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STUDIES

Soil chemistry, and not short-term (1–2 year) deer exclusion, explains understory plant occupancy in forests affected by acid deposition

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Abstract

The loss of species diversity and plant community structure throughout the temperate deciduous forests of North America have often been attributed to overbrowsing by white-tailed deer (*Odocoileus virginanus*). Slow species recovery following removal from browsing, or reduction in deer density, has been termed a legacy effect of past deer herbivory. However, vegetation legacy effects have also coincided with changes to soil chemistry throughout the north-eastern USA. In this paper, we assess the viability of soil chemistry (i.e. pH, extractable nutrients and extractable metals) and other factors (topography, light, overstory basal area and location) as alternative explanations for a lack of vegetation recovery. We compared the relative effects of soil chemistry, site conditions and short-term (1–2 year) deer exclusion on single-species occupancy probabilities of 10 plant taxa common to oak-hickory forests in central Pennsylvania. We found detection for all modelled species was constant and high ($\hat{p} > 0.65$), and occupancy probability of most taxa was best explained by at least one soil chemistry parameter. Specifically, ericaceous competing vegetation was more likely to occupy acidic (pH < 3.5), base cation-poor (K < 0.20 cmol$_c$ kg^{-1}) sites, while deer-preferred plants were less likely to occur when soil manganese exceeded 0.1 cmol$_c$ kg^{-1}. Short-term deer exclusion did not explain occupancy of any plant taxon, and site conditions were of nominal importance. This study demonstrates the importance of soil chemistry in shaping plant community composition in the north-central Appalachians, and suggests soil as an alternative, or additional, explanation for deer vegetation legacy effects. We suggest that the reliance on phyto-indicators of deer browsing effects may overestimate the effects of browsing if those species are also limited by unfavourable soil conditions. Future research should consider study designs that address the complexity of deer forest interactions, especially in areas with complex site-vegetation histories.

Keywords: Forest change; forest ecology; occupancy modelling; *Odocoileus virginianus*; plant–soil interactions; soil chemistry; understory plant communities; white-tailed deer.

Introduction

Forest plant communities are composed of species assemblages that result from a host of abiotic and biotic interactions. Factors that shape forest dynamics include, but are not limited to, successional stage (Vitousek and Reiners 1975; Matlack 1994), frequency of disturbance (Oliver 1981), topography (Drohan et al. 2002; Baldeck et al. 2013; Liancourt et al. 2013), herbivory (Anderson and Katz 1993; De la Cretaz and Kelty 2002; Rooney and Waller 2003; Begley-Miller et al. 2014; Habeck and Schultz 2015), soil chemistry (Demchik and Sharpe 2001; Kobe et al. 2002; Kogelmann and Sharpe 2006; Bigelow and Canham 2010) and trophic interactions (Hunter and Price 1992; Veresoglou et al. 2017). Over the last 30 years, several factors have been proposed as potential drivers of plant community dynamics in temperate deciduous forests. Of those, browsing by white-tailed deer (Odocoileus virginanus) has received the most attention, resulting in a multitude of studies linking overbrowsing to a lack of tree seedling regeneration and understory diversity (Marquis and Brenneman 1981; Whitney 1984; Tilghman 1989; Horsley et al. 2003; Carson et al. 2005; Thompson and Sharpe 2005; Long et al. 2012; Stout et al. 2013).

Exclusion experiments across the white-tailed deer range support deer as one of the primary factors shaping plant community composition (Tierson et al. 1966; Marquis and Grisez 1978; Augustine and Frelich 1998; Kay and Bartos 2000; Russell et al. 2001; White 2012; Hidding et al. 2013; Begley-Miller et al. 2014; Habeck and Schultz 2015). Homogenization of forest understories, including the dominance of browse-resistant grasses, sedges and ferns, is attributed to selective browsing pressure of deer populations that are near carrying capacity (Rooney 2001, 2009; De la Cretaz and Kelty 2002; Horsley et al. 2003; Rooney and Waller 2003; Côté et al. 2004; Rooney et al. 2004; Griggs et al. 2006; Goetsch et al. 2011). Research shows that the recovery of browse-sensitive species, specifically liliaceous forest herbs and tree seedlings (Kirschbaum and Anacker 2005; Wakeland and Swihart 2009), is often slow or inadequate in areas dominated by browse-resistant vegetation even after deer densities are reduced (Stromayer and Warren 1997; Webster et al. 2005; Collard et al. 2010; Royo et al. 2010; Goetsch et al. 2011; Stout et al. 2013; Nuttle et al. 2014). It is unclear why recovery of browse-sensitive species has been limited, but it is possible that browsing pressure is still too high or that vegetation dynamics have changed resulting in a competitive advantage for species that are browse-resistant (Griggs et al. 2006; Royo et al. 2010; Pennsylvania–Department of Conservation and Natural Resources, Bureau of Forestry-Ecological Services 2013; McWilliams et al. 2017). This lack of recovery has been termed a legacy effect of deer browsing, often described as the 'ghost of herbivory past' (Carson et al. 2005; Royo et al. 2010; Nuttle et al. 2011, 2014; White 2012; Hidding et al. 2013; Thomas-Van Gundy et al. 2014). However, it is also possible that other factors are limiting vegetation recovery contemporaneously or solely.

Throughout the north-eastern USA, vegetation legacy effects have coincided with widespread changes to soil chemistry attributed to acid deposition (Drohan and Sharpe 1997; Driscoll et al. 2001; Drohan et al. 2002; Johnson 2002; Bailey et al. 2005; Pabian et al. 2012). Hydrogen ions deposited during wet deposition of nitric and sulfuric acids have a higher affinity for negatively charged soil colloids, resulting in leaching of base cations (calcium, magnesium, potassium and sodium) from the soil exchange complex (Helling et al. 1964; Ulrich 1983; Cronan 1994; Altland et al. 2008; Moore and Houle 2013). Soil pH also declines, increasing availability of metals like aluminum and manganese, which are typically not available to plants above a pH of 5.0 (Ulrich 1983; Marschner 1991; Levin 1994). Despite being an essential plant micronutrient, accumulation of manganese in leaf tissues above >700 mg g^{-1} (5.8 cmol$_c$ kg^{-1}) is linked to disruption of photosynthetic processes (Horsley et al. 2000, 2008; St Clair and Lynch 2005). Aluminum has no nutritional value to plants and limits root growth, particularly in acidic soils (Delhaize and Ryan 1995; Panda et al. 2009).

Plants have species-specific responses to changes in soil chemistry. Throughout the north-east, crown dieback and mortality of sugar maple (Acer saccharum) has been attributed to declines in soil calcium and increases in aluminum availability (Long et al. 1997; Kobe et al. 2002; Moore et al. 2008; Bigelow and Canham 2010). Red oak (Quercus rubra) responses to soil chemistry have been mixed, with some studies suggesting sensitivity to both decreasing soil calcium and increases in soil aluminum and manganese (Demchik and Sharpe 2000; St Clair and Lynch 2005), particularly in acidic soils where metals concentrate at the root–mycorrhizal fungi interface (Wasserman et al. 1987). However, other studies of red oak have found no relationship between added soil calcium and magnesium and survival of tree seedlings (Bigelow and Canham 2010; Long et al. 2012). Red maple (Acer rubrum) does not appear to be sensitive to accumulating levels of soil aluminum or manganese (Bigelow and Canham 2010).

Less is known about the response of herbaceous plants to changes in soil chemistry; however, a study in central Pennsylvania found that liming improved nutritional quality of several species by increasing calcium, magnesium and phosphorous content and reducing foliar concentrations of aluminum and manganese (Pabian et al. 2012). White trillium (Trillium grandiflorum) and purple trillium (Trillium erectum) are limited to high calcium sites (>5 cmol$_c$ kg^{-1}). As a result, both species exhibited higher levels of calcium in their foliage compared to painted trillium (Trillium undulatum), which grew on sites with soil calcium levels <5 cmol$_c$ kg^{-1} (Thompson and Sharpe 2005). Horsley et al. (2008) found several species across the north-east to be associated with sugar maple and higher levels of soil calcium (i.e. maidenhair fern (Adiantum pedatum), silvery glade fern (Deparia acrostichoides), rattlesnake fern (Botrychium virginianum) and sweet cicely (Osmorhiza claytonii)). Overall, these studies suggest that in addition to deer browsing, acid deposition may explain vegetation patterns if species distributions are constrained by soil chemistry.

In this paper, we assess the viability of soil chemistry (i.e. pH, extractable nutrients and extractable metals) as an alternative explanation for vegetation legacy effects in the oak-hickory forests of the Ridge and Valley Physiographic Province of Pennsylvania. Due to a complex geologic history (Barnes and Sevon 2014), valleys in this region are dominated by soils derived from limestone parent material, while side slopes and ridges are dominated by shale and sandstone-derived soils, respectively. The oak-hickory forests that dominate the province are primarily located on ridges and side slopes, where soils are poorly buffered against the effects of acid deposition (Mutahhari 1985). Statewide, soil pH has decreased by about one-half unit and soil base cation nutrient pools have declined 50–75 % over the last 50 years, likely due to increased acid inputs (Drohan and Sharpe 1997; Bailey et al. 2005). As a result, there is concern about the effects of soil chemistry changes on oak-hickory forest communities (Demchik and Sharpe 2001; Schreffler and Sharpe 2003; Long et al. 2012).

