linear models and nonparametric multiplicative regression (NPMR).

3. Excluding deer altered sapling communities and several aspects of the understorey environment. Excluding deer from plots with lower overstory basal area increased sapling abundance, decreasing the amount of light available to groundlayer plants. Exclusion also reduced soil compaction and the thickness of the soil E horizon.

4. The composition of understorey communities covaried in apparent response to the environmental factors affected by exclusion. In several common species and groups, E horizon thickness, compaction, openness, and/or total (sapling and overstory) basal area were significant predictors of plant frequency.

5. Complementary analyses revealed that deer exclusion also altered the frequency distributions of several species and groups across environmental space.

6. *Synthesis.* Deer alter many facets of the understorey environment, such as light availability, soil compaction and thickness of the soil E horizon, which, in turn, appear to mediate variation in plant communities. Those environmental modifications likely compound direct impacts of herbivory as drivers of understorey community change. Our results provide evidence that deer effects on the environment have important implications for forest composition. Thus, we suggest a re-examination of the common assumption that understorey community shifts stem primarily from tissue removal.

Key-words: community composition, non-metric multidimensional scaling, nonparametric multiplicative regression, openness, soil compaction, soil E horizon, soil fertility, tree regeneration, understorey vegetation, white-tailed deer (*Odocoileus virgnianus*)

Introduction

Ungulates are widely regarded as keystone herbivores and ecosystem engineers in wetland, grassland and forest systems around the world (e.g. reviewed by Hobbs 1996; Waller & Alverson 1997; Knapp *et al.* 1999; Côté *et al.* 2004; Barrios-Garcia & Ballari 2012). Native and introduced ungulates shape plant community composition and structure directly via frugivory, grazing of grasses, and browsing of woody plants and forbs (Bodmer 1990). Selective browsing has profound influences on vegetation communities (reviewed by Hanley 1997), with deer (members

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of the Cervidae family) being common browsers in temperate forests (Putman 1988).

In temperate deciduous forests of eastern North America, white-tailed deer (*Odocoileus virginianus*) overabundance can markedly alter forest composition, structure and function (Rooney 2001; Russell, Zippin & Fowler 2001; Rooney & Waller 2003; Côté *et al.* 2004). In particular, large increases in deer abundance since the mid-1900s have led to tree regeneration failures (e.g. Rooney & Waller 2003; Côté *et al.* 2004; White 2012), pronounced declines in the relative abundance of palatable vs. less palatable plants (e.g. Frelich & Lorimer 1985; Tilghman 1989; Miller, Bratton & Hadidian 1992; Anderson 1994; Balgooyen & Waller 1995; Fletcher *et al.* 2001; Horsley, Stout & DeCalesta 2003; Frerker, Sabo & Waller 2014; Nuttle, Ristau & Royo 2014; Bradshaw & Waller 2016), losses of plant species richness and community diversity (e.g. Rooney & Dress 1997; Horsley, Stout & DeCalesta 2003; Bressette, Beck & Beauchamp 2012; Shelton *et al.* 2014; Habeck & Schultz 2015), changes in community developmental trajectories (Frelich & Lorimer 1985; Augustine, Frelich & Jordan 1998; Nuttle, Ristau & Royo 2014) and enhanced ecosystem vulnerability to biotic invasions (e.g. Baiser *et al.* 2008; Knight *et al.* 2009; Kalisz, Spigler & Horvitz 2014; Dávalos, Nuzzo & Blossey 2015; Dobson & Blossey 2015).

A number of these changes result directly from deer herbivory, which leads to declines in plant vigour, competitive ability and fecundity (e.g. Balgooyen & Waller 1995; Shelton & Inouye 1995; Augustine & Frelich 1998; Fletcher *et al.* 2001; Webster, Jenkins & Rock 2005), increased susceptibility to other biotic or abiotic stressors (e.g. Long, Pendergast & Carson 2007; Dávalos, Nuzzo & Blossey 2014), and in many instances, decreased survival (e.g. Tripler *et al.* 2005; Krueger *et al.* 2009). Moreover, the direct effects of herbivory, along with the impacts of associated deer activities (e.g. defecation, bedding and trampling), may perturb the forest understorey environment, e.g. by altering microclimate (Yamada & Takatsuki 2015), soil biotic and physical properties (e.g. Heckel *et al.* 2010; Bressette, Beck & Beauchamp 2012; Chips *et al.* 2014; Shelton *et al.* 2014), and the overall availability as well as spatial patterning of understorey light (Murray, Webster & Bump 2013) and soil resources (e.g. Seagle 2003; Jensen *et al.* 2011; Murray, Webster & Bump 2013; Tahtinen *et al.* 2014).

Results of several studies have indicated that deer-mediated environmental modifications may drive pervasive changes in the demography of woody and herbaceous plant species (Dufresne *et al.* 2009; Knight *et al.* 2009; Heckel *et al.* 2010; Holmes & Webster 2011; Nuttle, Ristau & Royo 2014; Tahtinen *et al.* 2014; Dobson & Blossey 2015). Here, we adopt a comprehensive approach, asking how such environmental perturbations interact with direct consequences of deer herbivory to reshape woody and herbaceous communities. We take advantage of the comparisons possible between conditions in- and outside deer exclosures located in hardwood-dominated forests in northern Wisconsin and the Upper Peninsula of Michigan, USA (Fig. 1). Previous work with these exclosures
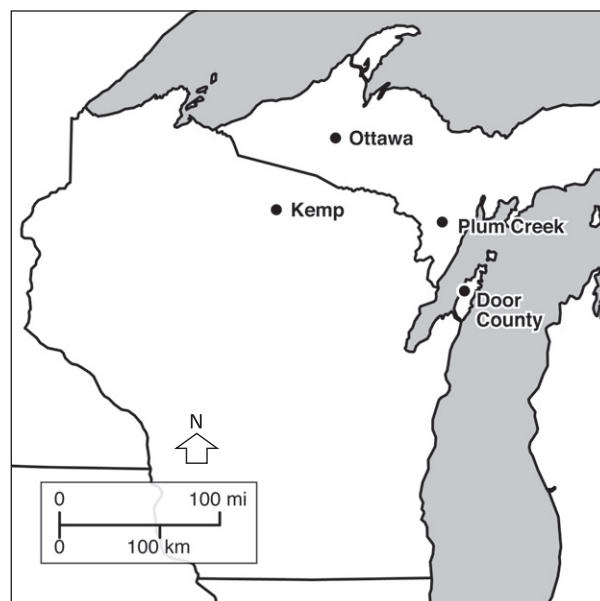

Fig. 1. Map showing exclosure locations in Wisconsin and the Upper Peninsula of Michigan, USA. Exclosures and paired deer-access plots were located in the Kemp Natural Resources Station ('Kemp'), three State Parks in Door County, Plum Creek industrial timberland ('Plum Creek') and Ottawa National Forest ('Ottawa').

