PREDICTIVE RELATIONSHIPS BETWEEN THE CANOPY OVERSTORY AND THE HERBACEOUS UNDERSTORY IN A NORTHEASTERN WISCONSIN FOREST

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ABSTRACT

The composition of the herbaceous understory can be largely influenced by the dominant canopy tree species. We sampled the herbaceous species composition underlying seven canopy types (eastern hemlock, eastern hemlock-northern hardwood mixture, northern hardwoods, red pine, second-growth disturbed, white cedar swamp, and white pine) from May–July of 2000 in a northeastern Wisconsin forest. We hypothesized that the herbaceous community should predictably differ among canopy types. Significant differences (nMANOVA, F = 5.02, P < 0.001) existed among the herbaceous compositions. Northern hardwood herbaceous assemblages were the most diverse (55 taxa, \( H' = 3.06 \), \( H_{\text{max}} = 4.00 \)) and white pine assemblages (4 taxa, \( H' = 0.95 \), \( H_{\text{max}} = 1.39 \)) were the least diverse. Discriminant analysis with resubstitution estimates strongly predicted six of seven canopy types from the herbaceous compositions at >85% accuracy; however, cross-validation estimates predicted only two of seven canopy types at >73% accuracy. These data demonstrate that herbaceous community can be used to predict canopy type, at least on an individual habitat scale, in the northeast Wisconsin forest but may lose validity outside this study area.

INTRODUCTION

Woodland ecosystems are complex environments involving biotic and abiotic interactions among light, soils, waters, understory herbaceous plants and shrubs, and canopy trees. Many studies have documented concomitant abiotic influences, rather than interspecific overstory-understory species interactions, that canopy trees have on the composition of underlying vegetation, including soil depth and microtopology (Hicks 1980), structural and habitat dynamics (Auclair & Goff 1971), throughfall precipitation and soil nutrients (Crozier & Boerner 1984), disturbance and resistance (McCormick & Platt 1980; Parker & Leopold 1983; Duffy & Meier 1992), microclimate (Whitney & Foster 1988), biogeography (Schluter & Ricklefs 1993), soil pH (Sagers & Lyon 1997), nitrate availability (Weltzin & Coughenour 1990; Qian et al. 1997), and tree architecture and shade (Berger & Puettmann 2000). Furthermore, other studies demonstrated that
understory community fidelity often appears to be highly individualistic and does not follow an environmental gradient or regional predictive paradigm (Gleason 1926; Curtis 1959; Rodgers 1980; McCune & Antos 1981). Additionally, Kotar et al. (1988; 2002) concluded that vegetation is generally not useful in uniformly categorizing large habitat types, but nonetheless confirmed it to be an important and distinguishing ecosystem characteristic in north temperate forests.

These studies demonstrate the difficulty in explicating unifying herbaceous trends at aggregate species levels across large ecosystems because species often demonstrate a range of tolerances (Curtis 1959). However, because the presence or absence of herbaceous species is governed by interactions of both biotic and abiotic factors, multivariate and ordination techniques could representatively capture these interactions and describe the distribution mosaic at a smaller local or regional habitat-level scale. Such techniques based exclusively on indicator herbaceous species composition, if accurate, would facilitate rapid assessments and dissemination of local and regional forest composition data when other assessment methods are logistically unfeasible.

For our study, we sought to segregate the composite herbaceous understory-canopy overstory relationships in a local forest, at an individual habitat scale, based solely on multivariate analyses of herbaceous species. Portions of Stockbridge-Munsee Mohican tribal forestlands (near Bowler, Shawano County, Wisconsin USA) were lost from reservation control over many decades, resulting in deforestation. Within recent years, these forestlands have been reacquired and managed for restoration. This offered an opportunity to assess the understory-overstory relationships in local tree stands over a large ecosystem with several dominant canopy assemblages, including second-growth restoration areas. We hypothesized, because of the presence of both undisturbed and disturbed tree stands in our study area, herbaceous understory compositions should be markedly and predictably different among each canopy type. Our goal was to generate a multivariate model predicting overstory canopy type from the understory herbaceous composition to demonstrate that the canopy overstory influences the herbaceous understory.