We compared the effects of soil chemistry and short-term (1–2 year) deer exclusion on single-species occupancy probabilities (MacKenzie et al. 2002) of 10 plant taxa common

to oak-hickory forests in central Pennsylvania (four browse-resistant shrubs and ferns: mountain laurel (*Kalmia latifolia*), huckleberry (*Gaylussacia* spp.), blueberry (*Vaccinium* spp.) and hay-scented fern (*Dennstaedtia punctilobula*); two browse-preferred species: Indian cucumber-root (*Medeola virginiana*), and brambles (*Rubus* spp.); and four tree seedling species: red maple, black birch (*Betula lenta*), red oak and chestnut oak (*Quercus montana*)). Occupancy models incorporate two stochastic processes: (i) the probability a site is occupied by a species and (ii) the probability the species is detected (MacKenzie *et al.* 2002). Detection is often an overlooked parameter in plant studies because plants are sessile, but because of non-observable life stages (i.e. dormancy) and/or observer error, detection is often <1. Conventional modelling approaches can yield spurious parameter estimates if detection is low (Kéry *et al.* 2005), and more plant studies should assess detection probabilities to determine the usefulness of conventional models. We also used two-species occupancy models (Richmond *et al.* 2010) to assess biotic interactions between species to determine if apparent competition from browse-resistant taxa explained vegetation trends.

Our analysis addresses three questions: (i) does soil chemistry or rapid species establishment following 1–2 years of deer exclusion explain patterns of species occupancy across central Pennsylvania; (ii) does the presence of browse-resistant taxa limit occupancy of browse-preferred taxa or seedlings; and (iii) do sampling site factors, such as total cover or date of visit, affect a species' detection probability? To our knowledge, this is the first study to assess alternative explanations of vegetation legacy effects in an occupancy framework. Even though soil chemistry and deer browsing have been proposed as explanations for current vegetation patterns throughout Pennsylvania (Marquis 1981; Horsley *et al.* 2003; Krueger and Peterson 2009; Miller *et al.* 2017), rarely have these factors been studied simultaneously (Thompson and Sharpe 2005; Long *et al.* 2012). Additionally, we assessed biotic interactions between browse-resistant and browse-preferred species to determine if vegetation dynamics were influenced by indirect effects of deer browsing (i.e. competitive release of browse-resistant taxa), and evaluated the importance of accounting for detection in studies of common plant taxa.

Methods

We randomly selected 24 vegetation sampling sites from 100 potential sampling locations established across two state forests (Rothrock and Bald Eagle state forests) in the Ridge and Valley Physiographic Province of central Pennsylvania (Fig.
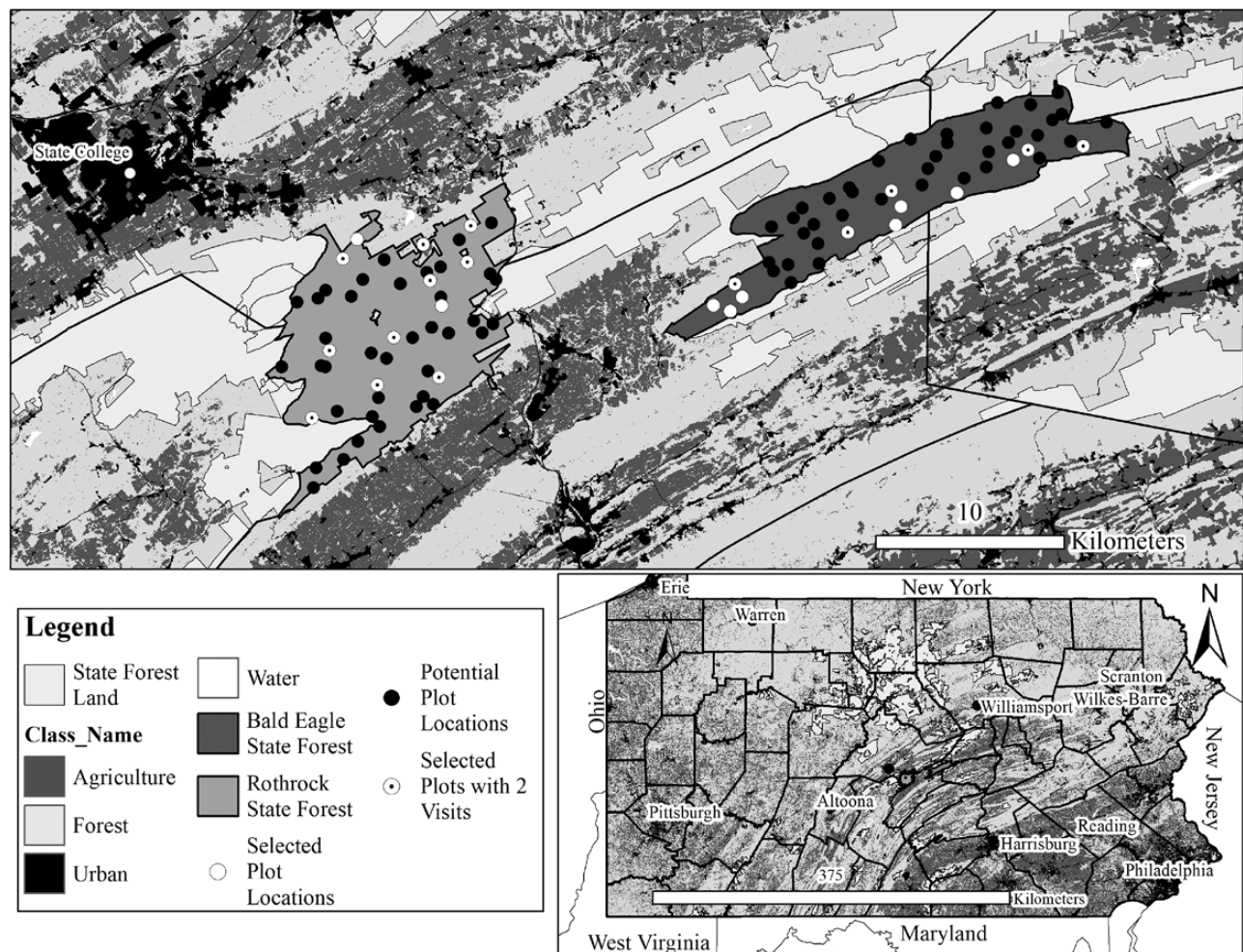

Figure 1. Map of the study area and Pennsylvania land cover (agriculture, forest, urban and water). The study area is highlighted by dark grey polygons (Rothrock State Forest, left; Bald Eagle State Forest, right), and is located on state forest land (light polygons). Open and closed circles on the larger map represent 100 potential sampling locations across the entire study area. Open circles indicate chosen sampling sites (plot locations) for this study, and open circles with a centre dot represent the 14 sites that were visited twice in 2015.

1). Selected sampling sites included one location within an already-established commercial deer exclosure. At each of the 24 sampling sites, we established 11 circular 14.62 m diameter subplots in a network such that a single subplot's centre was not more than 36.5 m straight-line distance from the next nearest subplot's centre (Fig. 2). We established five of these subplots (numbers 1–5) in 2013 and the other six (6–11) in 2014. At the same time, we nested a single smaller circular 3.30 m diameter microplot 3.66 m due east (90° azimuth) of each subplot's centre. We enclosed microplot 5, and three randomly selected microplots from subplots 6 through 11 with 1.82 m tall heavy-duty poly deer fencing to exclude deer. Throughout the text, sampling site to refers to the network of 11 subplots and nested microplots at a single sampling location.

Study area characteristics

Across the study area the climate is temperate, with mean annual precipitation of 104 cm, a night-time temperature range of 4.5 °C in winter and 16 °C in summer, and a daytime temperature range of 4 °C in winter and 29 °C in summer (National Oceanic and Atmospheric Administration 2017a). The growing season averages 182 days from 22 April to 21 October (National Oceanic and Atmospheric Administration 2017b). The study area is
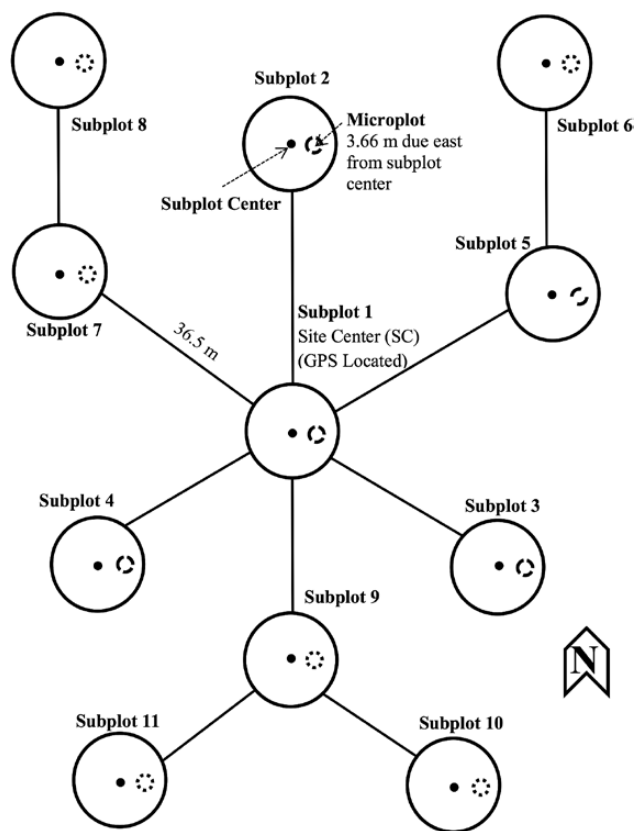