(Frerker, Sabo & Waller 2014) revealed that deer exclusion affects populations of common understorey species, increasing tree regeneration and shrub and forb cover, and decreasing the abundance of graminoids. To extend this study, we have coupled vegetation and environmental data from the same exclosures to test these hypotheses:

H_1: Deer exclusion alters the structure and composition of understorey plant communities;

H_2: Changes resulting from deer exclusion alter key facets of the understorey environment, such as light availability and soil properties;

H_{3a}: Changes in understorey communities following deer exclusion stem, in part, from changes in the understorey environment identified in H_2;

H_{3b}: Alternatively, or additionally, deer exclusion modifies the distribution of understorey plant species across environmental space by allowing palatable taxa to occupy a larger portion of their fundamental niche.

Materials and methods

STUDY LOCATIONS

In Summer 2011, we visited 17 exclosures in upland forests of northern Wisconsin and Michigan's Upper Peninsula (UP) in stands dominated by *Acer saccharum* with variable, but often substantial,

amounts of *Tsuga canadensis* in the overstory (Fig. 1, Table 1, Table S1, Supporting Information). In each stand, we sampled vegetation and measured key environmental variables inside the fences and in paired 'deer-access' plots outside the fences. The latter were in close proximity to the exclosures (always within 100 m), and were placed in locations with similar management histories and overstory structure and composition. Additional details about the study locations are provided in Frerker, Sabo & Waller (2014).

VEGETATION SAMPLING

We employed three sampling designs to accommodate the 100 m², 182 m² and 2–8 ha exclosures (Fig. 2). Depending on the size of each exclosure, we sampled herbaceous and woody understorey vegetation in 16 to 84 1-m² quadrats arrayed along transects that varied in arrangement, length and number (Table 1, Fig. 2). We measured two subplots (each 2500 m²) within the 2 ha and larger exclosures and paired deer-access plots. Within every quadrat, we recorded all vascular plant species present. Across larger areas within each plot, we identified the species and measured the diameter at breast height (DBH, 1·4 m) of saplings and trees. In 2 ha and larger plots (Ottawa and Plum Creek locations), we tallied small saplings (0·6 cm ≤ DBH <3·2 cm) within 1·5 m of the entire length of the transects. We also measured DBH of all large saplings (3·2 cm ≤ DBH <10 cm) and trees (DBH ≥10 cm) within 3 m of the transects (Fig. 2). In the smaller plots (100–182 m², in Door Co. and Kemp), we tallied all small saplings and recorded DBHs of all larger saplings within each plot. Additionally, we measured the diameter of trees ≥10 cm DBH that were tallied in variable-radius plots sampled with a prism (basal area factor = 2·3 m² ha^{-1}) held over the centre of each smaller plot. For plant species authorities, see USDA, NRCS (2016).
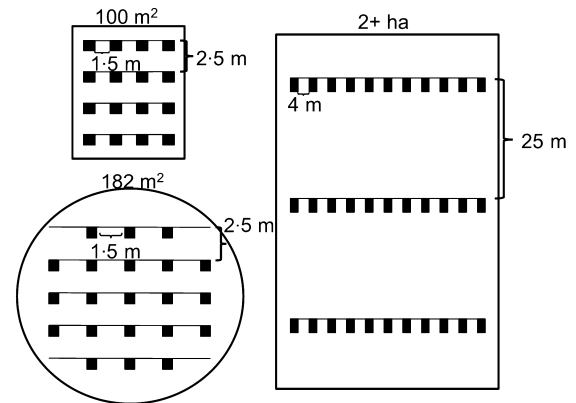
■ Groundlayer quadrat (3 additional consecutive quadrats, not pictured because randomly located, were added to each transect in 2+ ha plots at 2·5 m spacing)

Fig. 2. Vegetation sampling design for the 100 m² (Kemp), 182 m² (Door Co.) and one of two subplots in the 2+ ha (Ottawa and Plum Creek) exclosures and paired deer-access plots.

CHARACTERIZING THE UNDERSTOREY ENVIRONMENT

In all exclosure and paired deer-access plots, we measured biotic and abiotic variables to characterize the understorey environment. We estimated openness (a proxy for light availability) at the groundlayer, using fisheye lens photographs obtained at 0·5 m height (Promis *et al.* 2011), once in the centre of the 100-m² exclosure/deer-access plots, once in the centre of the first, third and fifth transects of the 182-m² paired plots, and every 15 m along each of the three transects within the large exclosure/deer-access subplots (Fig. 2). We recorded the diameter of coarse woody debris (CWD) that intersected each transect, and estimated the cross-sectional area per km of transect

Table 1. Site locations (latitude and longitude in decimal degrees), along with soil taxonomic class, number of exclosures (#) per location, installation date, size of exclosures and population density estimated by state natural resources agencies based on harvest data collected in deer management units during 2010–2011 (Michigan Department of Natural Resources and Environment 2010; Wisconsin Department of Natural Resources 2010). Also included are the overstory condition or manipulation just prior to exclosure installation and the total number of quadrats (Quad) sampled in each exclosure or paired deer-access plot. The three state parks (Peninsula SP, Whitefish Dunes SP, and Potawatomi SP) are located in Door County

Location	Lat, Long	Soil Taxonomic Class	#	Date	Size	Deer density km^{-2}	Overstory condition	Quad
Kemp NRS	45·84, −89·67	Sandy, mixed, frigid Entic Haplorthods	10	2001	100 m²	2–11	Undisturbed, blowdown	16
Peninsula SP	45·15, −87·22	Loamy, mixed, active, frigid Lithic Hapludolls; Coarse-loamy, mixed, superactive, frigid Typic Haplorthods; Rock outcrop	2	1991, 1992	182 m²	4–8	Undisturbed	21
Whitefish Dunes SP	44·93, −87·18	Loamy, mixed, active, frigid Lithic Hapludolls	1	1992	182 m²	4–8	Undisturbed	21
Potawatomi SP	44·87, −87·43	Coarse-loamy, mixed, superactive, frigid Typic Haplorthods	1	1992	182 m²	4–8	Undisturbed	21
Ottawa NF	46·40, −88·90	Sandy, isotic, frigid Typic Haplorthods; Sandy, mixed, frigid Entic Haplorthods – Sandy, mixed, frigid Alfic Haplorthods – Coarse-loamy, mixed, superactive, frigid Alfic Haplorthods	2	1998, 2002	2 ha	4–8	Gaps created	84
Plum Creek timberland	45·83, −87·51	Fine-loamy, mixed, active, frigid Inceptic Hapludalfs – Coarse-loamy, mixed, superactive, frigid Aquic Argiudolls	1	1996	8 ha	12	Thinned	84

(assuming a circular cross-section). Additionally, we used a rapid assessment protocol to rank exotic earthworm invasion (Loss *et al.* 2013) in one 1-m^2 quadrat near the centre of each 100-m^2 plot, once at a random location close to each transect for 182-m^2 plots, and twice at random locations between transects in each of the two sub-plots of 2 ha and larger plots. At each earthworm assessment site, we measured the thickness of leaf litter and surface soil horizons in a 20-cm core. We measured soil compaction once per quadrat with a soil compaction meter (Lang penetrometer, Inc., Gulf Shores, AL, USA). We also collected three soil cores (10-cm depth) per plot in areas with representative vegetation, and submitted mixed composite samples (one per plot) to the Soil Testing Laboratory at the University of Wisconsin-Madison. Samples were analysed for total N using the Kjeldahl method, P and K using the Bray and Kurtz P-1 procedure, Ca and Mg via ammonium acetate extraction, organic matter (OM) by loss-on-ignition and pH in a 1:1 soil:water slurry. Finally, for every plot, we extracted coarse-scale soil type and texture data from soil survey maps (USDA, NRCS 2013).

