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Ecological species groups of landform-level ecosystems dominated by jack pine in northern Lower Michigan, USA

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Abstract

A combination of field and tabular methods and multivariate analyses were used to develop groups of ground flora species (i.e., ecological species groups) that characterize and distinguish highly disturbed, landform-level ecosystems dominated by jack pine in northern Lower Michigan. The endangered Kirtland's warbler formerly or currently occupied the large glacial landforms for which species groups were developed. Eight such ecological species groups were created using 31 woody and herbaceous species sampled in 144 plots within a 20,000 km^2 geographic region of uniform climate and regional physiography. The groups were initially constructed using subjective, observation-based groupings of species with similar presence and abundance along soil moisture and fertility gradients. Species groups were corroborated using TWINSPAN and detrended correspondence analysis, and the environmental conditions indicated by each were described and contrasted based upon field observations and canonical correspondence analysis. Two of the eight species groups indicated very dry, infertile sites, and one was indicative of a very broad range of sites dominated by jack pine. The remaining five groups reflected a relatively gentle environmental gradient within the set of ecosystems we sampled, indicating small differences along a soil moisture gradient and less so along a soil fertility and light availability gradient. The groups were applied successfully for the majority of an area that had been repeatedly logged and/or burned for at least 120 years. In addition, the groups were successful when tested on sites with highly disturbed upper soil strata furrowed for the establishment of plantations between the 1960s and 1980s. Within the boundaries of the regional ecosystems for which they were developed, ecological species groups reflect the integrated effects of multiple site factors that control the height growth rates of jack pine trees that, in turn, determine the duration of Kirtland's warbler occupancy. While usually applied at the scale of ecosystem types, our results demonstrate that ecological species groups may also provide the ecological basis for distinguishing ecosystems at broader scales. When examined simultaneously in the field with physiography, microclimate, and soil factors, the groups are therefore useful in identifying and classifying ecosystem units at the scale of landforms, the appropriate scale of management for the Kirtland's warbler.

Introduction

Distinguishing plant associations has been at the heart of vegetation science for centuries, with a traditional focus on the distribution, composition and classification of plant communities. These floristic concepts of plant sociology, particularly as they involve ground flora, have their roots in many schools of community ecology, both European (e.g., Braun-Blanquet 1964; Ellenberg 1988 and Oberdorfer 1990) and North American (e.g., Clements 1916; Gleason 1926; Curtis 1959 and Whittaker 1962). The use of vegetation in describing and distinguishing associations and communities has proved applicable to practical problems of site classification, and the relationship of plant species and communities to site factors has also been the subject of extensive study.

The importance of ground flora in indicating relative site productivity also has a long history in ecology (Cajander 1926; Rowe 1956; Daubenmire 1976; Klinka et al. 1989). Because they are responsive to site conditions, understory plants act as phytometers that integrate many environmental factors that are difficult to measure directly (e.g., macroclimate, microclimate, physiography, soil, and light conditions) (Daubenmire 1976; Barnes et al. 1982; Spies and Barnes 1985; Barnes et al. 1998 p. 306-308). The ecological range of ground flora species over nutrient and moisture gradients is more restricted than overstory tree species, which may grow over a wider range of sites (Pregitzer and Barnes 1982; Pastor et al. 1984; Zak et al. 1986; Hix 1988; Host and Pregitzer 1991; Barnes et al. 1998, p. 306–308). Perhaps most importantly, regeneration and abundance of ground flora species are less affected by disturbances than are tree species (Westveld 1951; Archambault et al. 1989; Whitney 1991), a factor important for indicator species in heavily disturbed forests such as those in the Upper Great Lakes region.

Limitations of the use of ground flora for vegetation classification have been identified (Coile 1938; Rowe 1956, 1984), many of which are a direct result of the method used to determine the indicator value of the species. For example, a few key individual species may be used to classify a site using factors the species indicate, such as light conditions, soil water, or soil fertility (Daubenmire 1961; Beaufait and Brown 1962; Overlease and Overlease 1976; Heringa and Cormack 1963; Hawkes et al. 1997; Klinka et al. 1989). Such a single-species approach is often criticized because (*i*) only a small subset of the total ground flora is utilized, and (*ii*) the presence and abundance of many species are affected by factors that are poorly related to site conditions, such as herbivory, dispersal, plant competition and mutualisms, disturbance history, and chance (Coile 1938; Rowe 1956; Pregitzer and Barnes 1982; Spies and Barnes 1985; Archambault et al. 1989). Additionally, single indicator species often fail to provide sufficient discrimination needed to differentiate and classify ecosystems, particularly when occurrence and abundance of these species are not integrated with characteristics of climate, physiography, and soil (Rowe 1984; Barnes et al. 1998, pp. 308).

Alternatively, groups of indicator species (termed ecological species groups) may be used to indicate site quality. Ecological species groups are groups of plants that repeatedly occur together in areas with similar combinations of site factors, and that are perceived to have similar ecological requirements or tolerances (Spies and Barnes 1985; Host and Pregitzer 1991; Barnes et al. 1998). Ecological species groups represent the integrated effects of multiple-factor gradients (Pregitzer and Barnes 1982), given that the cooccurrence of plants in the field is due to multiple interacting physical and biotic factors (Barnes et al. 1998, p. 306–310). The presence of any member of the group assumes that the ecological conditions defined for the group are present. Often, groups are not limited to one ecosystem, but instead are more prevalent in some ecosystems than in others (Spies and Barnes 1985; Archambault et al. 1989; Simpson et al. 1990), reflecting a continuous change in composition across the underlying ecological gradients (Host and Pregitzer 1991).

The concept of ecological species groups is attributed to Duvigneaud (1946), although several methods have been developed and utilized (Ellenberg 1950; Daubenmire 1952; Rowe 1956; Schlenker 1964; Sebald 1964; Barnes et al. 1982; Klinka et al. 1989). The method used in this study was pioneered in the German state of Baden-Württemberg to classify and map ecosystems (Schlenker 1964; Sebald 1964; Mühlhäusser et al. 1983; Barnes 1984; Barnes et al 1998, p. 321–323). Differing from typical phytosociological techniques, the Baden-Württemberg method uses ecological species groups simultaneously with climate, physiography, and soil conditions to map and delineate ecosystems in the field. The approach has been adapted in the United States for mature and relatively undisturbed forested areas in Michigan (Pregitzer and Barnes 1982; Spies and Barnes 1985; Simpson et al. 1990), Ohio (Hix and Pearcy 1997), Wisconsin (Hix 1988), New England (Smith 1995), as well as elsewhere in Europe (Godart 1989). Species groups have also been developed for forests disturbed early in the last century in Lower Michigan (Archambault et al. 1989; Host and Pregitzer 1991; Pearsall 1995). Since ecological species groups may theoretically be developed for a range of disturbance regimes, our objective was to develop groups of ground flora species for use in heavily disturbed systems characterized by repeated burning, logging, and furrowing for plantations such as those dominated by jack pine (*Pinus banksiana* Lamb.) in northern Lower Michigan.