METHODS

Study Area

The Stockbridge-Munsee Mohican tribal forestlands (8747 ha, Bowler, Shawano County, Wisconsin, USA, N 44E 55.5, W 88E 50.5) consist of seven predominant canopy tree assemblages (G. Bunker, unpublished data): eastern hemlock Tsuga canadensis, eastern hemlock–northern hardwood mixture, northern hardwoods (sugar maple Acer saccharum, red maple Acer rubrum, white birch Betula papyrifera, beech Fagus grandifolia, red oak Quercus rubra, and basswood Tilia americana), red pine Pinus resinosa, second-growth disturbed, white cedar swamp Thuja occidentalis, and white pine Pinus strobus. Replicate stands of each canopy type are discretely mixed throughout the area. The most common canopy type is northern hardwoods and the most common tree (of 31 recorded species) is the eastern hemlock. The Bureau of Indian affairs has extensively monitored the forestlands and established a continuous forest inventory (CFI) matrix (ca 115 points) referenced with GPS and GIS applications. Each CFI point is equidistant from each other (50 chains) and collectively span the entire forest and all seven canopy types.
Herbaceous Survey

We surveyed 106 CFI locations between May 17 and July 7, 2000. Because we sampled the majority of CFI locations within the forest it was not possible to have an equal sample distribution of each canopy type; each canopy type had differing surface areas throughout the study region. However, based on GIS assessments of CFI points per each area unit of canopy type, no canopy types were proportionally underrepresented; each canopy type had approximately the same CFI point : canopy surface area ratio. At each CFI location, we sampled three random 1.0 m$^2$ quadrats within a 5 m radius of the matrix point and enumerated herbaceous species as stems per m$^2$ (but considered multiple stem species as one individual when such determinations were possible). We expressed diversity as both total taxa and with the Shannon-Weiner index (Hutcheson 1970).

Multivariate Analyses

To test our hypothesis that understory vegetation should differ among canopy types, we used a three-step multivariate approach following statistical methods in Johnson (1998). We used nonparametric methods throughout our analyses because each canopy type had a different number of CFI points.

1. We used stepwise selection at $\alpha = 0.05$ to choose the most significant indicator herbaceous species (expressed as mean individuals per m$^2$) used for defining the understory-overstory relationships in the next two steps.

2. We calculated nonparametric multivariate analysis of variance (nMANOVA) from the mean densities of the stepwise-selected plant species of each overstory canopy type using Wilk’s likelihood ratio test with a type-III sum of squares at $\alpha = 0.001$. These series of tests allow us to determine if differences exist in herbaceous compositions between canopy types; however, nMANOVA does not post-hoc segregate which compositions are different.

3. To determine which of the seven canopy types differed in herbaceous understory composition, we used nonparametric discriminant analysis (DA) with both resubstitution ($DA_{RS}$) and cross-validation ($DA_{CV}$) estimates. Mean densities of the stepwise-selected herbaceous species were the independent predictor variables and canopy types were the dependent test variables. Mahalanobis distances between herbaceous vectors were measured from the first nearest neighbor with proportional prior probabilities (prior probabilities were used to account for uneven distribution of CFI points per canopy type).

RESULTS AND DISCUSSION

Herbaceous Survey

We recorded 70 herbaceous taxa throughout the study area (Appendix 1). Wild lily-of-the valley *Maianthemum canadense*, the sedge *Carex pennsylvanica*, and Virginia waterleaf *Hydrophyllum virginianum* were the most commonly encountered species. The other species were patchy and had lower densities. Twelve species were found under only one canopy type: five in northern hardwoods (the grass *Brachyelytrum erectum*, prairie smoke *Geum triflorum*, miterwort *Mitella diphylla*, nettle *Urtica dioica*, and perfoliate bellwort *Uvularia perfoliata*) and seven in white cedar swamps (yellow marsh marigold *Caltha palustris*, pink lady’s slipper *Cypripedium acaule*, fragrant bedstraw *Galium triflorum*, royal fern *Osmunda regalis*, wood sorrel *Oxalis acetosella*, fringed milkwort *Polygala paucifolia*, and skunk cabbage *Symlocarpus foetidus*). Subsequently, northern hardwood (55 taxa, $H' = 3.06$, $H_{\text{max}} = 4.00$) and white cedar swamp (42 taxa, $H' = 2.50$, $H_{\text{max}} = 3.74$) herbaceous assemblages were the most diverse (Table 1). White pine herbaceous assemblages (4 taxa, $H' = 0.95$, $H_{\text{max}} = \ldots$)
TABLE 1. Overstory canopy type, the number of sites sampled, and the diversity of corresponding understory herbaceous species in the Stockbridge-Munsee Mohican tribal forest. Diversity was calculated from the Shannon-Weiner index (Hutcheson 1970). Canopy types are listed in descending diversity order.