STATISTICAL ANALYSES

For every plant species encountered in one or more quadrats across our 17 exclosure/deer-access pairs, we estimated plot-level frequencies as the proportion of plot quadrats containing that species. We also summed the proportional frequencies of species to form groups by plant family, growth form (e.g. vascular cryptogams, graminoids, forbs, etc.), ecological status (e.g. exotic species and late-successional shrubs – *Dirca palustris*, *Taxus canadensis*, *Acer spicatum*, *Cornus rugosa*, *Diervilla lonicera*, *Symphoricarpos albus*, *Viburnum acerifolium* and *Mitchella repens*), and for species found in at least 20% of the plots, by dispersal mode. We determined the dispersal mode of our 26 most common quadrat species by referring to a plant traits database compiled from literature and field specimens (Amatangelo *et al.* 2014). The sapling (0·6 cm ≤ DBH <10 cm) and tree tallies were converted to plot-level averages for hardwood and conifer sapling and overstory basal area (BA, m^2 ha^{-1}). We also generated plot averages for all the environmental data sampled at the quadrat, transect or subplot levels.

To test H$_1$, that deer exclusion alters community composition, we first employed non-metric multidimensional scaling (NMDS) to characterize variation in sapling, shrub plus tree seedling and herbaceous communities. Prior to ordinating the vegetation communities, we deleted species that occurred in fewer than 5% of our plots, leaving 131 herb, shrub and tree species for the frequency data and 20 species for the sapling BA dataset. Sapling abundance data were square-root transformed and Wisconsin double standardized (McCune, Grace & Urban 2002). We used Bray–Curtis distances to calculate all the species distance matrices. Using the same dataset, we then assessed the significance of differences in treatment centroids, after accounting for variation among location and plot pairs, for sapling, woody understorey and herbaceous communities using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). In addition, we tested for treatment differences in variance using permutational analysis of multivariate dispersions (PERMDISP; Anderson 2004). In an extension of the herb and shrub frequency analyses conducted in Frerker, Sabo & Waller (2014), we used mixed models, with plot pair and location as random effects, to determine the significance of deer exclusion on the sapling BA of tree species or genera that occurred in at least 20% of the plots. We include location in these models primarily to account for the potentially confounding influence of variation among locations in the number of plot pairs.

To test H$_2$, that deer exclusion altered key biotic and/or abiotic aspects of the understorey environment, we again used NMDS. This time, rather than ordinating species data, we characterized variation in the collective suite of environmental variables across all exclosure and deer-access plots. Separate NMDS ordinations were generated for the environments of the groundlayer communities (shrubs plus tree seedlings, and herbs) and sapling layer. All 20 environmental variables (Table S1) were included in the groundlayer environment NMDS, while 17 of the 20 variables were included in the sapling environment NMDS (excluding openness, the BA of conifer saplings, and the BA of hardwood saplings because they were confounded with the corresponding vegetation data). Prior to NMDS, we normalized environmental variables by the maximum so that each ranged between 0 and 1, and then calculated Euclidean dissimilarities. We assessed the influence of individual environmental variables on the NMDS axes using Kendall's Tau. Finally, we tested the significance of treatment differences in (i) environmental NMDS scores, after accounting for variation among location and plot pairs, using PERMANOVA and PERMDISP; and (ii) individual environmental variables, using mixed models with plot pair and location as random effects.

We adopted a multifaceted approach to test our two competing hypotheses (H$_{3a}$ and H$_{3b}$) that contrasts in species composition between exclosures and deer-access plots correspond with differences in the environment (H$_{3a}$), or that relationships between species composition and environmental gradients differ between exclosure and deer-access plots (H$_{3b}$). First, we fit environmental vectors to the NMDS ordinations of sapling, shrub plus tree seedling and herbaceous communities. Next, we employed several tactics to examine relationships between the environment and species abundances. We used Kendall's Tau to determine which environmental NMDS axes were correlated with plot-level vegetation NMDS axis scores. We employed mixed models, with location as a random effect, to assess the influences of deer exclusion or environmental variables (as fixed effects) on abundances (frequencies or BA) of individual species that occurred in at least 20% of the plots and species groups. We also calculated divergence in groundlayer species abundance, and divergence in environment, between paired plots by subtracting exclosure values from corresponding deer-access values. Finally, we again employed mixed models (with location as the random effect) to examine relationships between the species and environmental divergences. As detailed in tables in the results, we usually transformed abundances (e.g. with square-root) to reduce heteroscedasticity and/or improve model fit. Sapling abundances were not tested against deer-mediated environmental variables because they were frequently confounded.

We used nonparametric multiplicative regression (NPMR) to detect whether deer exclusion altered the manner in which individual species or species groups were distributed in environmental space. Unlike linear mixed models, NPMR does not require assumptions about model form and it simultaneously tests a set of predictors and their interactions (McCune 2006). We conducted NPMR using the stepwise free search function in Hyperniche 2.0 (McCune & Mefford 2011), with the model type set to local mean quantitative, Gaussian weighting and medium overfitting. The dependent variables again were vegetation NMDS axis scores and plot-level abundances (frequencies or BA) of individual species or groups, while the predictor variables were axis 1 and 2 scores from the corresponding environmental NMDS and a categorical variable indicating deer treatment. Among the resulting models, we deleted all but those with the highest cross-calibration R^2 (xR^2), which is calculated based on agreement between observed values and corresponding

predictions using a leave-one-out procedure during each of n model runs, where n is sample size. For species with best-fit models that included the deer treatment term and had a positive xR^2 value, we compared the best-fit model against one that included only our environmental NMDS axes 1 and/or 2 as predictors. When the increase in xR^2 resulting from addition of the deer treatment to the model was greater than the 3% convention used in Arkle, Pilliod & Welty (2012), we report the difference, recognizing that a small improvement in the cross-validated R^2 is more meaningful than comparable changes in traditional R^2 (Bruce McCune, personal communication). Tolerance values, model smoothing parameters that increase as species' distributions broaden across the range in predictor variables, and sensitivities, which increase with predictor importance (e.g. sensitivity equals 1·0 when a 10% change in the predictor produces a 10% change in the response and a sensitivity of zero means no change in the response), were provided for NMDS axis 1 and/or 2 when either or both appeared in the best-fit model. Tolerance and sensitivity were not calculated for treatment, as it was a categorical variable.