We constructed ecological species groups for use in multi-factor classification of landscape ecosystems occupied by the federally endangered Kirtland's warbler (*Dendroica kirtlandii* Baird) in northern Lower Michigan (Kashian and Barnes 2000; Kashian et al. (in press); Walker et al. (in press)). Landscape ecosystems are volumetric tracts of land consisting of interacting physical site factors of climate, physiography, soil, and water, as well as biota (Rowe 1988; Rowe and Barnes 1994; Barnes et al. 1998, p. 3–6). Landscape ecosystems exist, and may be classified, at multiple scales within a hierarchy (Albert et al. 1986; Albert 1995; Barnes et al. 1998, p. 3). Regions (approximately 16,000 to 60,000 km^2) and districts (2,000 to 20,000 km^2) are bounded at the broadest scale by an integration of macroclimatic and gross physiography. Within districts, subdistricts (300 to 13,000 km^2) containing uniform macroclimate are distinguished by differences in physiography, soil, and vegetation. Subdistricts may be further subdivided into physiographic systems (200 to 3,000 km^2) that correspond to glacial features, such as outwash plains, ice-contact terrain, and moraines. Physiographic systems contain landform-level ecosystems (hereafter referred to as "landforms"; 5 to 25 km^2), which in turn contain ecosystem types (often < 1 km^2).

Kirtland's warblers nest almost exclusively in northern Lower Michigan under young, dense stands of jack pine in a discontinuous area approximately 20,000 km^2. The availability of suitable breeding habitat is intensively managed by providing large jack pine plantations and preservation of known warbler breeding areas. Warblers nest only under jack pine of a specific height and density, and therefore occupy a given stand for a relatively narrow window of time. Warblers occupy landforms for different lengths of time due to interacting factors of physiography, microclimate, and soil that mediate the height growth of jack pine (Kashian et al. (in press); Walker et al. (in press)). Once developed, ecological species groups not only provide an understanding of the integrated effect of these physical site factors, but are also critical in guiding the selection of warbler management areas for plantations. Similar to several studies (Pregitzer and Barnes 1982; Spies and Barnes 1985; Hix 1988; Archambault et al. 1990; Simpson et al. 1990; Pearsall 1995), Barnes et al. (1989) developed preliminary ecological species groups for the dry sand plain, jack pine- and northern pin oak- (*Quercus ellipsoidalis* E.J. Hill) dominated local landscape ecosystems of the 10,000-ha Mack Lake burn in northern Lower Michigan. Given that wildlife management typically occurs at landform- or larger scales, this study appropriately expands our understanding of fine-scale ground flora species-site relationships at Mack Lake to the operational unit of landforms occupied by the warbler across northern Lower Michigan. The objectives of this study were: (*i*) to determine the ecological species groups for landforms occupied by Kirtland's warblers in northern Lower Michigan, (*ii*) to describe the site indicator value of each of the groups, and (*iii*) to evaluate the applicability of the groups to heavily disturbed areas planted with jack pine for warbler management.

Methods

Field sampling

Ground flora data were collected from landforms dominated by jack pine and formerly or currently occupied by the Kirtland's warbler in northern Lower Michigan (centered at approximately 44°43′ N, 84°27′ W). Kashian et al. (in press) classified the range of landforms occupied by the warbler in this region using several parameters including macroclimate and physiography. Soil factors, including the presence of fine-textured soil bands or lenses which have been shown to increase site productivity in this region (Hannah and Zahner 1970; Host et al. 1988), were also utilized in classifying landforms. For this study, the range of landforms was sampled in accordance with two criteria. First, ground flora were sampled only within the Grayling Subdistrict (8.2) of the Highplains District (8), a regional ecosystem of relatively uniform climate and physiography (Figure 1; Albert et al. 1986). Second, sampling used for species group development was limited to areas burned by wildfire or naturally regenerated following clear-cutting. Clear-cut areas were included because ground flora species are known to persist on a site after such disturbance (Hix and Barnes 1984). Plantations were sampled but not included in the development of species groups due to the young age of many plantations and thus heavy disturbance of the upper soil strata by furrowing. In developing ecological species groups, the landform classification described in Kashian et al. (in press) was collapsed into five landform groups: 1)