<table>
<thead>
<tr>
<th>Canopy Type</th>
<th>Number of Sites</th>
<th>Number of Taxa</th>
<th>H′</th>
<th>H_{max}</th>
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</thead>
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<tr>
<td>Northern Hardwoods</td>
<td>56</td>
<td>55</td>
<td>3.06</td>
<td>4.00</td>
</tr>
<tr>
<td>White Cedar Swamp</td>
<td>10</td>
<td>42</td>
<td>2.50</td>
<td>3.74</td>
</tr>
<tr>
<td>Second Growth-Disturbed</td>
<td>12</td>
<td>40</td>
<td>2.57</td>
<td>3.56</td>
</tr>
<tr>
<td>Hemlock-Mixed Hardwoods</td>
<td>7</td>
<td>24</td>
<td>2.22</td>
<td>3.18</td>
</tr>
<tr>
<td>Eastern Hemlock</td>
<td>15</td>
<td>23</td>
<td>1.86</td>
<td>3.13</td>
</tr>
<tr>
<td>Red Pine</td>
<td>4</td>
<td>17</td>
<td>1.54</td>
<td>2.83</td>
</tr>
<tr>
<td>White Pine</td>
<td>2</td>
<td>4</td>
<td>0.95</td>
<td>1.39</td>
</tr>
</tbody>
</table>

1.39) were the least diverse. Since the number of species generally increases with area (Connor & McCoy 1979), our observed rare species and diversity indices may be area-dependent. However, we feel that rarefaction estimates are not necessary and that our data proportionally represent all habitats because we sampled a uniform ratio of CFI points per unit area among canopy types.

**Multivariate Analyses**

Stepwise selection reduced the 70 taxa to 15 significant predictor species (Table 2). Selection removed the ubiquitous wild lily-of-the valley _Maianthemum canadense_, the sedge _Carex pennsylvanica_, and Virginia waterleaf _Hydrophyllum virginianum_ while including the infrequently-encountered wood sorrel _Oxalis acetosella_ and pink lady’s slipper _Cypripedium acaule_. Overall, the

<table>
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<th>Species</th>
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<tbody>
<tr>
<td>Bunchberry <em>Cornus canadensis</em></td>
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<tr>
<td>Common clubmoss <em>Lycopodium clavatum</em></td>
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<tr>
<td>False solomon seal <em>Smilacina racemosa</em></td>
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<tr>
<td>Goldenthread <em>Coptis groenlandica</em></td>
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<tr>
<td>Large-flower trillium <em>Trillium grandiflorum</em></td>
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<tr>
<td>Long beech fern <em>Thelypteris phegopteris</em></td>
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<tr>
<td>Marsh marigold <em>Caltha palustris</em></td>
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<tr>
<td>Oak fern <em>Gymnocarpium dryopteris</em></td>
</tr>
<tr>
<td>Partridgeberry <em>Mitchella repens</em></td>
</tr>
<tr>
<td>Pink lady’s slipper <em>Cypripedium acaule</em></td>
</tr>
<tr>
<td>Sensitive fern <em>Onoclea sensibilis</em></td>
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<tr>
<td>Sessile bellwort <em>Uvularia sessilifolia</em></td>
</tr>
<tr>
<td>Sharp-lobe hepatica <em>Hepatica americana</em></td>
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<tr>
<td>Wood anemone <em>Anemone quinquefolia</em></td>
</tr>
<tr>
<td>Wood sorrel <em>Oxalis acetosella</em></td>
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</table>
selection process included patchy species with variable distributions among canopy types that offered a determinant discrimination basis.

Significant differences existed between at least one canopy type and the others according to the 15 significant indicator species compositions (nMANOVA, \( F = 5.02, P < 0.001 \)). Moreover, \( D_{\text{RS}} \) strongly predicted six of the seven canopy types at >85% accuracy from herbaceous compositions, further demonstrating that herbaceous understory communities differ by canopy overstory type (Table 3). Only the white pine canopy was misclassified, but this error may be expected from low degrees of freedom and discrimination basis. (Only two white pine stands were sampled and had low species diversity. However, to assess any potential sampling bias, after we took our random quadrat samples, we visually inspected the white pine habitat area for any additional herbaceous species we may have not captured, but found none). While \( D_{\text{RS}} \) was strong, \( D_{\text{CV}} \) was weaker and estimated only two of seven canopy types at >73% accuracy (Table 3). Only northern hardwood mixture and eastern hemlock stands were strongly estimated. This may be due to northern hardwoods having the greatest herbaceous diversity and eastern hemlocks having near the lowest herbaceous diversity.