Parametric statistics and Kendall's Tau correlations were conducted in JMP Pro 11, while NMDS ordination, PERMANOVA and PERMDISP were performed using the metaMDS, adonis and betadisper functions, respectively, in R v. 3.2.2 and Vegan package 2.0–10 (Oksanen *et al.* 2013). The sample sizes for analyses were 34 when examining data across all plots, and 17 for tests of divergence between deer-access and exclosure treatments in plot pairs. Regarding results of mixed models, the significance of treatment effects, relationships between community composition and environment, and their interactions, was evaluated using the sequential Bonferroni procedure (Rice 1989) to account for an increased risk of type I error that accompanies repeated tests of the same hypothesis on many species.

Results

EXCLOSURE EFFECTS ON THE UNDERSTOREY PLANT COMMUNITY

Composition varied considerably (Sabo *et al.* 2017), both within and across study locations, in communities of tree saplings (Fig. 3a), shrubs plus tree seedlings (Fig. 3b), and herbs (Fig. 3c). Scores of common species along vegetation NMDS axes are presented in Table S2. In support of H_1, results of PERMANOVA indicated that exclosures differed from deer-access plots in the composition of saplings ($P = 0.003$) but not groundlayer woody plants (shrubs plus tree seedlings, $P = 0.11$) or herbs ($P = 0.34$). According to results of PERMDISP, dispersion of ordination data about their respective centroids did not differ between treatments for any understorey community ($P \geq 0.31$, data not shown).

For saplings, the treatment difference in the average score along NMDS axis 2 coincided with increases in the BA of *Betula papyrifera*, *Populus* spp. and *Tsuga canadensis* inside exclosures ($P < 0.05$ after square-root transformation of BA, although none of these increases were significant according to the sequential Bonferroni test). Correspondingly, under less dense overstories, sapling BA was higher inside than outside of exclosures (Fig. 4a). This divergence was driven largely by treatment differences in the abundance of hardwood rather than conifer saplings (Table S1).
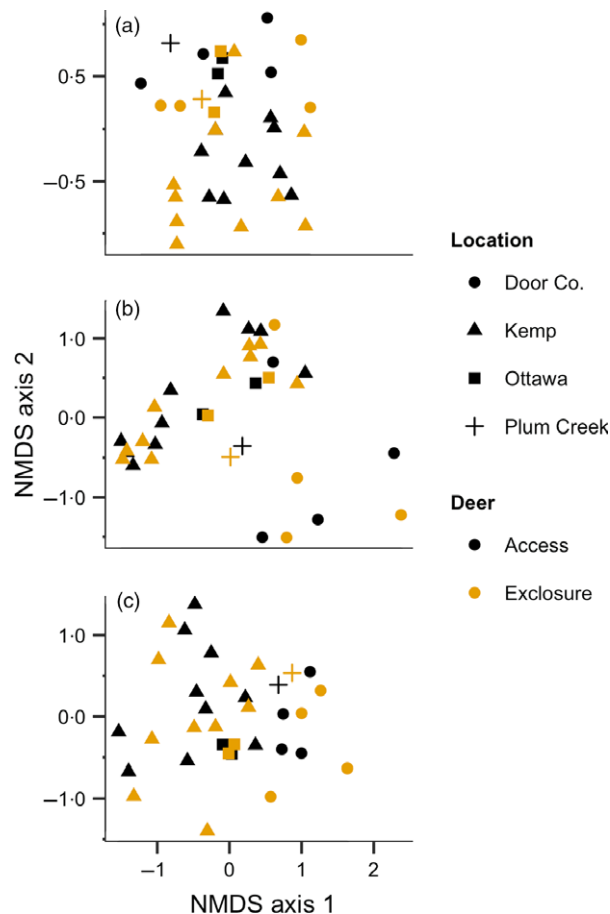

Fig. 3. Plot positions in ordinations of sapling basal area (a, stress = 0·24), tree seedling plus shrub frequency (b, stress = 0·13) and herb frequency (c, stress = 0·19). Based on results of PERMANOVA, sapling non-metric multidimensional scaling (NMDS) scores differed between exclosure and deer-access plots ($P \leq 0.01$). [Colour figure can be viewed at wileyonlinelibrary.com]

EXCLOSURE EFFECTS ON THE UNDERSTOREY ENVIRONMENT

NMDS ordinations of the sapling and groundlayer environments (Fig. 5) revealed substantial overlap between exclosure and deer-access plots in environmental space. In a test of H_2, results of PERMANOVA revealed that, after accounting for variation among location and plot pairs, deer exclusion modified the groundlayer environment ($P = 0.02$) but not the sapling environment ($P = 0.11$). Relationships between environmental NMDS axes and individual environmental variables are provided in Table S3.

Openness was higher outside than inside exclosures, on average ($P < 0.05$, 12·4% v. 7·5%, Table S1), and the contrast became larger as overstory BA (B_O) decreased (Fig. 4b). This trend was closely coupled with the aforementioned effect of deer exclusion on sapling BA (B_S), which was amplified under sparse overstories (Fig. 4a). Consequently, while openness declined with increasing B_O ($P = 0.009$, $n = 34$), it was more strongly and negatively related to variation in total BA (B_T), calculated as the sum of B_O and B_S ($P < 0.0001$,
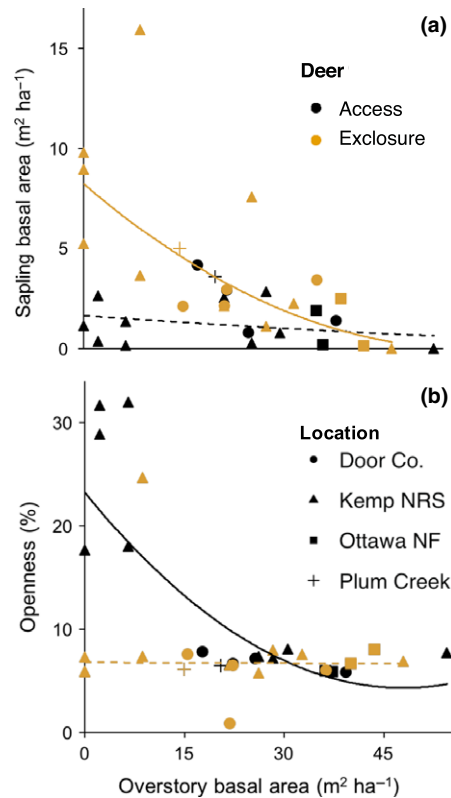
Fig. 4. Plots of (a) sapling basal area (B_S, m^2 ha^{-1}) and (b) openness (*O*) against overstory BA (B_O). B_S was negatively related with B_O in the exclosures (solid line), but not in the deer-access plots (dashed line). Conversely, *O* was negatively related with B_O in the deer-access plots (solid line), but not in the exclosures (dashed line). Mixed models, with location as a random effect, and B_O, exclosure treatment (*D*), and their interaction as fixed effects, were based on data from all 34 plots, and response variables were square-root transformed: (a) $B_S{}^{0.5} = 2 \cdot 87 - 0 \cdot 048 B_O - 1 \cdot 59 D + 0 \cdot 039 B_O D$, (b) $O^{0.5} = 2 \cdot 61 - 0 \cdot 003 B_O + 1 \cdot 88 D - 0 \cdot 054 B_O D$. All fixed effects and their interactions were significant ($P \leq 0 \cdot 05$) except for B_O ($P = 0 \cdot 81$) in the openness model. [Colour figure can be viewed at wileyonlinelibrary.com]