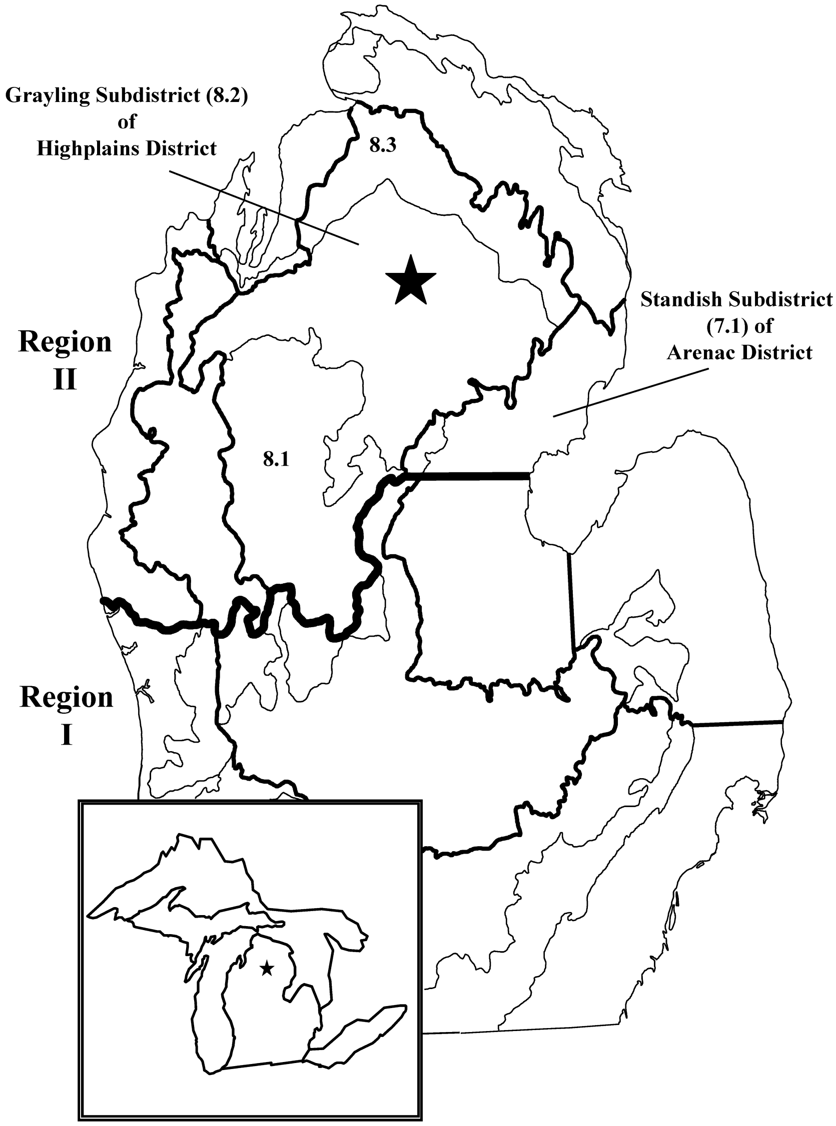

Figure 1. Regional landscape ecosystems of northern Lower Michigan (Albert et al. 1986) with general location of study area (denoted by marker) within the Grayling Subdistrict (8.2) of the Highplains District (8).

outwash channel landforms, 2) unbanded outwash plain landforms, 3) banded outwash plain landforms, 4) water table-influenced outwash plain landforms, and 5) ice-contact terrain and outwash plains associated with ice-contact physiographic systems (Table 1).

One-hundred forty-four 5- × 20-m (100 m^2) rectangular sampling plots were established using a stratified random sampling design, and all ground flora species including tree seedlings (other than jack pine), shrubs, forbs, and grasses were identified to species where possible and their aerial coverage calculated by percent coverage classes using a 12-class scale (0.25, < 0.005%; 0.5, 0.005–0.01%; 1, 0.01–0.1%; 2, 0.1–0.5%, 3, 0.5–1%; 4, 1–2%; 5, 2–4%; 6, 4–8%; 7, 8–16%; 8, 16–32%; 9, 32–64%; 10, > 64%). Coverage estimates were standardized using a wooden sampling frame that was 0.1% of the entire plot. Nomenclature follows Voss (1972, 1984, 1997) for vascular plants; all non-vascular plants except *Cladina* were recorded as "mosses" or "lichens." Species not found within the plot but within five meters of the plot perimeter were recorded and assigned the lowest coverage-class value.

Table 1. Landform groups occupied by the Kirtland's warbler in the Grayling Subdistrict (8.2) of northern Lower Michigan. The five landform groups originate from an aggregation of 12 landform-level ecosystems distinguished by Kashian et al. (in press).

Landform Group	Description	Landforms (Kashian et al. (in press))	Number of plots
Glacial outwash channels	Low-lying, extremely flat topography; coarse and medium-coarse sand with pebbles and cobbles; banding uncommon or absent; excessively drained; cold and very infertile.	1	20
Unbanded outwash plains	Flat to moderately sloping or pitted; medium-coarse sand and gravel to medium-fine sand; banding uncommon or absent; excessively drained; infertile.	2, 3, 4, 7, 8	47
Banded outwash plains	Flat to moderately sloping or pitted; medium to very fine sand; banding common to frequent; somewhat excessively drained; moderately infertile.	6, 8	35
Water table-influenced outwash plains	Flat topography; medium-fine to fine sand; banding occasional to absent; somewhat poorly drained; water table within 2 meters of surface; infertile.	5	30
Ice-contact terrain and associated outwash plains	Flat to slightly or steeply sloping topography; medium sand to sandy loam; banding common to absent; excessively to well drained; infertile to moderately infertile.	9, 10, 11	12

Analyses

Species groups are typically developed using two methods or a combination of them. Tabular methods were used in Baden-Württemberg (Barnes et al. 1998, p. 322–323) and by Spies and Barnes (1985) that arrange species and sites in a manner that allows the worker to detect species with similar distributions across a series of sites, and that utilizes abundance as well as presence/absence data. A detailed understanding of species-site relationships is required before accurate and useful groups may be constructed, although this subjective clustering of species allows the appropriate grouping of climate, topography, and soil data of an ecological unit with its vegetation data. Multivariate statistics are also useful in constructing ecological species groups (Gauch 1982), although many such techniques are particularly sensitive to ecological "noise" in the data set (Spies and Barnes 1985). An integration of the two approaches appears to be most often successful and has been used in several studies (Host and Pregitzer 1991; Smith 1995).

Combining the field methods of Baden-Württemberg (Spies and Barnes 1985; Archambault et al. 1989; Barnes et al. 1998, p. 322–323) and a tabular method modified from a standard European method described by Mueller-Dombois and Ellenberg (1974), the coverage-class values of the species (abundances) were recorded in a table in which the species formed the rows and the sample plots formed the columns. Following detailed field observations during sampling, the plots (columns) were arranged along environmental gradients of soil water and fertility from very dry and infertile to moist and moderately fertile based on field reconnaissance, plot sampling, and soil laboratory analysis. Tabular methods were then automated and repeated using two-way indicator species analysis (TWINSPAN; Hill 1979), which utilizes polythetic, divisive clustering. Rare species (occurring in less than 5% of all plots) were excluded from the analysis, a technique that has been shown to remove very little information from the data set (Gauch 1982). The synthesis table obtained from TWINSPAN was then compared to the species group approximations developed by tabular methods.

Ecological profiles similar to those of Spies and Barnes (1985), Archambault et al. (1989), and Host and Pregitzer (1991) were used to examine the occurrence of the species groups across the landforms. Ecological profiles are useful in verifying within-group similarity by examining the ecological amplitudes of the species within the groups and comparing the degree of limitation of the group to a particular landform group. Based on the value of the coverage class, the rank mean was determined for each species in every landform group. The percent deviation of the rank mean of each landform group for each species from the pooled rank mean across all landforms was determined and plotted as either a negative or positive deviation along the sequence of landforms.

Graphed together, the profiles of each species in a species group should exhibit similar deviations from the pooled rank mean in similar landform groups.

Coverage values of each species group for each landform group were determined by summing the coverage-class values of all species within a species group at each plot and determining the mean value for the landform group. Because of the large numbers of zeros in the data, the difference in mean coverage values of each species group across all landforms were examined using the non-parametric Kruskal-Wallis test (Conover 1980). Species groups constructed with tabular methods were corroborated with detrended correspondence analysis (DCA; ter Braak 1992), which identified clusters of species in ordinate space and verifed groups of species identified by tabular methods.