Figure 2. Configuration of subplots 1–11 at each sampling site. The centre of subplot 1 is defined as site centre (SC). Subplots 1–5 were established in 2013, while subplots 6–11 were established in 2014. Each circular subplot is 14.62 m in diameter with a total area of 1/60th ha (168 m²). Nested inside each subplot circle is a smaller 3.30 m diameter microplot with an area of 1/2500th ha (small dashed circle only; 4.05 m²). Microplots indicated by long dashes are controls, while microplots outlined with short dashes (dots) indicate potential fencing locations. Fencing treatment was randomly assigned to three of the microplots labelled 6 through 11 at each site. Microplot 5 (two-line dash) was consistently fenced across sites.

located within the Ridge and Valley Physiographic Province of Pennsylvania, and sampling sites range in elevation from 400 to 700 m above sea level. Based on county-level 1:12 000 digital soil survey data (Pennsylvania Spatial Access Database 2014), soils at each sampling site were classified into one of four soil taxonomic classes that encompass several soil series: Fine-loamy, mixed, semi-active, mesic Typic Hapludults (competing series: Ungers, Clymer, Gilpin, Leck Kill, Murrill soil series, six sites); Fine-loamy, mixed, semi-active, mesic Aquic Fragiudults (competing series: Buchanan series, six sites); Loamy-skeletal, siliceous, active, mesic Typic Dystrudepts (competing series: Hazleton, Wallen and Dekalb series, six sites); and Sandy-skeletal, siliceous, mesic Entic Haplorthods (competing series: Leetonia series, six sites). All sites are forested hardwood stands dominated by red oak, chestnut oak, black oak (*Quercus velutina*) and scarlet oak (*Quercus coccinea*) at higher elevations, and red oak and yellow poplar (*Liriodendron tulipifera*) at lower elevations (Fike 1999).

Vegetation monitoring

From 26 May to 10 August 2015, we conducted overstory vegetation inventories across all subplots and understory vegetation inventories across all microplots at all 24 sampling sites. At 14 of those sites, we collected vegetation data twice across two separate sampling dates with a minimum of 20 days between visits (mean = 38 days). We divided data into three categories for collection: (i) overstory trees, (ii) tree seedlings and (iii) vegetative cover. We classified all arborescent, woody species ≥ 12.7 cm diameter at breast height (DBH) as overstory trees, and live, arborescent, woody species ≤ 2.54 cm DBH as tree seedlings. We identified, measured for DBH and recorded the live/dead status of all overstory trees within 14.62 m diameter subplot, and counted the total number of individuals of tree seedling species by height category (categories were: 1 = <0.15 m, 2 = 0.15–0.3 m, 3 = 0.3–0.9 m, 4 = 0.9–1.5 m, 5 = >1.5 m) in each 3.30 diameter microplot. We excluded tree seedlings <0.3 m tall (categories 1 and 2) from analysis to reduce variability in counts due to differences in overstory seeding.

We defined vegetative cover as any understory vegetation not considered a tree seedling or overstory tree. Cover data included several different vegetation types (e.g. shrubs, herbs, ferns, grasses, sedges, rushes and vines), and due to identification challenges (e.g. lack of reproductive structure present at the time of sampling), we assigned some taxa to a vegetation category rather than species (e.g. grasses (Poaceae), sedges (Cyperaceae), rushes (Juncaceae), some polypod ferns (Polypodiaceae), blackberries (*Rubus* spp.), blueberries (*Vaccinium* spp.), huckleberries (*Gaylussacia* spp.), goldenrods (*Solidago* spp.), asters (Asteraceae) and violets (*Viola* spp.)). For each cover taxon, we recorded percent cover in 10 % increments, ranging from 0–10 % (category 0) to 90–100 % (category 9), and converted each category to a midpoint single value (ratio scale) for each estimate. Because taxa can overlap at different heights, the amount of cover in each microplot frequently exceeded 100 %.

Environmental covariates

We modelled occupancy and detection probabilities across subplots as a function of several environmental covariates using a suite of candidate models and selected the best model using Akaike's Information Criteria adjusted for sample size (AIC$_c$, Burnham and Anderson 2002; see the Data analysis section for more information on model selection). For occupancy, we considered several soil and non-soil covariates separately as potential drivers of occupancy relationships across the study area. Soil covariates included uppermost organic and mineral

horizon measurements for soil pH (*pHO* and *pHM*), calcium (*CaO* and *CaM*), magnesium (*MgO* and *MgM*), potassium (*KO* and *KM*), manganese (*MnO* and *MnM*), aluminum saturation (*AlSatO* and *AlSatM*), effective cation exchange capacity (*ECECO* and *ECECM*) and total base cations (*SumBasesO* and *SumBasesM*). Non-soil covariates included microplot topography (*slope*, *elevation* and *aspect* (north or south)), light availability (*pctopen*), subplot basal area (*ba*), location (Rothrock or Bald Eagle state forest (*sf*)) and deer exclusion status (*fence*, yes or no).

Within each candidate model for occupancy, we modelled detection probabilities one of three ways: (i) as a constant (no relationship with any covariate), (ii) as a function of visit day (*calendar day*) or (iii) as a function of total microplot percent cover (*tpc*). Again, the best candidate model was chosen using AIC$_c$. These covariates were considered because the presence of dense cover had the potential to decrease detection of taxa hidden underneath layers of vegetation, whereas visits early or late in the growing season could have caused us to miss taxa (e.g. spring ephemerals) that were not present above the soil surface or had senesced. We did not include correlated covariates (Pearson correlation coefficient, $r > 0.55$) in the same model.

We collected soil samples by hand from a 0.6 m diameter soil pit to 40 cm depth at subplots 1, 5, 6, 7, 8, 9, 10 and 11 at each sampling site and at subplots 2–4 when time allowed. We subdivided samples according to horizon characteristics rather than depth, and most commonly collected two primarily organic horizons (Oe/Oi and Oa/A) followed by 1–3 mineral horizons at each subplot. The Oa and A horizons were collected together because the A horizon was thin and indistinguishable from the Oa horizon. Following collection, we dried each sample on kraft paper at ~23 °C, ground it by hand using mortar and pestle and sieved it to 2 mm to remove coarse debris. We removed 5.00 g of soil from the sample and sent it to the Ag Analytical Services Laboratory in University Park, PA for analysis of pH using 0.01 M CaCl$_2$ with a 1:5 soil-to-solution ratio (Hendershot *et al.* 2008). pH was extracted using the same method for all samples.

The USDA-NRCS Kellogg Soil Survey Laboratory (KSSL) in Lincoln, NE extracted extractable Ca and K (cmol$_c$ kg^{-1}) from the remaining samples at unbuffered soil pH using ammonium acetate (NH$_4$OAc) and displacement with 2 M KCl (Hendershot *et al.* 2008; Soil Survey Staff 2014). The KSSL also analysed extractable metals (Mn (mg kg^{-1})) separately using 1 N KCl (Long *et al.* 1997, 2011; Soon *et al.* 2008). To calculate aluminum saturation, we divided the total extractable aluminum by the effective cation exchange capacity (ECEC; sum of base cations + Na + Al) and logit transformed the percentage. We have listed the manual reference number for each method (Soil Survey Staff 2014) in the supporting information [see **Supporting Information—Table A**], and we converted Mn values to cmol$_c$ kg^{-1} for consistency. To ensure consistency in our assessment of soil chemistry, we only included extracted values from the uppermost organic horizon (the Oa/A horizon) and the uppermost mineral horizon (the E or B horizon) during analysis.

To estimate slope, elevation and aspect for microplot locations, we used 10 m × 10 m Pennsylvania DCNR Digital Elevation Models (DEMs) accessible through Pennsylvania Spatial Data Access (PASDA) website (Department of Conservation and Natural Resources 2006) to extract elevation and derive aspect and slope from field-collected GPS coordinates. We converted degrees aspect to categorical cardinal direction (N or S) and adjusted north and south categories by 25° azimuth to include the effect of ridge direction on aspect (Long *et al.* 2010). North facing slopes were classified as aspects > 245° but <65° and south facing slopes were classified as aspects > 65° but <245°.

For understory openness, we used the proportion of open sky at 1 m above ground level as a surrogate for light availability for each microplot during the growing season (Gonsamo *et al.* 2013) (methods and equipment described by Frazer (1999)). We photographed all microplots at a sampling site in the same 2-h window, and calculated mean percent sky openness for each microplot from all analysed photos. We logit transformed openness values prior to analysis.

We assigned deer exclusion category (1 = yes or 0 = no) based on whether a microplot was inside of a functioning deer exclosure. One sampling site occurred within already established DCNR Bureau of Forestry (BoF) deer exclosure meant to minimize browsing effects on tree seedling regeneration following timber harvest. Additionally, we fenced 4 of the 11 microplots at each sampling location (regardless of deer exclusion status prior to site establishment). Fences were ~3 m × 3 m and established 1–2 years prior to 2015 vegetation surveys (24 in 2013, and the remaining 72 in 2014). Eleven fences occurred within a 5-year commercial deer exclosure. We found no statistical differences in stem counts or vegetative cover between 5-year and other fenced subplots across sampling sites, so we did not include fence age as a covariate. We assigned state forest as a categorical variable, and we reported basal area as the sum of live tree total area (m^2 = 0.00007854 * DBH^2) per subplot extrapolated to m^2 ha^{-1} (the standard reporting unit). Basal area is a surrogate variable for overstory light availability because lower basal areas are typically associated with more recent overstory disturbance (e.g. harvest, disease or insect mortality).