Our DA models were effective in describing the herbaceous understory-canopy overstory relationships at a habitat scale in the Stockbridge-Munsee Mohican tribal forestlands but lose validity outside our study area. In general, if significant differences exist, \( D_{\text{RS}} \) estimates perform strongly with the original data used in creating the rule determinations but may perform weakly with exogenous data (Johnson 1998). Conversely, \( D_{\text{CV}} \) is a more rigorous stepwise procedure often used to simulate corroboration with exogenous data. Subsequently, we are confident in our \( D_{\text{RS}} \) model estimates within our study area but acknowledge that our DA rules are likely weaker elsewhere.

Our herbaceous understory-canopy overstory results are consistent with other studies (e.g., Gleason 1926; Curtis 1971; Rodgers 1980; McCune & Antos 1981; Kotar et al. 1988; 2002), in that our DA models suggest these patterns are highly individualistic and cannot be generalized from one large region to another. However, our DA models suggest that localized, habitat scale, understory-canopy species-dependent relationships can be demonstrated independently from a suite of measured abiotic correlates (e.g., topology, precipitation, nutrients, shade, etc.). Our study sampled more herbaceous taxa, more forest points, and/or more canopy types than other previous studies that comparatively found less conclusive unifying herbaceous trends (e.g., Hicks 1980; McCune & Antos 1981; Whitney & Foster 1988; Berger & Puettman 2000). Subsequently, the species-DA technique, when derived from a large study area, may facilitate rapid assessment and dissemination of localized, habitat scale, forest composition data when extensive sampling of abiotic metrics is not practical.
TABLE 3. DA estimates of canopy type from herbaceous understory. The row headers represent the actual data and the column headers represent model predictions. The top numbers in each cell represent DA_{RS} model predictions and the bottom numbers in each cell represent DA_{CV} model predictions. The bold-faced percentages along the central diagonal indicate the successful prediction of actual canopy type from the DA model rules derived from herbaceous understory.

<table>
<thead>
<tr>
<th>Into type → From type ↓</th>
<th>Eastern Hemlock</th>
<th>Eastern Hemlock-Hardwoods Mixture</th>
<th>Northern Hardwoods</th>
<th>Red Pine</th>
<th>Second-Growth Disturbed</th>
<th>White Cedar</th>
<th>White Pine</th>
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<tbody>
<tr>
<td><strong>Eastern Hemlock</strong></td>
<td>100.00%</td>
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<td>73.33%</td>
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<td><strong>Eastern Hemlock- Hardwoods Mixture</strong></td>
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<td><strong>Northern Hardwoods</strong></td>
<td>7.15%</td>
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<td><strong>92.85%</strong></td>
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<td>17.85%</td>
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<td><strong>73.21%</strong></td>
<td>1.76%</td>
<td>1.27%</td>
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<td><strong>Red Pine</strong></td>
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<tr>
<td><strong>Second-Growth Disturbed</strong></td>
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<td><strong>91.67%</strong></td>
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<td>41.67%</td>
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<tr>
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ACKNOWLEDGMENTS

This research was funded by a United States Environmental Protection Agency grant to the Stockbridge-Munsee Mohican Tribe. Chad Miller maintained the GIS database. Ondrej Podlaha assisted with fieldwork and Chrystal Kosowski provided logistical support. Michael Chadwick offered suggestions that improved an earlier draft of this manuscript.

LITERATURE CITED

APPENDIX 1. Herbaceous species list of the Stockbridge-Munsee Mohican tribal forest. An “X” indicates that species was present under that canopy type.

<table>
<thead>
<tr>
<th>Species</th>
<th>Eastern Hemlock</th>
<th>Eastern Hemlock-Hardwoods Mixture</th>
<th>Northern Hardwoods</th>
<th>Red Pine</th>
<th>Second Growth Disturbed</th>
<th>White Cedar</th>
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<td>Actaea pachypoda</td>
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<td>Adianium pedatum</td>
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<td>x</td>
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<tr>
<td>Allium canadense</td>
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<tr>
<td>Amphicarpaea bracteata</td>
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<td>Dicentra cucullaria</td>
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