Once species groups were identified using both tabular and multivariate techniques, relationships of the groups to measured environmental variables were examined by constraining the ordination of species groups with various environmental parameters using canonical correspondence analysis (CCA) in the program CANOCO (ter Braak 1992). A set of 11 variables likely having the strongest effect upon plant community composition was selected for the analysis. Variables included the percentage of coarse sand (20–40 cm), percentage of fine sand (20–40 cm), percentage of silt and clay (20–40 cm), accumulated banding above and below 150 cm (cm), depth to banding (cm), surface soil pH, soil pH (20–40 cm), depth to neutral (pH = 7.0) soil (cm), depth to water table (cm), and percent canopy coverage. The significance of each environmental variable to the analysis was determined using a stepwise Monte Carlo permutation procedure (ter Braak 1992) with $\alpha = 0.05$.

To examine the applicability of the ecological species groups under highly disturbed conditions (plantations), the coverage of each species group in each of 29 plots established in plantations was entered into discriminant analysis (Gauch 1982). Error rates in discriminant analysis were tested using the jackknife method. Assumptions of discriminant analysis, multivariate normality and equal covariances, were not tested.

Results and discussion

Species group descriptions

Eight ecological species groups were developed (Table 2) using 31 of the 124 species observed (25% of all species observed) in 144 non-plantation plots in the Grayling Subdistrict. Each group was named after a characteristic member of the group. Most species not included in the groups were either too rare or were unidentifiable to species, which prevented an assessment of their indicator value. Site quality variation among the landform groups results from slight differences in soil texture, fertility, and soil water status. Soil fertility differences between the landform groups are subtle, and the dominant gradient distinguishing the groups is soil water. Detailed descriptions of the relationships of each group to soil water, soil fertility, and light conditions are described below in the order in which they are presented in Table 2.

The *Danthonia* group is the largest of the eight groups, and includes *Danthonia spicata* (L.) R&S, *Andropogon scoparius* Michx., *Andropogon gerardii* Vitman., and *Arctostaphylos uva-ursi* (L.) Sprengel. *Hieracium venosum* L. and *Hieracium floribundum* Wimmer&Grab. are less common but are also widespread. The group has its highest coverage on very infertile, very dry, outwash channels and unbanded outwash plain ecosystems (Table 3). Ecosystems in which these species occur typically are characterized by coarse, very infertile soils, often having sparse tree cover and consequently open light conditions. The group is most often associated with the *Solidago* and *Vaccinium* groups.

The *Solidago* group is most commonly represented by *Solidago spathulata* DC; *Anemone quinquefolia* L. and *Viola pedata* L. also characterize the group, but they are less common. The group is found in very dry to dry, very infertile to infertile soils and is most commonly found in outwash channels and unbanded outwash plain ecosystems, though it is also common in banded outwash ecosystems (Table 3). Although similar to the *Danthonia* group in site requirements, it is less widespread. The group is found under open to light canopy coverage, often in association with the *Danthonia* and *Vaccinium* groups.

The *Vaccinium* group is the most common and widespread of all the species groups. *Vaccinium angustifolium* Aiton is the most common member of the group, although all other members, *Prunus pumila* L., *Melanpyrum lineare* Desr., *Comptonia peregrina* (L.)

Table 2. Ecological species groups of landform groups occupied by the Kirtland's warbler in the Grayling Subdistrict, northern Lower Michigan.

1. *Danthonia* group: Characteristic of very dry, very infertile sites and open light conditions.
   Danthonia spicata (L.) R&S
   Andropogon gerardii Vitman.
   Andropogon scoparius Michx.
   Arctostaphylos uva-ursi (L.) Sprengel
   Hieracium floribundum Wimmer&Grab.
   Hieracium venosum L.

2. *Solidago* group: Characteristic of very dry to dry, very infertile to infertile sites and open conditions to light shade.
   Solidago spathulata DC
   Anemone quinquefolia L.
   Viola pedata L.

3. *Vaccinium* group: Characteristic of a broad range of soil water, soil fertility, and light conditions.
   Vaccinium angustifolium Aiton
   Carex pensylvanica Lamb.
   Comptonia peregrina (L.) Coulter
   Melanpyrum lineare Desr.
   Prunus pumila L.

4. *Gaultheria* group: Characteristic of very dry, very infertile to somewhat moist, moderately fertile sites and all light conditions.
   Gaultheria procumbens L.
   Amelanchier sanguinea (Pursh) DC
   Epigaea repens L.
   Solidago hispida Willd.

5. *Maianthemum* group: Characteristic of dry, infertile to somewhat moist, moderately fertile sites and light to moderate shade.
   Maianthemum canadense Desf.
   Amelanchier spicata (Lamb.) K.Koch
   Oryzopsis asperifolia Michx.

6. *Crataegus* group: Characteristic of moderately dry, infertile to moderately moist, moderately fertile sites and moderate to moderately-heavy shade.
   Crataegus spp. L.
   Convolvulus arvensis L.
   Rosa blanda Aiton

7. *Fragaria* group: Characteristic of somewhat dry to somewhat moist, moderately fertile sites and light to moderate shade.
   Fragaria virginiana Miller
   Prunus serotina Ehrh.
   Rubus flagellaris Willd.
   Salix humilus Marsh.
   Schizachne purpurascens (Torr.) Swallen.

8. *Rubus* group: Characteristic of moist, infertile sites and open conditions to moderate shade.
   Rubus hispidus L.
   Spiraea latifolia (Aiton) Borkh.

Table 3. Mean coverage-class values of ecological species groups in five landform groups occupied by the Kirtland's warbler in the Grayling Subdistrict, northern Lower Michigan. Values are mean coverage classes, standard deviations are in parentheses; p-values are for the Kruskal-Wallis test with $\alpha = 0.05$.