n = 34, data not shown). Correspondingly, after accounting for variation due to B_O, B_T increased significantly in exclosures. Specifically, in a mixed model with location as a random effect and B_O and exclosure treatment (*D*) as fixed effects: $B_T{}^{0.5} = 2 \cdot 61 + 0 \cdot 57 B_O{}^{0.5} - 1 \cdot 91 D + 0 \cdot 33 B_O{}^{0.5} D$, where *D* = 0 and 1 for exclosures and deer-access areas, respectively ($P \leq 0 \cdot 05$ for both fixed effects and their interaction, *n* = 34, data not shown).

Additionally, based on mixed models with location and plot pair as random effects and treatment as the fixed effect, soil compaction was 9% lower ($P = 0 \cdot 003$, Table S1) and soil E horizon was 27% thinner ($P = 0 \cdot 03$, Table S1) in exclosures compared with deer-access plots. Soil organic matter and nutrient concentrations, pH, A and O horizon thickness, volume of CWD and earthworm invasion scores did not differ between treatments (all $P > 0 \cdot 10$ in mixed models, Table S1). We did not test for treatment differences in soil texture (i.e. % sand, silt or clay) because, for these data, we relied on coarse-level mapping rather than direct field sampling in our plots.

RELATIONSHIPS BETWEEN UNDERSTOREY COMMUNITIES AND ENVIRONMENT

Patterns of community composition correlated with several aspects of the understorey environment (Table 2). Environmental variables were more closely related to woody and herbaceous groundlayer communities than to the sapling community. Of the environmental variables that differed by treatment, thickness of the soil E horizon was correlated with NMDS axis scores for all three communities and openness was correlated with scores for the two groundlayer communities (Table 2). Additionally, axis 1 of the environmental NMDS was positively correlated with axis 2 of the sapling vegetation NMDS ($P = 0 \cdot 03$) as well as axis 1 of both the woody and herbaceous groundlayer NMDS ($P \leq 0 \cdot 0001$),
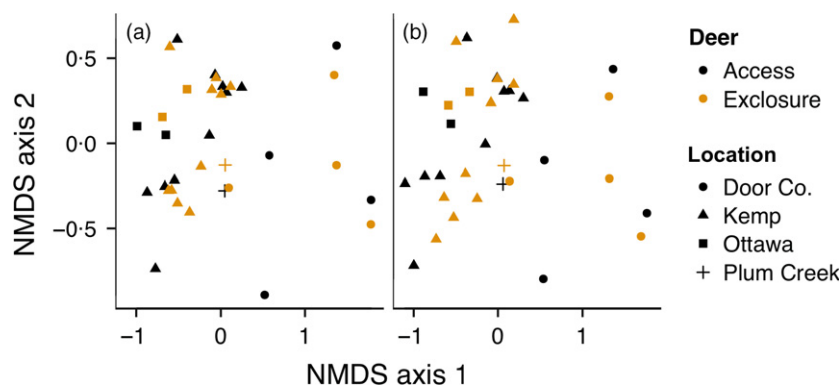

Fig. 5. Ordinations of environmental conditions across all deer-access and exclosure plots. To depict the understorey environment for tree saplings (a), we conducted non-metric multidimensional scaling (NMDS) of 17 plot-level abiotic (soil surface horizons, chemistry, texture and compaction) and biotic (earthworm invasion rank, CWD and basal area of trees) environmental variables. Stress = 0·14. To depict the groundlayer environment for herbs, shrubs and tree seedlings, we generated an NMDS of 20 plot-level environmental variables (b), which included all variables from (a) with the addition of openness, the basal area of hardwood saplings and the basal area of conifer saplings. Stress = 0·12. Based on results of PERMANOVA, NMDS scores of the groundlayer environment differed between exclosure and deer-access plots ($P \leq 0 \cdot 05$). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 2. Environmental loadings that were correlated to non-metric multidimensional scaling (NMDS) ordinations of sapling, seedling and shrub and herb communities (Fig. 3) by significance category

| Community | Significance of environmental correlates | | | |
	$P \leq 0.001$	$P \leq 0.01$	$P \leq 0.05$	$P \leq 0.10$
Saplings	Hardwood overstory basal area		N, % organic matter, Ca, Mg, % sand, % silt, thickness of E and A horizons	O horizon thickness
Seedlings and shrubs	N, pH, Ca, Mg, K, % organic matter, % sand, thickness of E and A horizons, hardwood overstory basal area	Openness, % silt		Conifer sapling basal area, O horizon thickness
Herbs	N, pH, Mg, % organic matter, % sand, thickness of E horizon	Ca, openness, hardwood overstory basal area, thickness of A horizon	% silt	K

while axis 2 of the environmental NMDS was positively correlated with axis 2 of both the woody and herbaceous ground-layer NMDS ($P \leq 0.04$) (data not shown).

In support of H$_{3a}$, results of mixed models reveal that the abundances of numerous species and species groups (46 of 55 tested) covaried with one or more environmental variables that were modified by the exclosure treatment (Tables S4–S7). For example, graminoid frequency increased in more compacted soils ($P \leq 0.0001$, Fig. 6a), while Liliaceae frequency declined as the soil E horizon thickened ($P = 0.003$, Fig. 6b). Moreover, the frequencies of 15 species and groups ($n = 34$, Table 3) were explained by mixed models that included additive combinations of compaction, E horizon, openness and/or total BA. When included as a fixed effect in these additive models, deer exclusion was never significant ($P \geq 0.16$). Divergence between the paired plots (deer-access minus exclosure) in the frequency of several common species and groups correlated with the corresponding paired plots' divergence in environmental conditions (Fig. 7, Table S8). In several cases (e.g. *Carex arctata* and common herbs with unassisted dispersal), these correlations matched the significant overall relationships we observed between species/group frequency and environmental conditions (Tables 3 and S4–S7).