Missing covariates

After we removed subplots from the data set that were missing covariates, some species had parameters (either occupancy probability (Ψ) or probability of detection (p)) that were not estimable due to small sample size. We pooled all covariate data by sampling site and applied this pooled value to subplots that were missing data when variability within site was less than variability between sites (Cochran 1977). Within-site variability was calculated as:

$$\sigma_{within}^2 = \frac{\sum_{i=1}^{n} \sum_{j=1}^{m} (y_{ij} - \bar{y}_i)^2}{n(m-1)},$$

where y_{ij} is the covariate value at subplot (j) within site (i), $\bar{y}_i$ is the mean covariate value across sites (i), m is the total number of subplots with full covariate data (171) and n is the total number of sampling sites (24). The equation for between-site variability is:

$$\sigma_{between}^2 = \frac{\sum_{i=1}^{n} (\bar{y}_i - \bar{\bar{y}})^2}{n-1},$$

where $\bar{y}_i$ is the mean covariate value at site (i), $\bar{\bar{y}}$ is the mean covariate value across all sites and n is the total number of sampling sites (24). If $\sigma_{within}^2 < \sigma_{between}^2$, then we pooled samples within a site [see **Supporting Information—Table B**]. After pooling, we used 250 of the 261 possible subplots to assess occupancy across all taxa.

Data analysis

Occupancy models

We determined which covariates most explained occupancy across the study area for 10 taxa with single-species occupancy models (MacKenzie *et al.* 2002) in program MARK (White and Burnham 1999). Occupancy models account for missed observations that would be otherwise interpreted as plant absence. Taxa modelled were mountain laurel, huckleberry,

blueberry, hay-scented fern, red maple, black birch, red oak, chestnut oak, Indian cucumber-root and brambles. We chose these taxa because they are relatively common throughout the study area and represent a wide variety of deer browsing preferences. We assumed populations were closed (no immigration or emigration), and did not assume that detection probability was 1.0. Imperfect detection is often an overlooked parameter in plant studies, despite its effect on the accuracy of population abundance and survival estimates (Kéry *et al.* 2005; McCarthy *et al.* 2013). For each taxon, we use single-species occupancy models to estimate detection probability, occupancy probability and odds ratios (ORs; Szumilas 2010) for the best model [see Supporting Information—Tables C and D] according to Akaike's Information Criterion (AIC_c). Variables were added to the null model one at a time to create separate models and we compared their AIC_c values. Covariates that could affect detection were added first, and if $\Delta AIC_c < 2$ the covariate was retained in the model. If two models with different variables were competitive ($\Delta AIC_c < 2$), we included those variables in a single model and compared its AIC_c to the null model. We repeated this process for occupancy, starting instead with the best model for detection instead of the null model for both detection and occupancy. Finally, we inverted the model selection process, starting again with a null model, but we performed model selection on occupancy first, then detection. Models converged on the same result regardless of the order the parameters were modelled. We visited some sites only once but their encounter histories were included in the analysis to help increase the precision of estimates of occupancy (Shannon *et al.* 2014).

To assess if the two most abundant non-preferred shrubs (mountain laurel or huckleberry) affected occupancy of other taxa, we used two-species occupancy models in program MARK. Two-species occupancy models assess biotic interactions between two species only, specifically focusing on whether a dominant species (species A) affects occupancy of a non-dominant species (species B) by assessing levels of co-occurrence between both species (Richmond *et al.* 2010). Encounter histories of dominant species A (mountain laurel or huckleberry, depending on the model) were paired with encounter histories of a non-dominant species B (hay-scented fern, huckleberry, Indian cucumber-root, red maple, red oak or chestnut oak) for each visit and compared using a single model. Again, we compared a suite of candidate models where occupancy was a function of both soil and non-soil covariates (see Environmental covariates section for full list) by adding variables to the null model and selected the best model according to AIC_c [see Supporting Information—Tables E and F].

When occupancy probability of species B varied with the presence of the dominant species (species A), we reported the Species Interaction Factor (SIF). The SIF measures the level of co-occurrence of both species relative to the number of single occurrences of each species, and it is mathematically defined as:

$$\text{SIF} = \psi^{BA}/(\psi^A * \psi^{Ba}),$$

where ψ^{BA} is the occupancy probability for species B when species A is also present, ψ^A is the occupancy probability for species A when species B is absent and ψ^{Ba} is the occupancy probability for species B when species A is absent. A SIF >1 indicates that both species are more likely to co-occur than expected by chance, while a value <1 indicates the inverse.

For all two-species occupancy models, a fully parameterized model has eight derived parameters: three for occupancy and five for detection (Table 1). Occupancy probabilities are calculated for the dominant species (ψ^A), the non-dominant species when dominant species is absent (ψ^{Ba}) and the

Table 1. List of estimable parameters in a fully parameterized two-species occupancy model.

Model parameter	Dominant species (A)	Non-dominant species (B)
ψ^A	Present	Absent
ψ^{Ba}	Absent	Present
ψ^{BA}	Present	Present
p^B	Absent	Present
p^A	Present	Absent
r^A	Present, detected	Present
r^{Ba}	Present, not detected	Present, detected
r^{BA}	Present, detected	Present, detected

non-dominant species when the dominant species is present (ψ^{BA}). The five detection parameters are split into two groups: detection when one species is absent (p) and detection when both species are present (r). Detection parameters are further subdivided based on which species were present (p^B, p^A), and whether the dominant or non-dominant species was detected (r^A, r^{Ba}, r^{BA}). We did not expect detection of the either the non-dominant (p^B) or dominant species (p^A) to depend on presence (r^A) or detection of the other species (r^{Ba} or r^{BA}); therefore, we set $p^B = r^{Ba} = r^{BA}$ and $p^A = r^A$ for all models.

State forest differences

Location (state forest) was an important predictor of occupancy for three of the four tree seedling taxa. We assessed three potential causes for the state forest effect: (i) differences in responses to deer exclusion (change in mean stem counts of tree seedlings in fenced areas from 2014 to 2016), (ii) differences in soil chemistry across the entire soil profile (uppermost organic and mineral horizons [Oa/A and E (or B if E was absent)], plus the bottommost mineral horizon [B]) and/or (iii) differences in topography (slope, elevation and aspect). Statistically, differences in mean tree seedling stem counts were compared using linear regression, aspect was compared using Pearson's chi-squared test and all other covariates (all soil chemistry measures, elevation and slope) were compared using a multivariate analysis of variance (MANOVA).

Results

Single-species occupancy models

Probability of detection (p) was best modelled as a constant, and detection probabilities were high ($\hat{p} > 0.65$) for all 10 taxa (Fig. 3). Common taxa that were considered browse-resistant shrubs and ferns had the highest detection probabilities ($\hat{p} > 0.92$ for all taxa), while Indian cucumber-root and tree seedlings (red maple, black birch, red oak and chestnut oak) had variable but similar detection probabilities ($\hat{p} > 0.66$ for all taxa). Brambles had a 100 % detection probability ($p = 1$). The probability of detecting any species across two visits was ≥89 %.

Huckleberry occupancy increased with decreasing organic horizon pH, and decreased with increasing levels of uppermost mineral horizon potassium (Fig. 4, top right). For every 1-unit increase in organic horizon pH, huckleberry was 91 % less likely to occur, and for every 0.1 $cmol_c$ kg^{-1} increase in mineral horizon extractable potassium, that decrease was 50 % (Table 2). Occupancy of mountain laurel was negatively associated with increasing manganese and increasing pH (Fig. 4, top left). The probability of mountain laurel occurrence on a site decreased by more than 90 % for every 1-unit increase in organic horizon
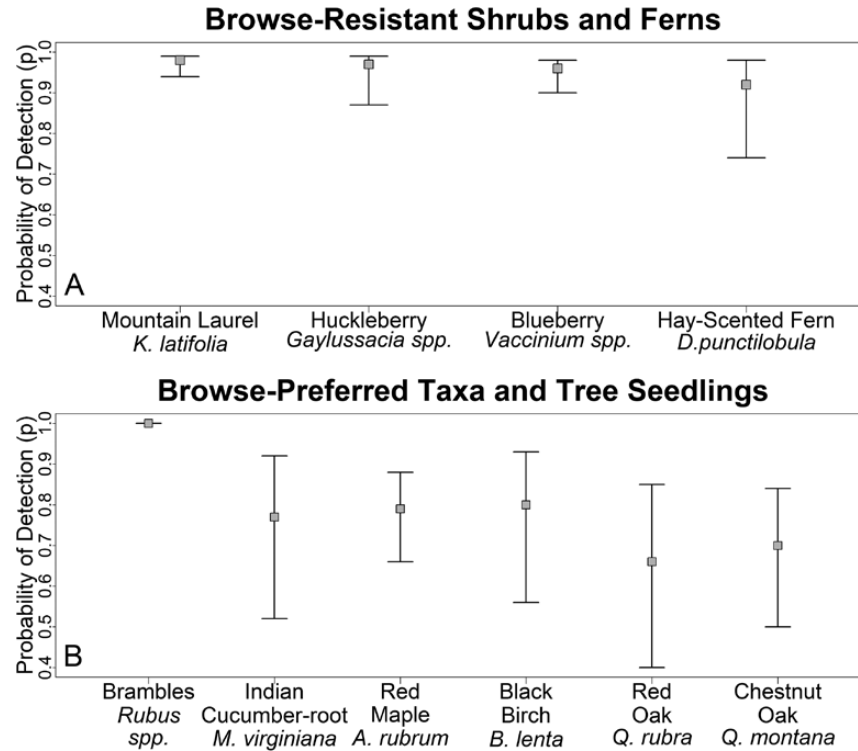
Figure 3. Probability of detection for browse resistant shrubs (mountain laurel, huckleberry and blueberry) and ferns (hay-scented fern) (panel A), and browse-preferred taxa (brambles and Indian cucumber-root) and tree seedlings (red maple, black birch, red oak and chestnut oak) (panel B). Error bars represent 95 % confidence intervals.