Species Group	Outwash Channels (n = 20)	Unbanded Outwash (n = 47)	Banded Outwash (n = 35)	Ice-contact (n = 30)	Water table -influenced outwash (n = 12)	p-value
Danthonia	7.89 (3.68)	6.32 (3.75)	4.19 (4.58)	3.33 (3.01)	2.67 (2.88)	< 0.01
Solidago	0.69 (0.79)	0.60 (0.16)	0.45 (0.58)	0.15 (0.48)	0.13 (0.31)	< 0.01
Vaccinium	16.50 (3.62)	16.90 (5.59)	13.86 (3.62)	14.75 (3.95)	17.45 (5.73)	0.05
Gaultheria	1.54 (1.49)	2.07 (1.67)	1.75 (1.25)	3.46 (2.61)	3.48 (2.33)	0.04
Maianthemum	0.75 (1.33)	1.10 (3.54)	1.49 (2.05)	1.49 (1.74)	2.38 (1.72)	0.03
Crataegus	0.09 (0.27)	0.46 (0.93)	0.47 (1.13)	0.54 (1.40)	1.10 (1.56)	0.04
Fragaria	0.90 (0.19)	1.28 (1.93)	1.51 (3.02)	2.27 (2.75)	7.29 (6.63)	< 0.01
Rubus	0.00 (0.00)	0.00 (0.00)	0.03 (0.17)	0.07 (0.37)	2.67 (2.64)	< 0.01

Coulter, and *Carex pensylvanica* Lamb., are also very common. The group is well distributed across all landform groups (Table 3). The group is also tolerant of a wide range of light conditions; it is absent only in areas of heavy shade. *Melanpyrum* is particularly characteristic of ecosystems supporting older stands of jack pine, and *Carex* may be a very aggressive colonizer after disturbance, often outcompeting all other ground flora and forming a dense, continuous mat across the forest floor (Abrams and Dickmann 1982).

The *Gaultheria* group is characterized by *Gaultheria procumbens* L.*,* *Epigaea repens* L., and *Amelanchier sanguinea* (Pursh) DC, and the less common *Solidago hispida* Willd. The group is widespread, though less so than the *Vaccinium* group, and is found on all levels of soil water and fertility, although it is most predominant on the moist landform groups (Table 3). The group occurs in a very wide range of light intensities and may tolerate moderately heavy shade. It is associated with the *Vaccinium* and *Maianthemum* groups.

The *Maianthemum* group includes *Maianthemum canadense* Desf., *Amelanchier spicata* (Lamb.) K.Koch, and the less common *Oryzopsis asperifolia* Michx. The group is characteristic of dry to moderately moist sites of infertile to moderately fertile soils, occurring most often on sites with fine-textured banding or fine-textured soil in the upper horizons, particularly banded outwash plains and ice-contact terrain, or on moist sites (Table 3). The group is most often found in light to moderate shade, although it may tolerate open light conditions to heavy shade. The group is most often associated with the *Gaultheria* group.

The *Crataegus* group is characterized by several species of *Crataegus* L., *Rosa blanda* Aiton, and *Convolvulus arvensis* L. The group is characteristic of moderately dry to moderately moist, infertile to moderately fertile soils. It is common on all but the driest sites and is most common on moist sites (Table 3). The group is commonly found under moderate to moderately heavy shade. The site relationships of the group are similar to those of the *Maianthemum* group, but it is found on slightly better sites often where moisture is relatively high, such as in ice-contact terrain and water table-influenced outwash plains. It is most often associated with the *Maianthemum* group, although it may occur with the *Fragaria* group as well.

The *Fragaria* group is most often represented by *Fragaria virginiana* Miller, *Prunus serotina* Ehrh., and *Salix humilus* Marsh.; *Rubus flagellaris* Willd. and *Schizachne purpurascens* (Torr.) Swallen. are less common. The group is found on the best soil water and fertility conditions of any of the species groups, characterized by moderately dry to moist soils that are moderately fertile. It is most often found on ice-contact terrain and on outwash plains influenced by the water table (Table 3). It is most typical of light- to moderately shady conditions. It is most often associated with the *Rubus* group on wetter sites and the *Crataegus* and *Maianthemum* groups on drier sites.

The *Rubus* group consists of *Rubus hispidus* L. and *Spiraea latifolia* (Aiton) Borkh. The group is nearly restricted to moist, infertile soils of water table-influenced outwash plains, where the water table is above 150 cm during part of the growing season (Table 3). Although the members of the group require high soil water during part of the growing season, the soil of these sites is very often coarse and infertile. The group characterizes landform-level ecosystems rarely occupied by the Kirtland's warbler, and as a result the group is not widespread across the landform groups. The group is found in open light conditions to moderate shade.

No species group occurred exclusively on one landform group, although the *Rubus* group, being the most mesic species group, was almost exclusively found on water table-influenced outwash plain sites (Table 3). Such patterns are the rule and have occurred in other studies (Pregitzer and Barnes 1982; Spies and Barnes 1985; Archambault et al. 1990; Simpson et al. 1990; Host and Pregitzer 1991; Pearsall 1995). The *Danthonia* and *Vaccinium* groups, and to a lesser extent the *Gaultheria* group, are abundant on every landform. The dry species groups (e.g., *Solidago*) and those found on the moderately moist end of the soil moisture gradient (e.g., *Fragaria*), while found on most landform groups, had higher coverage in some landform groups than in others, differing in the relative abundance of the individuals of species in the group. The attempt to develop species groups for large-scale, landform-level ecosystems presents the situation of relatively high within-ecosystem variation compared to studies of smaller-scale ecosystems. As a result, the majority of the species groups are found on all or nearly all landform groups.

Quantitative comparisons of species groups

TWINSPAN classified the ground flora data into groups of species that were similar to those determined using tabular methods and knowledge of physical factors of physiography, soils, and microclimate. Using the groups developed by TWINSPAN, plots located on banded outwash and ice-contact, two landform groups very similar in site conditions, were not clearly separated. In general, however, TWINSPAN results corroborated species groups developed with tabular methods.

Ecological profiles demonstrated that each species is unique in its occurrence across the landform groups (Figs. 2a–2c). However, all species of an ecological species group have similar ecological amplitudes in relation to the five landform groups. For example, ubiquitous groups such as *Vaccinium* and *Gaultheria* contain high within-group variation due to their common occurrence on nearly every landform (Figs. 2a and 2b). The major source of the within-group variation of the *Maianthemum* and *Fragaria* groups occurs in ice-contact terrain, where site variability is likely high enough to affect the presence and abundance of species most sensitive to slight changes in site factors (Figs. 2b and 2c). In contrast, the *Rubus* group, which is the species group most restricted to a single landform group (water table-influenced outwash plains), shows very little within-group variation (Fig. 2c), nor do the *Danthonia* and *Crataegus* groups (Figs. 2a and b). The location of these groups near the extremes of the soil-water and fertility gradient is probably a major reason for their limited within-group variation.