Despite indications that shifts in composition are linked to changes in key environmental conditions, we also found evidence, albeit limited, that excluding deer altered relationships between understorey composition and environment, supporting our final hypothesis (H$_{3b}$). Across environmental space, the abundance of four species or groups differed across the fence, as was evidenced in the NPMR results for *Betula papyrifera* saplings, several shrubs and one native forb (*Trientalis borealis*) (Table S9). The genus *Lonicera*, with both native and exotic species, was generally more common in deer-access plots (Fig. 8a). Higher abundances of *B. papyrifera*, late-successional shrubs and *T. borealis*, were observed across a broader environmental space in exclosures compared to deer-access plots (Fig. 8b–d, Table S9). For most species, however, distributions across environmental space were best explained with models containing only the two environmental NMDS axes (Table S10).

Discussion

Although our study focused on temperate forests dominated mostly by northern hardwoods, there was considerable variation, both within and across exclosure sites, in key ecosystem properties, including edaphic conditions, forest structure and
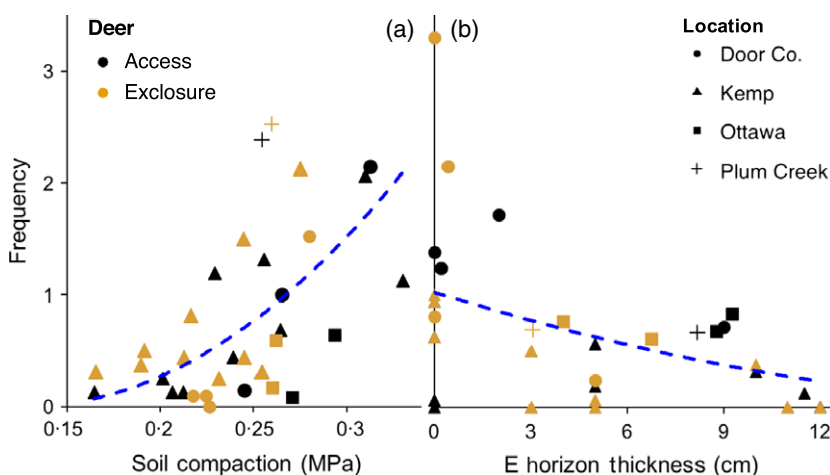

Fig. 6. Plots of (a) graminoid frequency against soil compaction, and (b) Liliaceae frequency against thickness of the soil E horizon, across all 17 exclosures (orange symbols) and deer-access plots (black symbols). Mixed models, in which frequency was square-root transformed, yielded significant trends (dashed line) for graminoids ($P \leq 0.001$) and lilies ($P = 0.003$). In neither case was the effect of deer treatment, or its interaction with the continuous independent variable, significant ($P > 0.1$). Thus, a single trend was fit to all 34 data points. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 3. In additive models, environmental factors affected by deer exclusion, including thickness of the soil E horizon (E, cm), soil compaction (C, MPa), openness (O, %) and total BA (B_T = overstory BA + sapling BA, m^2 ha^{-1}) each explained a significant amount of variation, across exclosure and deer-access plots, in the frequencies of several groundlayer species and species groups. Mixed models, which included location as a random effect, and soil compaction and one of the other three environmental variables as fixed effects, were based on data from all 34 plots. Collinearity precluded models with more than two environmental variables and certain variable combinations, $E + B_T$, $E + O$, or $B_T + O$. Frequencies were square-root transformed to decrease heteroscedasticity. Below, we provide intercepts and fixed effect coefficients for models with significant effects and, for species with more than one significant model, corrected Akaike's information criterion (AICc)

Species/group	Model parameter coefficients					AICc
	a	E	C	O	B_T	
Tree seedlings						
Abies balsamea	−0·21	−0·018**	1·53*	–	–	0·7
	−0·59**	–	2·03**	–	0·006**	4·0
Acer rubrum	−0·57**	–	2·37***	–	0·008****	−4·1
	−0·04	−0·013*	1·45*	–	–	3·4
Pinus strobus	−0·22	−0·013**	1·41**	–	–	–
Tilia americana	0·22	–	−0·98**	–	0·003**	–
Herbs						
Carex arctata	−0·59***	–	3·32****	−0·009***	–	−12·6
	0·90****	–	3·63****	–	0·006***	−12·0
	−0·54***	−0·011*	3·05****	–	–	−9·2
Dryopteris carthusiana	0·48****	0·010*	−1·90***	–	–	–
Maianthemum canadense	−0·74*	–	3·65***	–	0·017****	20·0
	0·19	−0·032**	2·38*	–	–	30·4
	0·05	–	2·81*	−0·017**	–	34·1
Oryzopsis asperifolia	−0·98**	–	3·81****	–	0·01***	15·3
	−0·38	−0·02**	2·84*	–	–	17·7
Taraxacum officinale	−0·41**	−0·015**	2·99****	–	–	–
Trientalis borealis	−0·27	−0·030***	2·73**	–	–	21·3
	−0·36	–	2·99**	−0·016**	–	24·0
	−0·84**	–	3·39**	–	0·009**	25·2
Veronica officinalis	−0·44**	−0·011*	2·59***	–	–	–
Abiotic dispersal	−0·36	–	3·67**	–	0·010*	–
Ingestion dispersal	−0·39	–	2·97**	–	0·017****	–
Exotics	−0·27	−0·035**	4·36**	–	–	–
Graminoids	−0·85*	−0·023*	7·47****	–	–	36·9
	−1·48***	–	8·44****	–	0·010**	37·3

Asterisks denote significance of individual model coefficients: *$P \leq 0.10$; **$P \leq 0.05$; ***$P \leq 0.01$; ****$P \leq 0.001$.

disturbance histories. Thus, detection of a consistent exclusion-mediated shift towards a more abundant and diverse sapling community, supporting H_1, is notable. Regarding the absence of a discernible shift in the groundlayer, studies demonstrating an unambiguous effect of deer on the overall composition of herbaceous communities are particularly uncommon (Mudrak, Johnson & Waller 2009; Jenkins *et al.* 2014; Pendergast *et al.* 2016). Signatures are often confined to variation in individual or population-level attributes (e.g. Anderson 1994; Kirschbaum & Anacker 2005; McGraw & Furedi 2005; Frerker, Sabo & Waller 2014; Dobson & Blossey 2015). Habeck & Schultz (2015) identified several potential causes for the paucity of reported impacts on community-level metrics of herbaceous species composition, including legacy effects of chronic deer overabundance leading to slow groundlayer responses. A growing body of evidence provides compelling support for this tenet (Royo *et al.* 2010; Tanentzap, Kirby & Goldberg 2012; Nuttle, Ristau & Royo 2014; Pendergast *et al.* 2016). We propose an additional possibility:

deer effects on community composition are often partially obscured by complex species responses to the array of influences deer exert on the understorey environment.