pH (Table 2), and decreased 48 % for every 0.1 cmol$_c$ kg^{-1} increase in organic horizon extractable manganese (Table 2). Similarly, increasing levels of mineral horizon extractable manganese decreased blueberry occupancy, and increasing levels of mineral horizon extractable potassium were associated with a decline in blueberry occupancy probability (Fig. 4, bottom left). For every 0.1 cmol$_c$ kg^{-1} increase in organic horizon extractable manganese, blueberry was 36 % less likely to occur, whereas the chances of occurrence decreased by more than 35 % for each 0.1 cmol$_c$ kg^{-1} increase in mineral horizon extractable potassium (Table 2). Hay-scented fern occupancy increased as a function of increasing organic horizon pH only (Fig. 4, bottom right), and with each half-unit increase in pH, hay scented fern was nearly 8 times more likely to occur (Table 2).

Tree seedling occupancy differed between state forests for all species except black birch, with Rothrock having higher occupancy compared to Bald Eagle for all species (Fig. 5). Comparatively, Rothrock had higher levels of total extractable bases (Ca, Mg and K) in the organic soil horizon ($t_{(170)}$ = 3.36, *P* = 0.001), Mg ($t_{(170)}$ = 4.68, *P* < 0.001), K ($t_{(170)}$ = 3.44, *P* = 0.001) in the mineral horizons, and higher pH ($t_{(170)}$ = 2.57, *P* = 0.011) in the bottommost mineral horizon than did Bald Eagle [see **Supporting Information—Table G**]. Conversely, Bald Eagle had higher levels of soil Ca ($t_{(170)}$ = −2.17, *P* = 0.032) and ECEC ($t_{(170)}$ = −3.24, *P* = 0.001) in the bottommost mineral soil horizon than did Rothrock, indicating nutrient losses to a depth of ~40 cm [see **Supporting Information—Table G**]. Additionally, Bald Eagle sites were steeper ($t_{(170)}$ = −2.95, *P* = 0.004) and found more frequently on north facing slopes ($\chi^2_{(1,171)}$ = 14.707, *P* < 0.001) compared to sites in Rothrock [see **Supporting Information—Table H**], but there were no differences by state forest in responses to fencing [see **Supporting Information—Table I**]. Overall, covariate differences by state forest suggest that differences in occupancy

relationships were probably due to soil chemistry changes throughout the entire soil profile. These changes are most likely attributed to differences in leaching due to topography, including slope and aspect.

Red oak occupancy probability differed by state forest but not individual measures of soil chemistry (Fig. 5, top right), with occurrence of red oak 28 times more likely in Rothrock compared to Bald Eagle (Table 2). Chestnut oak occupancy increased with decreasing openness and decreased with increasing organic horizon extractable calcium across both state forests (Fig. 5, bottom left and bottom right), but overall occurrence was three times more likely in Rothrock compared to Bald Eagle (Table 2). For every 5 % increase in open sky, chestnut oak was 33 % less likely occur, and for every 1.0 cmol$_c$ kg^{-1} increase in organic horizon extractable calcium, the chances of occurrence were reduced by 22 % (Table 2). Red maple was also three times more likely to occur in Rothrock compared to Bald Eagle, but red maple occupancy was unrelated to individual measures of soil calcium and instead increased with increasing mineral soil ECEC (Fig. 5). For every 1.0 cmol$_c$ kg^{-1} increase in ECEC, red maple was 25 % more likely to occur (Table 2). Black birch occupancy patterns were not explained by any measured covariate, and as a result black birch occupancy was best modelled as a constant (Table 2).

Bramble occupancy was best modelled as a function of both mineral horizon manganese and subplot basal area, and Indian cucumber-root occupancy was best modelled as a function of both microplot canopy openness and organic horizon extractable manganese. Brambles were eight times more likely to occur with each 0.1 cmol$_c$ kg^{-1} increase in mineral horizon extractable manganese (Fig. 6, left), and occupancy was zero whenever basal area was >24 m^2 ha^{-1} regardless of the amount of mineral soil extractable manganese present (Table 2). Indian cucumber-root had greater occupancy at low levels of extractable manganese
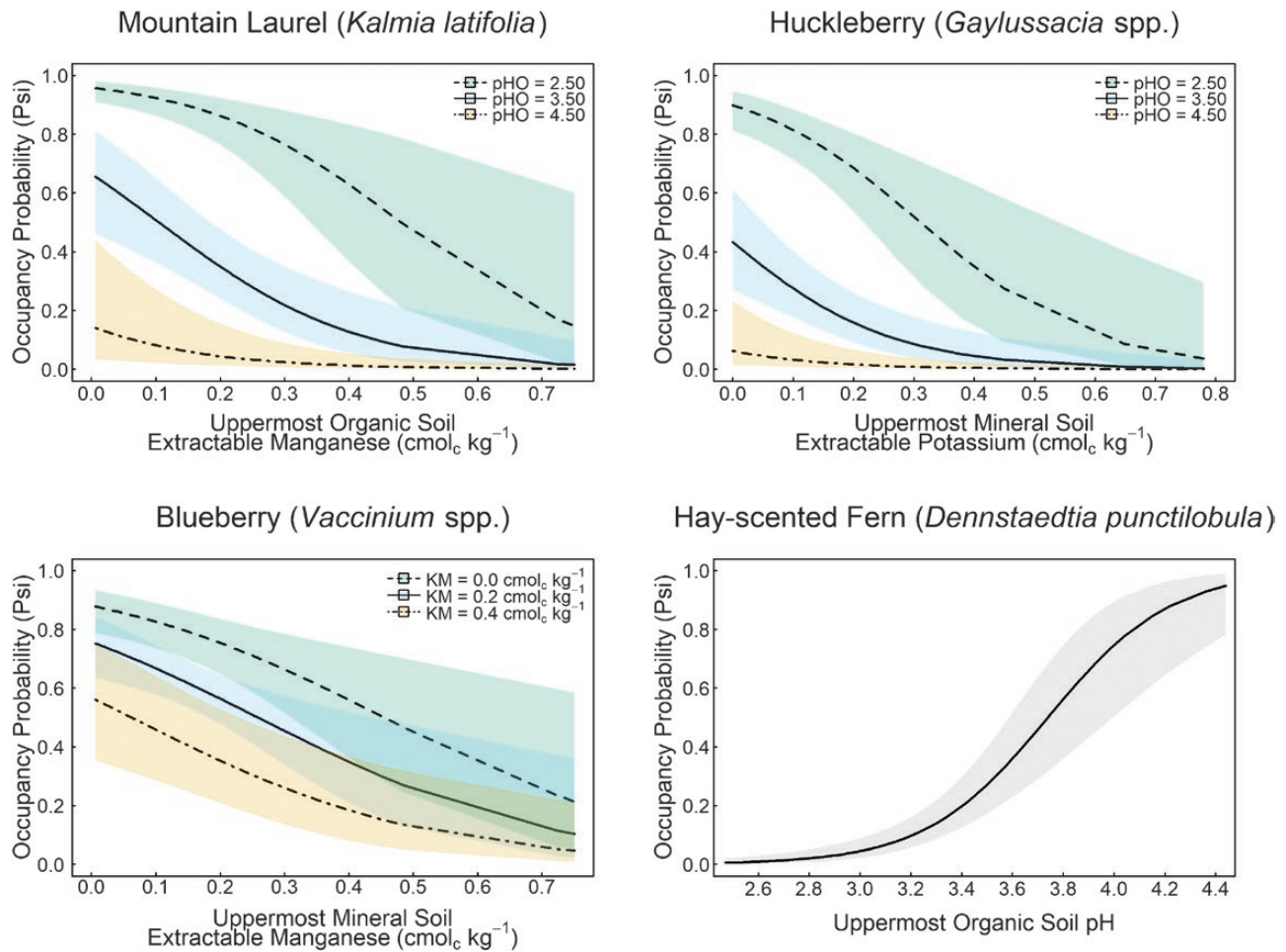
Figure 4. Occupancy probability as a function of environmental covariates for mountain laurel (top left), huckleberry (top right), blueberry (bottom left) and hay-scented fern (bottom right). Graphs represent the best model for each taxon selected using AIC$_c$, and x axes represent the range of covariates sampled. Shaded areas (regardless of colour) represent 95 % confidence intervals. Colours represent different levels of a covariate as indicated in the subfigure legend.