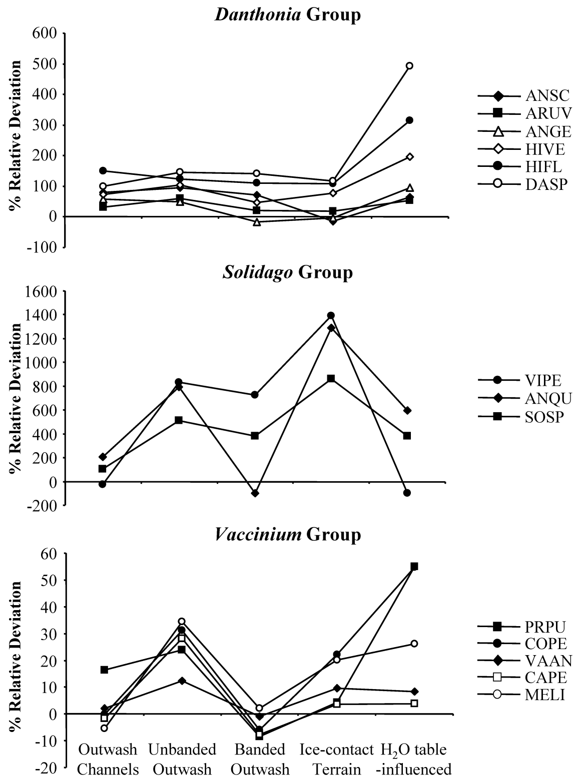

Figure 2a. Percent relative deviation from mean coverage of species of the *Danthonia*, *Solidago*, and *Vaccinium* species groups. Landform groups are arranged left to right in order of increasing soil moisture.

The mean coverage values of all eight ecological species groups differed significantly among the five landform groups (Table 3). The ubiquitous *Vaccinium* and *Gaultheria* groups exhibited the least differences and the groups representing the extremes of the moisture/fertility gradient (*Danthonia, Solidago, Fragaria*, and *Rubus*) exhibited the strongest differences. It is notable that the coverage of all species groups differed among the landforms even as the

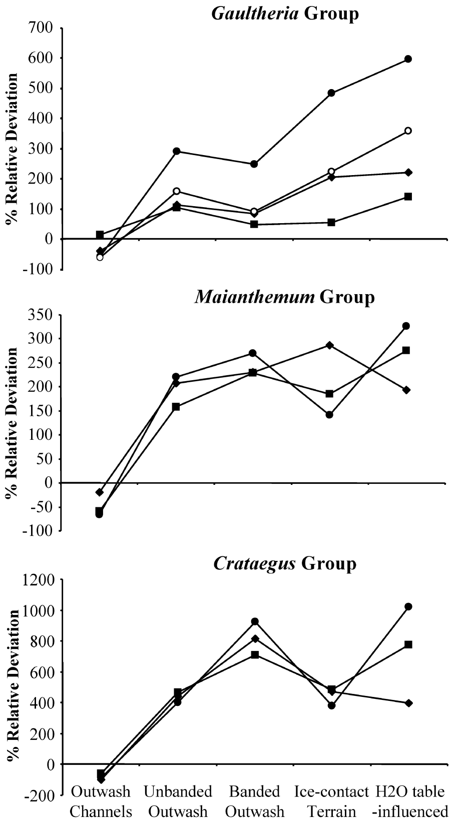

Figure 2b. Percent relative deviation from mean coverage of species of the *Gaultheria*, *Maianthemum*, and *Crataegus* species groups. Landform groups are arranged left to right in order of increasing soil moisture.

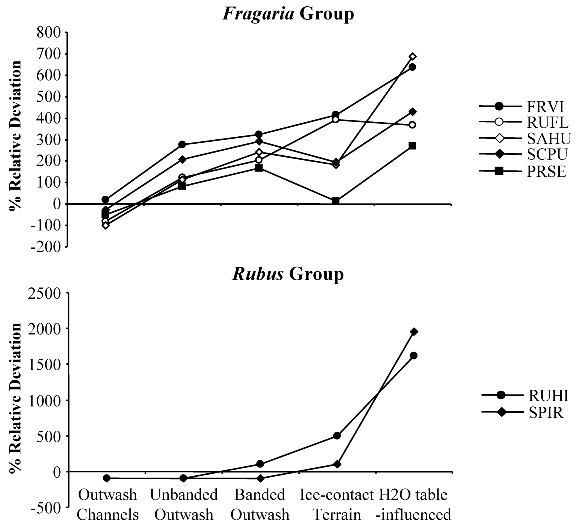

Figure 2c. Percent relative deviation from mean coverage of species of the *Fragaria* and *Rubus* species groups. Landform groups are arranged left to right in order of increasing soil moisture.

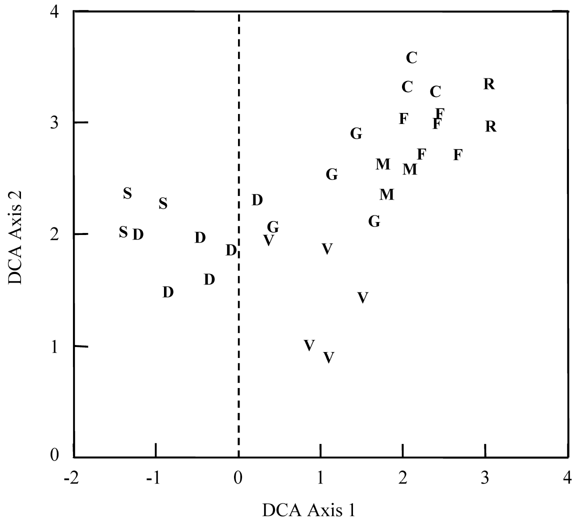

Figure 3. Detrended correspondence analysis of 31 species used to construct eight ecological species groups in the Grayling Subdistrict, northern Lower Michigan. Letters represent ecological species group membership: D, *Danthonia*; S, *Solidago*; V, *Vaccinium*; G, *Gaultheria*; M, *Maianthemum*; F, *Fragaria*; C, *Crataegus*; R, *Rubus*.

power of the Kruskal-Wallis test was reduced due to the many zero-ties in the analysis.

The species groups developed with tabular methods were substantiated with the results of detrended correspondence analysis (DCA; Figure 3). The strong within-group clustering of species and the relatively clear separation of clusters in the DCA ordination supports the constitution of the species groups. The first DCA axis explains much of the variation in the data set and represents a gradient of increasing soil water. Species characteristic of infertile, dry sites have negative axis scores (*Solidago* and *Danthonia* groups), whereas water table-influenced sites (the *Rubus* group) and those characteristic of sites with high soil water (*Fragaria, Crataegus*, and *Maianthemum* groups) have high positive first-axis scores. The broad distribution of groups occurring across a wide range of soil water conditions (*Danthonia, Vaccinium*, and *Gaultheria*) is illustrated by their relatively loose clusters. The second DCA axis represents a weak light gradient. Species found in relatively low light intensity (e.g., *Crataegus*) received high Axis 2 scores and are located near the top of the diagram, whereas those found in open conditions (e.g., *Danthonia*) received lower second-axis cores and are located near the middle of the diagram.