Thus, we encourage further exploration of deer impacts on individual environmental variables, and their subsequent indirect effects on community composition. In our study, exclosures clearly affected both biotic and abiotic environmental factors (H_2), including sapling abundance and light availability. Because saplings compete for soil resources as well as cast shade, increases in their abundance within exclosures (e.g. Kuijper *et al.* 2010; Kain *et al.* 2011; Tanentzap *et al.* 2011; Bressette, Beck & Beauchamp 2012) could have strong cascading effects on groundlayer vegetation. Notably, while it was not a focus of our hypotheses, we also observed, as have others (e.g. Kuijper *et al.* 2010), that variation in local environment can exert an important influence on understorey responses to deer. In particular, deer exclusion impacts on the sapling community varied substantially across the locations we studied, and were especially pronounced in stands with
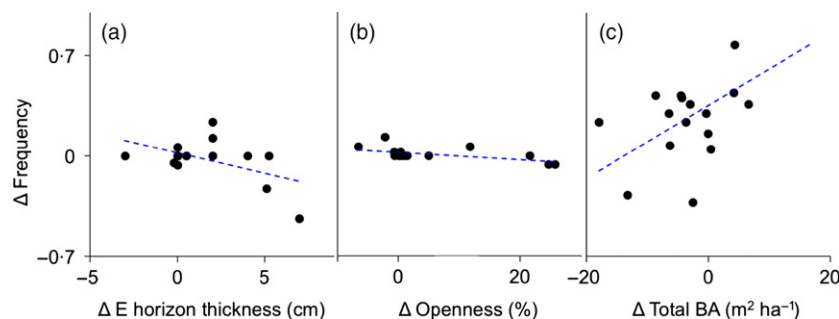
Fig. 7. Treatment divergences (Δ) in species or group frequency plotted against corresponding divergences in environment: (a) Δ *Viola* spp. frequency against Δ E horizon thickness, (b) Δ *Carex arctata* frequency against Δ openness, and (c) Δ ingestion-dispersed herbs against Δ B_T (total basal area). To calculate divergence (Δ), exclosure values were subtracted from deer-access values for each of the 17 plot pairs. Trends were significant in all cases ($P \leq 0.04$ in mixed models with location as a random effect, Table S8). [Colour figure can be viewed at wileyonlinelibrary.com]
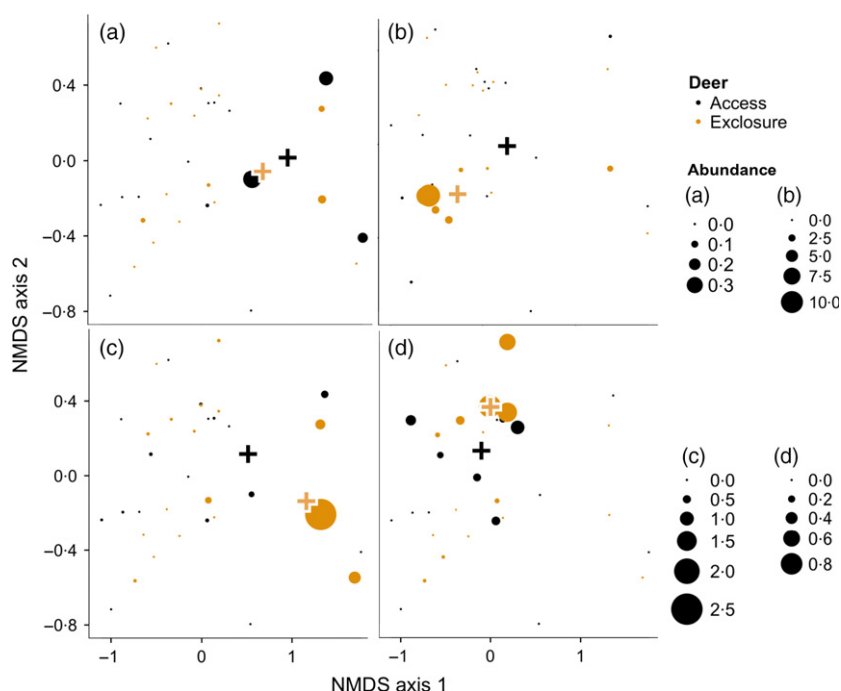

Fig. 8. Variation in species abundances (basal area [$m^2 ha^{-1}$] or frequencies) across our ordination-based characterization of environmental space (NMDS axes 1 and 2 from Fig. 5). Data are values from each of the 34 exclosure and deer-access plots. Circle size denotes basal area or frequency and '+' marks the location of abundance-weighted centroids. The genus *Lonicera* (native and invasive shrubs) was more frequent in deer-access plots (a), while *Betula papyrifera* saplings (b), late-successional shrubs (c) and *Trientalis borealis* (d) were more abundant with broader distributions across environmental space in exclosures compared to deer-access areas. [Colour figure can be viewed at wileyonlinelibrary.com]

lower canopy coverage (less overstory BA), as was also reported by Wright *et al.* (2012) in New Zealand forests with introduced ungulates. These results highlight the context dependency of deer impacts on forest systems (Horsley, Stout & DeCalesta 2003; Tripler *et al.* 2005; Tremblay, Huot & Potvin 2007; Dufresne *et al.* 2009; Collard *et al.* 2010).

Several other studies have also assessed the effects of deer exclusion on understorey light environments. Similar to our study, light availability was greater in deer-access plots than 20-year-old exclosures corresponding with exclusion-mediated increases in understorey tree density (Tanentzap *et al.* 2011). In another case (Nuttle *et al.* 2011), leaf area index was still lower in controls due to species composition differences, despite tree basal areas converging after fences were removed. In contrast, two studies concluded that light availability was not significantly different between exclosures and deer-access areas (Holmes & Webster 2011; Murray, Webster & Bump

2013). Such results could reflect the fact that these studies differed from ours in measurement protocols, exclosure ages, overstory composition and structure, and stand disturbance histories, any of which could affect light levels or their relation to deer exclusion.

Our study corroborates findings by Heckel *et al.* (2010) and Shelton *et al.* (2014) that soil compaction is lower in exclosures than in adjacent deer-access areas. This may reflect the direct effect of deer trampling, as we found no differences in leaf litter thickness or fine root abundance (data not shown). Heckel *et al.* (2010) surmised that recovery from trampling could account for the similar effect they saw in 15-year-old exclosures but Shelton *et al.* (2014) questioned the importance of trampling in driving differences observed just 2 years after exclusion, suggesting instead that deer exert indirect effects like reducing mycorrhizal activity (or fine root abundance).