Table 2. Odds ratios from single-species occupancy models for each covariate. Parameters are: uppermost organic horizon pH (*pHO*), uppermost organic horizon extractable manganese (*MnO*), uppermost mineral horizon extractable potassium (*KM*), state forest (*sf*), uppermost organic horizon extractable calcium (*CaO*), uppermost mineral horizon effective cation exchange capacity (*ECECM*), basal area (*ba*) and understory microplot canopy openness (*pctopen*). Correlated covariates were not included in the same model (Pearson correlation coefficient, *r* > 0.55).

| Taxon	Parameter	Odds ratio	95 % LCL	95 % UCL
Mountain laurel (*Kalmia latifolia*)	*pHO*	0.09	0.03	0.22
	MnO	0.52	0.37	0.73
Huckleberry (*Gaylussacia* spp.)	*pHO*	0.09	0.03	0.22
	KM	0.50	0.35	0.71
Blueberry (*Vaccinium* spp.)	*MnO*	0.64	0.49	0.84
	KM	0.65	0.50	0.84
Hay-scented fern (*Dennstaedtia punctilobula*)	*pHO*	7.91	3.90	16.04
Red oak (*Quercus rubra*)	*sf*	28.04	3.68	213.65
Chestnut oak (*Quercus montana*)	*CaO*	0.78	0.64	0.95
	pctopen	0.67	0.49	0.93
	sf	3.36	1.33	8.46
Red maple (*Acer rubrum*)	*sf*	3.10	1.57	6.10
	ECECM	1.25	1.07	1.46
Brambles (*Rubus* spp.)	*ba*	0.69	0.55	0.87
	MnM	8.23	2.16	31.30
Indian cucumber-root (*Medeola virginiana*)	*MnO*	0.04	0.01	0.21
	pctopen	1.48	1.12	1.97
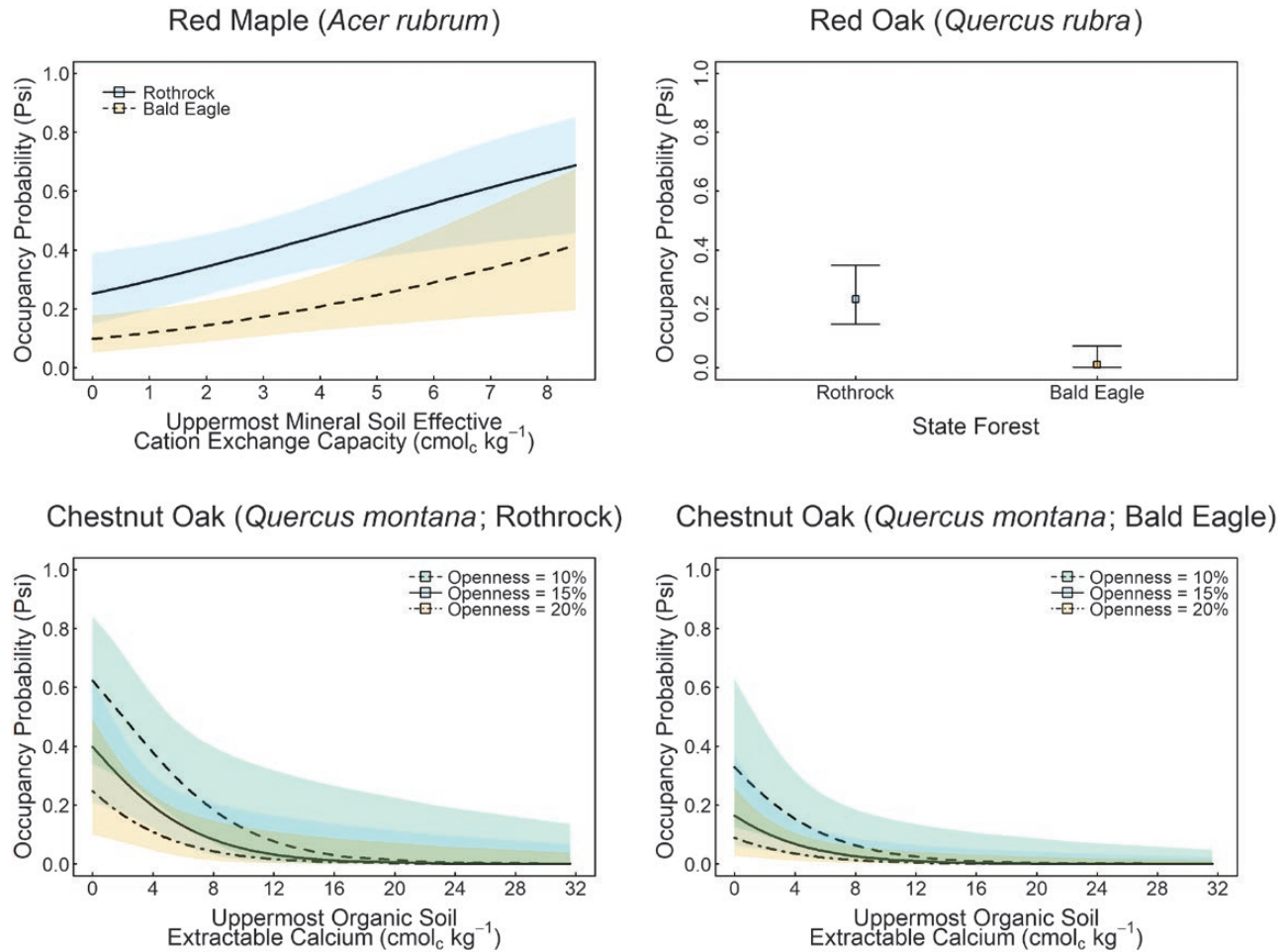
Figure 5. Occupancy probability as a function of environmental covariates or red maple (top left), red oak (top right) and chestnut oak (bottom left and bottom right). Graphs represent the best model for each taxon selected using AIC_c, and x axes represent the range of covariates sampled. Shaded areas (regardless of colour) represent 95 % confidence intervals. Colours represent different levels of a covariate as indicated in the subfigure legend.

and high openness (Fig. 6, right), and was 96 % less likely to occur with every 0.1 $cmol_c$ kg^{-1} increase in organic horizon extractable manganese (Table 2). Additionally, for every 5 % increase in open sky, Indian cucumber-root was 48 % more likely to occur (Table 2). The best models for occupancy of browse-preferred plants did not include deer exclusion as a covariate for any taxon.

Two-species occupancy models

Detection probability for both species (*A* and *B*) in all two-species occupancy models was best modelled as constant between visits, indicating that total percent cover and date of visit did not influence detection. Additionally, because detection for both species *A* and species *B* was modelled as equal for all detection parameters, the detection probabilities for species *A* (*pA*) and *B* (*pB*) were equal to the detection probabilities for that species (*A* or *B*) found in Fig. 3.

Red oak and chestnut oak occupancy was higher when mountain laurel was present, but their occupancy was best modelled as constant and unaffected by huckleberry presence (Table 3). The SIF between red oak and mountain laurel overlapped 1 (SIF = 1.19, 95 % CI = 0.97–1.42) indicating that red oak was not more or less likely to co-occur with mountain laurel across sites than expected by chance. The SIF for chestnut oak and mountain laurel also overlapped 1 (SIF = 1.19, 95 % CI = 0.96–1.41), indicating, again, that chestnut oak was not more likely to co-occur with mountain laurel across sites than expected by chance.

Indian cucumber-root, hay-scented fern and black birch occupancy was unaffected by the presence of mountain laurel or huckleberry; occupancy was best modelled as constant regardless of the presence of either dominant ericaceous shrub (Table 3). Red maple was more likely to occupy sites where either mountain laurel or huckleberry was present than where either species was absent (Table 3). The SIF for red maple and mountain laurel was >1 (SIF = 1.17, 95 % CI = 1.03–1.31), which indicated that red maple was more likely to co-occur with mountain laurel than expected by chance. The same trend also was true for red maple and huckleberry (SIF = 1.31, 95 % CI = 1.03–1.59).