Table 4. Eigenvalues and inter-set correlations for the first two axes of canonical correlation analysis of eight ecological species groups constrained by 11 environmental variables on 5 landform groups in the Grayling Subdistrict, northern Lower Michigan.

	Axis 1	Axis 2
Eigenvalue	0.125	0.110
Cumulative % variance	29.2	55.5
Correlations		
Depth to water-table, cm (WATER)	–0.147	–0.664
% silt and clay, 20–40 cm (S+C)	0.457	–0.167
% fine fraction, 20–40 cm (FINES)	–0.174	0.528
Percent canopy cover (TREECOV)	0.281	–0.316
Depth to banding, cm (BANDING)	–0.414	0.225
pH of soil surface (SURFPH)	0.351	–0.173
Accumulated banding > 150 cm, cm (DEEPBND)	0.247	0.831
% coarse fraction, 20–40 cm (COARSE)	0.180	–0.497
Accumulated banding < 150 cm, cm (SHALBND)	0.303	–0.016
Depth to pH 7.0, cm (PH7)	–0.038	–0.072
pH of soil, 20–40 cm (SOILPH)	0.149	–0.307

Species group-environment relationships

In general, the species group-environment relationships revealed with canonical correspondence analysis (CCA) confirm those observed in the field and described above (Table 4). The first two axes of the CCA account for 56% of the species group-environment variation, and both had F-ratios significant at $p < 0.01$ based upon Monte Carlo simulations using 99 permutations. The first CCA axis was related to percent silt and clay, depth to banding, and soil surface pH (Table 4). The second axis is correlated with deep accumulated banding, depth to water table, and percent fine sand (20–40 cm). All 11 variables were significant at $p < 0.05$; the six most important variables (all $p < 0.01$) explaining variation in the data set, as selected by the stepwise Monte Carlo procedure, in order, were: depth to water table, percent silt and clay, percent fine sand, tree coverage, depth to banding, and soil surface pH.

Results of the CCA suggest that the groups are related to different combinations of the same set of environmental variables (Figure 4). Axis 1 corresponds to gradients in both depth to banding and percent silt+clay, with percent silt+clay having a slightly greater influence on species variation (represented by a slightly longer vector). Species having positive Axis 1 scores, such as those in the *Maianthemum*, *Fragaria*, *Crataegus*, and *Rubus* groups, are therefore correlated with higher soil moisture, having higher percentages of silt and clay and shallower depths to banding than species with negative scores. Axis 2 represents a gradient of depth to water table, and species with positive axis scores (e.g., those in the *Rubus* group) tend to be associated with a high water table at some point during the growing season as compared to those with negative Axis 2 scores. Other variables, such as percent canopy coverage, have influence along both axes; species with positive Axis 1 scores and negative Axis 2 scores (e.g., those in the *Crataegus* group) are found beneath heavy shade.

The species groups are differentiated along soil water and fertility gradients using the 11 environmental parameters, although different combinations of light and/or site factors may be responsible for the presence or absence of each group (Figure 4). For example, the *Rubus* group is located on the negative end of the depth-to-water table gradient, indicating its affinity for high water tables, but also appears to be related to high percentages of fine sand. In contrast, although the *Crataegus* and *Maianthemum* groups are similar in site requirements and are both related to high percentages of silt and clay and increasing soil surface pH, the *Crataegus* group appears to be more strongly related to light availability (percent canopy coverage). The *Fragaria* group, observed in the field to be associated with the best sites dominated by jack pine, appears to reflect similar percentages of silt and clay as the *Maianthemum* group, but also reflects higher percentages of fine sand and shallower depths to water table. The ubiquitous *Vaccinium* group is found clustered around the origin of the CCA ordina-

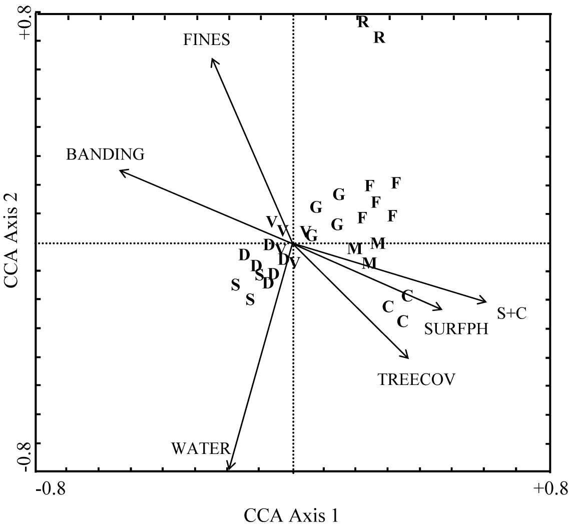

Figure 4. Ordination of 31 ground-cover species constrained by eleven environmental variables using canonical correspondence analysis. Letters represent ecological species group membership and are the same as in Figure 3. Arrows indicate the direction and magnitude of the influence of environmental variables. Codes for environmental variables are the same as those given in Table 4. The six most important variables as determined by Monte Carlo procedures (α = 0.05) are shown.

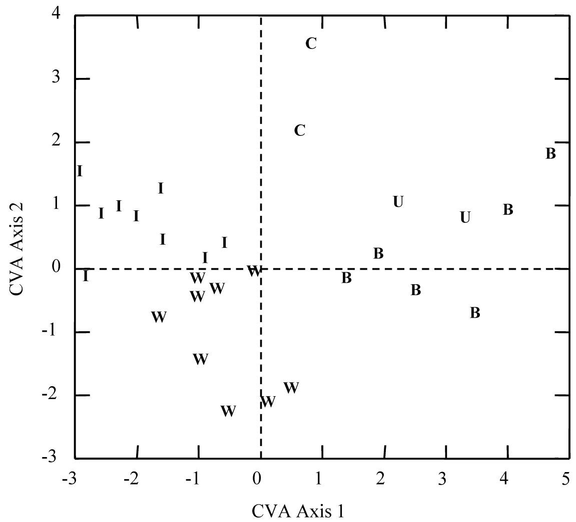

Figure 5. Ordination of 29 plantations plots located in five landforms groups in the Grayling Subdistrict, northern Lower Michigan along the first two canonical variates of an analysis of eight ecological species groups. Letters represent landform group to which the plot belongs: C, outwash channels; U, unbanded outwash plains; B, banded outwash plains; I, ice-contact terrain and outwash plains associated with ice-contact terrain; W, water table-influenced outwash plains.

tion. Although the *Danthonia, Vaccinium*, and *Gaultheria* groups are abundant on every landform, the *Gaultheria* group appears to be more strongly related to increased percentage of fine sand and decreased depth to water table, especially compared to the *Danthonia* group. The dry species groups (*Danthonia* and *Solidago*) are located at the furthest points along the depth to banding gradient and further than all other groups along the depth to water table gradient, indicating their propensity for dry, poor soils.