We also observed that excluding deer reduced the thickness of the E horizon in forest soils. This appears to be the first report of this soil effect. Characteristics of the E horizon and soil podsolization are shaped by a complex suite of climatological, geological and biological factors (Sanborn, Lamontagne & Hendershot 2011). Thus, exclusion impacts could result from the effects deer have on vegetation composition and nutrient inputs. Thinner E horizons may be associated with increases in hardwood sapling BA, as podsolization tends to be negatively related to the abundance of hardwood species relative to conifers (Nørnberg, Sloth & Nielsen 1993; Sanborn, Lamontagne & Hendershot 2011). Without deer depositing urea and faeces, soils within exclosures may also experience less leaching of soil dissolved organic carbon (Chantigny 2003). However, total N concentrations were similar in- vs. outside exclosures, as has been noted by others (e.g. Hobbs 1996; Pastor *et al.* 1998; Persson, Danell & Bergström 2000; Seagle 2003).

Several lines of evidence support our basic premise that responses of understorey species to deer exclusion often reflect the effects deer have on environmental factors such as light availability, soil compaction and E horizon thickness (H$_{3a}$). The frequencies of several species covaried with these key environmental variables. This covariation is also consistent with the ecology of these species, such as the shade tolerance of forest herbs, *Maianthemum canadense* and *Trientalis borealis*, the intolerance of *Rubus idaeus*, and known demographic responses to these environmental factors. Godefroid & Koedam (2004) also reported that the abundance of several congeners of the graminoid taxa present in our study increased with more soil compaction at their sites. Furthermore, increased soil compaction is implicated as an important non-consumptive consequence of deer contributing to declines in growth and fecundity of several forest groundlayer species (Heckel *et al.* 2010).

While few studies have explored how the E horizon affects understorey communities, Wilde & Leaf (1955) found strong relationships between the abundances of many species (including several studied here – Table S4) and the extent of podsolization in temperate hardwood-conifer forests. The thickness of the E horizon may reflect the extent to which organic matter, base cations and other nutrients in upper soil horizons are depleted via leaching of organic acids (Lundström, van Breemen & Bain 2000). Indeed, across our sites, E horizon thickness was inversely correlated with nearly every measure associated with soil fertility (e.g. OM, N, P, Ca, Mg, pH, R^2 for linear relationships ranging from 0·13 to 0·28, results not shown). Therefore, E horizon thickness may provide an integrative index of fertility in the rhizosphere that, in turn, appears to drive understorey community composition (Fig. 3; Hutchinson *et al.* 1999; Burton *et al.* 2011; McEwan & Muller 2011).

Excluding deer had fairly modest effects on the environmental variables, we measured (9–18% of the observed range for each variable, Table S1), which could reflect the relatively young age of these exclosures (i.e. that deer effects on soils persist long after exclusion). Nevertheless, there was a discernible treatment difference in the environmental ordination space for the groundlayer community (Fig. 5) and excluding deer had important effects on community and environmental properties known to affect the distribution and abundance of species (Figs 6–8, Tables 3 and S4–S8). In combination over several years, subtle environmental changes appear to have substantial cumulative impacts on understorey communities.

Lastly, we found some support for the hypothesis (H$_{3b}$) that deer can modify differences between the realized and fundamental niches of plant species (Hutchinson 1959). This perturbation, manifested by shifts in species' relative abundances along environmental gradients, might have resulted from the removal of key stressors (e.g. herbivory) and/or the amplification of others (e.g. competition for light and other resources) within exclosures. In one of the few studies addressing niche shifts due to ungulates, two native herb species expanded their spatial distributions to exploit a wider range of environmental conditions when ungulate pressure was removed (Gómez 2005). The opposite effect has also been found in exotic herbs, where abundances can drop rapidly following deer exclusion (Kalisz, Spigler & Horvitz 2014; Dávalos, Nuzzo & Blossey 2015). However, the best-fit models for few species/groups included both deer and environmental predictors. Thus, responses of understorey species to deer exclusion may actually reflect the effects that deer have on environmental factors to a greater degree than the direct impacts of deer on understorey species via herbivory.

Variation in ecosystem properties among our study locations precluded certain potentially informative data analyses. For example, three of the four oldest exclosures lie on fertile soils derived from dolomitic parent material in Door County (Table S1) and have also had the highest historic deer population densities (15 deer km^{-2}, or potentially much higher, reflecting historical hunting restrictions in state parks – Wisconsin Department of Natural Resources 2010). Because location-to-location variation in edaphic traits and deer population density was conflated with exclosure age, we do not present data on how age influenced community change, although we recognize that it may be an important source of variation (Collard *et al.* 2010; Royo *et al.* 2010; Hidding, Tremblay & Côté 2013; Habeck & Schultz 2015; Pendergast *et al.* 2016).

Results from this study and Frerker, Sabo & Waller (2014) support the contention that regional abundances of many native forb, shrub and palatable tree species may be threatened by overabundant deer. Deer impacts are not only due to the direct effects of herbivory on susceptible plants but also the alteration of a broad suite of environmental conditions. When deer increase light availability and soil resources by reducing sapling abundance, they also alter soil structure and morphology. Such indirect effects act in concert with browsing damage to alter understorey communities in complex and potentially long-lasting ways. However, we acknowledge that inferences drawn from our data are based primarily on correlation, and firmer conclusions regarding causes vs. consequences of the various deer impacts on forest understoreys await the results of future studies manipulating specific

aspects of the environment and/or plant community. Additional research could examine how species' distributions along environmental gradients change across a continuum of deer population densities, paying particular attention to how species perform at their environmental extremes. Results from such studies will help us understand and predict how species and community assemblages are likely to respond to both the direct effects of herbivory and the complex effects that deer can have on environmental conditions.

Authors' contributions

A.S., D.W., K.F. and E.K. designed the study. A.S. ad K.F. collected and processed data. A.S. and E.K. conducted data analyses. A.S. generated the first draft of the manuscript, and all authors contributed substantially to revisions.

Data accessibility

Data used in this study deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.4nf75 (Sabo *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Means (with standard deviations) and ranges, by location and deer treatment, for the 20 biotic and abiotic environmental variables used in our environmental NMDS ordinations.

Table S2. Scores of common species along vegetation NMDS axes for saplings, seedlings and shrubs, and herbs.

Table S3. Correlation coefficients of the relationships between environmental NMDS axes and their individual environmental components.

Table S4. The abundances of several species and species groups were significantly related to thickness of the soil E horizon.

Table S5. The abundances of several species and species groups were significantly related to soil compaction.

Table S6. The frequencies of several groundlayer species and species groups were significantly related to openness.

Table S7. The frequencies of several groundlayer species and species groups were significantly related to total basal area.

Table S8. Relationships between exclosure effects on the frequency of a particular groundlayer species or group and those on individual environmental parameters.

Table S9. Results of nonparametric multiplicative regression (NPMR) for species or groups in which patterns of abundance across our ordination of environmental space differed between exclosure and deer-access treatments.

Table S10. Results of nonparametric multiplicative regression (NPMR) for common species in which abundance varied across our ordination of environmental space but did not differ between exclosure and deer-access treatments.