Discussion

Soil chemistry most explained occupancy patterns of plant taxa across the study area, as evidenced by the final model output for each taxon (research question i). Expectedly, ericaceous, browse-resistant shrubs (huckleberry and mountain laurel) were associated with acidic (pH < 3.5), potassium-poor (K < 0.20 $cmol_c$ kg^{-1}) sites. Ericaceae have specialized ericoid mycorrhizal fungi associations that allow for efficient nutrient extraction in acidic, nutrient-poor soil environments. Statewide, soil pH has declined at all depths by a half unit over the last 50 years, resulting in 50–75 % decrease in macronutrients, and a 50 % increase in exchangeable metals (Drohan and Sharpe 1997; Bailey *et al.* 2005). In general,
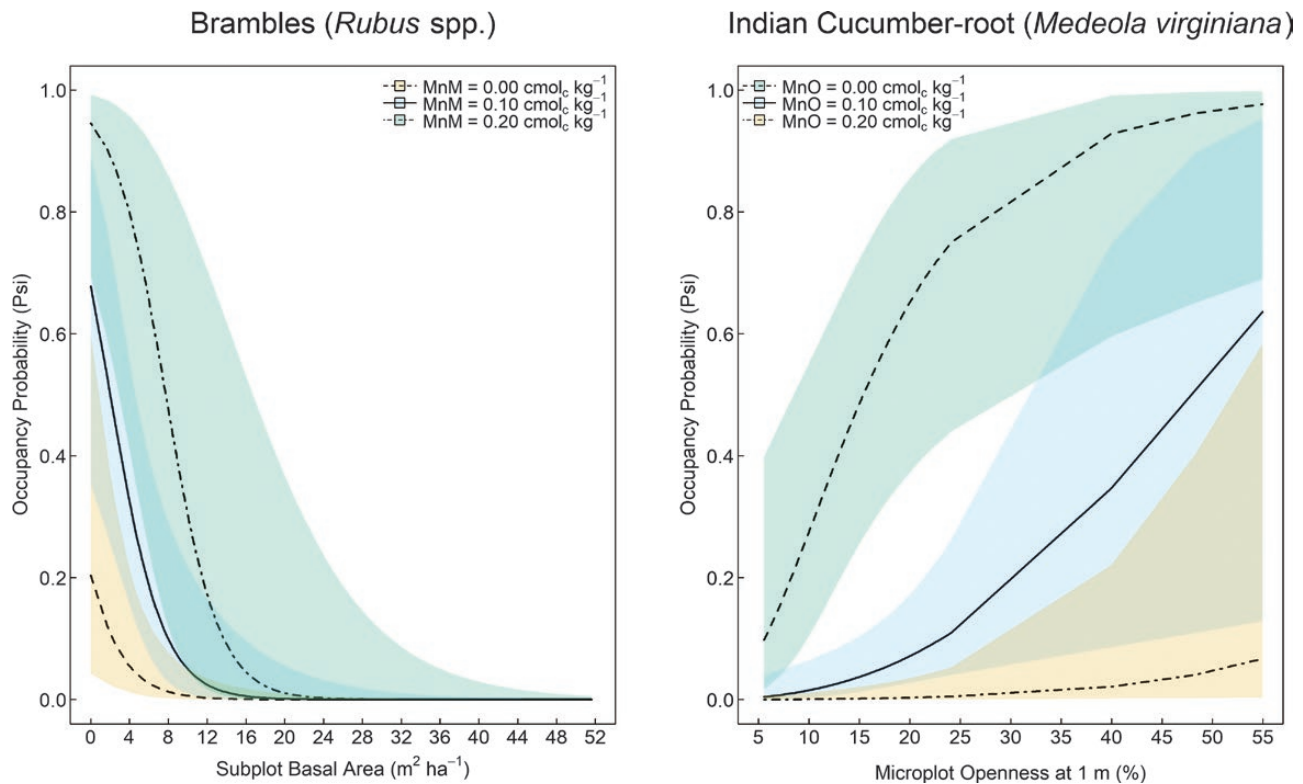
Figure 6. Occupancy probability as a function of environmental covariates for brambles (left) and Indian cucumber-root (right). Graphs represent the best model for each taxon selected using AIC_c, and x axes represent the range of covariates sampled. Shaded areas (regardless of colour) represent 95 % confidence intervals. Colours represent different levels of a covariate as indicated in the subfigure legend.

Table 3. Parameter estimates for two-species occupancy models where A represents the dominant species and B the subdominant species. Occupancy estimates for species B are listed along with their 95 % confidence intervals. Parameters are: occupancy of species B when A is present (ψ^{BA}), occupancy of species B when A is absent (ψ^{Ba}) and occupancy of species B regardless of species A occupancy (ψ^{B}). Estimates are not comparable across species pairs (rows).

Species A	Species B	Parameter	Ψ	95 % LCI	95 % UCI
Mountain laurel	Red oak	ψ^{BA}	0.06	0.02	0.17
		ψ^{Ba}	0.03	0.01	0.11
Huckleberry	Red oak	ψ^{B}	0.05	0.02	0.14
Mountain laurel	Chestnut oak	ψ^{BA}	0.13	0.07	0.22
		ψ^{Ba}	0.06	0.02	0.15
Huckleberry	Chestnut oak	ψ^{B}	0.10	0.06	0.17
Mountain laurel	Indian cucumber-root	ψ^{B}	0.01	0.00	0.04
Huckleberry	Indian cucumber-root	ψ^{B}	0.01	0.00	0.04
Mountain laurel	Hay-scented fern	ψ^{B}	0.05	0.03	0.10
Huckleberry	Hay-scented fern	ψ^{B}	0.05	0.03	0.10
Mountain laurel	Red maple	ψ^{BA}	0.30	0.22	0.40
		ψ^{Ba}	0.16	0.09	0.27
Huckleberry	Red maple	ψ^{BA}	0.32	0.23	0.44
		ψ^{Ba}	0.18	0.11	0.28
Mountain laurel	Black birch	ψ^{B}	0.11	0.07	0.16
Huckleberry	Black birch	ψ^{B}	0.11	0.07	0.16

these soil chemistry changes suggest a more favourable soil environment for ericaceous taxa. However, both mountain laurel and blueberry occupancy was reduced by increasing levels of soil extractable manganese, suggesting that mycorrhizal associations likely yield a competitive advantage when base cations are limited

(Cairney and Meharg 2003), but not when soil manganese is plant available. None of the best models of plant occupancy retained short-term deer exclusion as a covariate for any taxon.

Hay-scented fern was less likely to occupy sites where pH was low (2.5–3.5). There is no evidence in the literature

that hay-scented fern would exhibit a pH sensitivity (Conard 1908; Sharpe and Halofsky 1992), suggesting that there may be other causes of the apparent trend. Because single-species occupancy models do not account for interactions between species, a competitive interaction between hay-scented fern and mountain laurel would be masked as a hay-scented fern pH sensitivity if mountain laurel is a better competitor at low pH. Accounting for pH as a covariate for occupancy of both species, the best two-species occupancy model that explained occupancy of both mountain laurel and hay-scented fern held occupancy of fern constant regardless of whether the site was occupied by mountain laurel. This result suggests that competitive interactions do not result in competitive exclusion and that a lower bound of pH tolerance exists for hay-scented fern.

To our knowledge, this is the first documented case of potential pH sensitivity for hay-scented fern. Although pH was not correlated with any covariates excluded during analysis, several other unmeasured variables (e.g. organic matter content and soil moisture) may be correlated with pH. We acknowledge it is possible that organic horizon pH is acting as a surrogate for one of these other variables, and that occupancy is better explained by additional covariates. Furthermore, overall occupancy of hay-scented fern was low (5 % of sites), which is a small subset of total locations compared to other taxa. We suggest future studies consider organic matter content and soil moisture as predictors during analysis and sample across other regions. If hay-scented fern does exhibit a pH sensitivity in the Ridge and Valley Physiographic Province it has implications for management, especially if soil amendments are added to raise soil pH and control ericaceous vegetation. An increase of soil pH from 3.5 to 4.5 could improve soil conditions for hay-scented fern such that it replaces ericaceous taxa as the dominant browse-resistant vegetation.

The best single-species occupancy model for all tree seedlings included state forest as a covariate, and for all models, occupancy was higher in Rothrock compared to Bald Eagle. State forest differences suggest that management activity or some other landscape variable (e.g. deer density, land-use history, climate, soil chemistry or parent material) played a role in occupancy of tree seedlings. We evaluated three potential causes: white-tailed deer effects, soil chemistry effects and topographical differences to explain the location effect, and found complex soil chemistry differences between each state forest. Bald Eagle had steeper, more north facing slopes and soil nutrients concentrated at deeper depths (40 cm) within the soil profile compared to Rothrock. Leaching of soil nutrients from surface soil horizons suggests that there are fewer nutrients available in the rooting zone of newly established seedlings or shallowly rooted forest herbs. Soil nutrition is crucial for plant development and growth (Bache 1976; Cronan and Grigal 1995), and nutrient limitations likely explain vegetation differences across state forests. Future plant occupancy studies comparing state forests should consider adding additional covariates regarding management history (e.g. land use, harvest, fire or herbicide application) or deer density, if available.

Beside state forest effects, red maple occupancy had a positive relationship with mineral horizon ECEC. Effective cation exchange capacity represents the capacity of the soil to adsorb cations onto the exchange complex regardless of cation identity (Hendershot *et al.* 2008). Across the study area, increases in ECEC are driven primarily by either added calcium or aluminum to the exchange complex, suggesting that red maple is not sensitive to exchangeable aluminum. Tolerance of a wide range of soil chemistry conditions may explain why

red maple is common and abundant throughout Pennsylvania, especially in areas affected by acid deposition (Driscoll *et al.* 2001). Similarly, chestnut oak occupancy was inversely related to soil calcium, suggesting that calcium levels < 4 $cmol_c$ kg^{-1} are not limiting chestnut oak presence. Oaks are well-known for their dominance in dry, upland communities (Spira 2011), and these communities tend to be associated with sandstone geologies and lower calcium levels in Pennsylvania (Drohan *et al.* 2002). However, occupancy of red oak was not related to any soil chemistry covariate, suggesting that red oak occupancy is most likely influenced by several interacting factors, including competition from other plant taxa. Similarly, black birch occupancy was not explained by any covariate (soil chemistry or otherwise), suggesting its distribution is related to interacting or unmeasured factors.

Occupancy of both browse-preferred taxa was explained by a measure of soil extractable manganese and one other non-soil chemistry covariate. Bramble occupancy was positively associated with both lower subplot basal area (recent harvest or disturbance/high overstory openness) and higher mineral horizon manganese, whereas Indian cucumber-root was sensitive to understory shading and organic horizon extractable manganese ≥ 0.10 $cmol_c$ kg^{-1}. Brambles are an early successional species associated with disturbance (Rhoads and Block 2007), and are considered resistant to both micronutrient and heavy metal accumulation (Kowalenko 2005; Marques *et al.* 2009). Unlike brambles, Indian cucumber-root occupancy was negatively associated with soil manganese and positively associated with openness, suggesting Indian cucumber-root may accumulate metals in its tissues and be light limited.

Understory forest herbs are generally considered shade-tolerant, but very little research has been done on Indian cucumber-root and its associated habitat conditions (Barrett and Helenurm 1987; Meier *et al.* 1995; Hill and Garbary 2011). These results suggest that in addition to documented deer browsing effects on reproduction (Kirschbaum and Anacker 2005; Royo *et al.* 2010; Goetsch *et al.* 2011; Pierson and DeCalesta 2015), both light and metal availability may affect the presence of this species. Indian cucumber-root's apparent relationship with soil manganese combined with past studies on foliar nutrition (Gilliam and Roberts 2003; Gilliam 2006; Pabian *et al.* 2012) indicate that soil chemistry is important to the ecology of forest herbs.

The presence of browse-resistant ericaceous taxa did not limit occupancy of browse-preferred taxa (research question ii). Occupancy of Indian cucumber-root was unaffected by the presence of huckleberry or mountain laurel, and occupancy of all tree seedlings (excluding black birch, which was not correlated with either browse-resistant shrub) was higher when browse-resistant vegetation was present. Neither of these results suggests a strong competitive advantage for ericaceous taxa resulting in competitive exclusion of browse-preferred taxa. Contrary to expectations (Wurzburger and Hendrick 2007), co-occurrence of tree seedlings and browse-resistant ericaceous taxa suggests potential facilitation between both vegetation groups (Barley and Meeuwig 2017). Identifying potential causes of facilitation is beyond the scope of our paper, but this result provides an interesting avenue for future research.

Site factors had no effect on detection probability (research question iii), and detection was best modelled as constant across both visits for all taxa. Overall, browse-resistant taxa had higher detection probabilities than browse-preferred taxa and tree seedlings, most likely due to higher frequency of occurrence across sites. Detection probability increases as abundance

increases (McCarthy *et al.* 2013), and browse-resistant vegetation is usually abundant when present (Rooney 2009; Beguin *et al.* 2011). The combination of regular occurrence ($\psi > 0.49$ for all ericaceous taxa), and high abundance on sites when occupied allowed for high detection probability ($\hat{p} > 0.90$) for browse-resistant taxa. Browse-preferred taxa and tree seedlings had comparable detection probabilities (between 0.66 and 0.80), with the exception of brambles, which had detection equal to 1.

A detection probability of 0.80 translates to a 20 % probability of missing a species even if it is present, which could bias downward traditional estimators of occurrence, such as parameters in logistic regression models. Based on current detection probabilities of taxa in this study, a two-visit approach would result in detection probabilities of at least 89 % for all measured taxa. Additionally, two visits would decrease the total number of missed detections by at least 34 %. Future studies can improve accuracy of occupancy estimates by revisiting sampling locations more than once over the growing season and estimating a detection probability for all species.

Conclusions

Soil chemistry is an important component shaping plant community composition across the north-central Appalachians, with browse-resistant vegetation more likely to occupy sites with acid-leached soil chemistry (low pH, higher metals and lower base cations) than browse-preferred species. The strong occupancy responses to soil chemistry suggest that past studies attributing legacy effects of deer browsing to changes in competitive relationships and extirpation may also be attributed to unfavourable soil chemistry. Despite reductions in acid inputs over the last 20 years (Driscoll *et al.* 2001), and due to their poor buffering capacity and low base saturation (Ulrich 1983; Mutahhari 1985; Bailey *et al.* 2005), study soils are unlikely to recover within the span of a few human lifetimes without the use of soil amendments. Consequently, plant communities occupying similarly acid-leached sites are tolerant of these conditions and unlikely to shift without direct management.

We found that patterns of co-occurrence of browse-resistant, browse-preferred and tree seedling taxa further support the role of soil chemistry in shaping plant community composition. The presence of ericaceous taxa had no negative effect on occupancy of browse-preferred taxa or tree seedlings, despite the apparent competitive advantage given to ericaceous vegetation because of their tolerance of unfavourable soil conditions. Furthermore, red maple and both oak species were actually positively associated with ericaceous shrubs, suggesting some undocumented benefit to growing in concert with browse-resistant vegetation. We found no evidence that ericaceous shrubs are interfering with occupancy of any other taxa.

Finally, it is worth noting that the influence of multiple factors, other than deer exclusion, on occupancy of Indian cucumber-root has implications for deer management. Indian cucumber-root is often used as a phyto-indicator of deer browsing (Kirschbaum and Anacker 2005) because browsing results in observable changes in reproductive output and stature of most lilaceous forest herbs (Beardall and Gill 2001; Rooney and Gross 2003; Goetsch *et al.* 2011). However, when considered without assessments of habitat suitability (i.e. low manganese, high openness), instances of absence of Indian cucumber-root may sometimes be incorrectly attributed to deer browsing. Additional factors including above-ground and below-ground conditions could be alternative explanations for absence. Little is known about the demography of Indian cucumber-root, and its value as a phyto-indicator

hinges on consistent responses to deer herbivory regardless of other environmental conditions. Future research is needed to understand if this is a reasonable assumption for the species.

In this study, detection was moderate to high across all taxa, indicating conventional methods that assume 100 % detection still may be useful, especially if surveys are conducted across two visits. Occupancy estimates are limited to evaluations of presence/absence data, and other metrics (e.g. abundance, species interactions beyond two taxa and changes to reproductive output) may better evaluate the relative importance of soil chemistry in the context of deer exclusion. Furthermore, continued monitoring of exclosures is recommended to better quantify the effects of deer browsing in this region, because 85 of the 96 fences included in the analysis had been excluding deer for 2 years or less. Typically, deer exclusion studies do not report results until 4–5 years post-fencing due to the slow nature of vegetation responses (Rooney 2009; Beguin *et al.* 2011; Long *et al.* 2012; Miller *et al.* 2017). Resurveying exclosures after 5 years will likely better demonstrate the importance of both browsing and soil chemistry on plant community composition.

Supporting Information

The following additional information is available in the online version of this article—

Table A. Kellogg Soil Survey Laboratory Manual Reference Numbers for soil extraction methods.

Table B. Variance (σ^2) comparisons of covariate values within and between sampling sites.

Table C. Full model output for top single-species occupancy models considered during analysis by taxon (KALA: *Kalmia latifolia*, GASP: *Gaylussacia* spp., VASP: *Vaccinium* spp., DEPU: *Dennstaedtia punctilobula*, RUSP: *Rubus* spp., MEVI: *Medeola virginana*, ACRU: *Acer rubrum*, QURU: *Quercus rubra*, BELE: *Betula lenta* and QUMO: *Quercus montana*).

Table D. Parameter estimates for the best single-species occupancy model underlined in Supporting Information—Table C.

Table E. Full model output for the top two-species occupancy models for Mountain laurel (*Kalmia latifolia*)* as the dominant species (species A) and six additional non-dominant (species B) taxa (ACRU: *Acer rubrum*, BELE: *Betula lenta*, DEPU: *Dennstaedtia punctilobula*, MEVI: *Medeola virginana*, QURU: *Quercus rubra* and QUMO: *Quercus montana*). *All detection probabilities are equal for species A (mountain laurel) and species B for each model regardless of species A presence and detection ($pA(.)=rA(.)$ $pB(.)=rBA(.)=rBa(.)$).

Table F. Full model output for the top two-species occupancy models for huckleberry (*Gaylussacia* spp.)* as the dominant species (species A) and six additional non-dominant (species B) taxa (ACRU: *Acer rubrum*, BELE: *Betula lenta*, DEPU: *Dennstaedtia punctilobula*, MEVI: *Medeola virginana*, QURU: *Quercus rubra* and QUMO: *Quercus montana*). *All detection probabilities are equal for species A (huckleberry) and species B for each model regardless of species A presence and detection ($pA(.)=rA(.)$ $pB(.)=rBA(.)=rBa(.)$).

Table G. Results summary table from a multivariate analysis of variance (MANOVA) comparing site parameters across location (state forest). Bolded values indicate the largest value within a parameter, and abbreviations are consistent with the abbreviations listed in the Methods section. Tested parameters with P-values > 0.05 are not reported in the table.

Table H. Table of Pearson's chi-squared test and contingency table comparing aspect (N = North, S = South) between location (state forest).

Table I. Analysis of variance (ANOVA) summary table from generalized linear regression comparing the change in the total number of tree seedlings > 0.3 m tall from 2014 to 2016 by location (state forest).

Data

All data are available at the Dryad Digital Repository: doi:10.5061/dryad.dr48cf6.

Contributions by the Authors

All authors contributed to study design, and D.R.B.-M., D.R.D, P.J.D., and M.E.M. developed study methods and protocols for project implementation. DRB-M and DRD conducted data analysis; D.R.D., M.E.M., C.S.R., E.H.J.D. provided project resources; D.R.B.-M. was responsible for data curation, and wrote the original draft of this manuscript. All authors reviewed and edited each version of this manuscript following its original preparation through its final submission.

Conflict of Interest

None declared.

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