Applicability to plantations

Using the eight species groups, plots located in plantations across the five landform groups are differentiated very clearly using discriminant analysis, forming relatively tight, non-overlapping clusters in ordination space (Figure 5). The first canonical variate is positively correlated with species groups on the moist end of the soil water gradient, such as *Crataegus, Fragaria*, and *Rubus*, and negatively correlated with those on the dry end of the soil water gradient (*Danthonia, Solidago*, and *Vaccinium*; Table 5). The landform groups are also differentiated along a gradient of soil fertility represented by CVA Axis 2 (Figure 5). The second canonical variate is strongly positively correlated with the dry species groups, such as *Solidago* and *Vaccinium*, and is negatively correlated with moist groups such as *Fragaria* and *Rubus*. The second variate separates drier and infertile sites, such as outwash channel and unbanded outwash landforms, from moister and more fertile landforms, particularly water table-influenced landforms.

Overall, the landform groups are well separated by the eight species groups except for the banded and unbanded outwash, which is not unexpected (Figure 5). The first three canonical variates account for 77, 96, and 99% of the cumulative variance (Table 5). The overall misclassification rate is moderate (18%), and the jackknife misclassification rate is 31%. Unbanded- and banded outwash plain landform groups are those most often misclassified. The clear differentiation of landform groups in plantation plots using species groups suggests that the eight groups are functional and applicable even in highly disturbed (furrowed) soil conditions.

General discussion

Ecological species groups, in conjunction with physiography, microclimate, and soil factors, are useful in

Table 5. Comparison of results of canonical variates analysis conducted with eight ecological species groups for 29 plots located in jack pine plantations in the Grayling Subdistrict, northern Lower Michigan. Species groups are arranged from driest to moist.

Canonical variate	1	2	3
Eigenvalue	4.785	1.143	0.216
Cumulative % variance explained	77.1	95.5	99.0
Variable	**Correlation coefficient**		
Danthonia group	0.267	0.082	–0.111
Solidago group	0.384	0.532	–0.372
Vaccinium group	0.437	0.314	–0.052
Gaultheria group	–0.006	–0.034	–0.277
Maianthemum group	–0.010	0.065	–0.100
Crataegus group	0.688	–0.002	0.448
Fragaria group	0.740	–0.252	–0.121
Rubus group	0.776	–0.217	–0.012

distinguishing landscape ecosystems at both broad and fine scales. Several studies have defined species groups for many different geographic areas of Michigan, each at the scale of local landscape ecosystems (Pregitzer and Barnes 1982; Spies and Barnes 1985; Hix 1988; Archambault et al. 1990; Simpson et al. 1990; Pearsall 1995). Development of species groups for larger ecological units is likely avoided because: (*i*) groups developed for broad-scale ecosystems contain an inherently high within-group variability of species within a group, and (*ii*) the development and use of ecological species groups necessarily requires a keen understanding of the local landscape ecosystem types within the landforms and physiographic systems in order to comprehend the occurrence, range, and tolerances of species. These problems are magnified in dry, sandy ecosystems such as those dominated by jack pine, where steep environmental gradients are lacking. Our research shows that fine-scale ecological understanding of ground flora species may be utilized successfully in developing ecological species groups for broad-scale ecosystems, and that the construction of ecological species groups is an integral and necessary part of understanding landscape ecosystems at multiple scales.

Although each group was found in more than one landform, and several in every landform, variation in the relative abundance of the species groups differed between landforms. The use of coverage values rather than simple presence and absence is therefore crucial in defining and using the groups. As in similar studies (Pregitzer and Barnes 1982; Spies and Barnes 1985; Archambault et al. 1989; Host and Pregitzer 1991; Kashian et al. (in press)), the overlap suggests that a combination of physiography, soil and vegetation would likely be more successful in distinguishing the landforms than species groups would be alone, and that the species groups should be used in conjunction with physical site factors in ecological classification. Furthermore, CCA results suggest that differences in soil (in addition to light availability) are the primary factors explaining variability in species presence and abundance in our study. The soil factors are strongly mediated by physiographic factors, which, together with climate, form the basis of the ecological classification built by Kashian et al. (in press). It is in this sense that our research differs from a typical Braun-Blanquet approach, which emphasizes a floristic rather than an ecological approach.

The original grouping of species based on field observations and tabular analysis of presence/absence and abundance data was confirmed by multivariate analyses. The development of ecological species groups is an example of an approach in which subjective, qualitative data based on field observations and reconnaissance are equally as valuable as objective, quantitative data. Multivariate methods used exclusively would be only partially successful in creating meaningful ecological groups, since it is likely that some unrealistic groupings of species may result from procedures such as TWINSPAN or DCA. Therefore, caution must be exercised in using and interpreting multivariate methods without thorough knowledge of species-site relationships gained through extensive field observations and the *a priori* understanding of compensating factors. Simultaneous examination and integration of physiography, soil, and vegetation completed in the field is necessary for successful use of multivariate statistics (Spies and Barnes 1985).

Disturbance is a well-known limiting factor to the use of vegetation for ecological classification, especially where grazing, agriculture, logging, plantations, fire, or fire exclusion may have dramatically altered the native vegetation in a manner that may not reflect site conditions (Albert et al. 1986). The development of species groups has only sparingly been applied to disturbed landscapes (Archambault et al. 1989; Simpson et al. 1990; Host and Pregitzer 1991; Meilleur et al. 1992), and has usually dealt with past disturbances at least 50–100 years old. In our study, the eight species groups appear to be useful in young jack pine plantations where the surface-soil horizons and plant communities have been heavily disturbed by furrowing as recently as 15 years prior to sampling. Together with the results of other studies, these data confirm that ground flora species are fairly resilient even to recent disturbance. Working in Upper Michigan, Hix and Barnes (1984) found that the original ground flora might remain on a site many years after a clear-cut. In fact, 20 of the 31 species in the eight groups constructed in this study were found by Abrams and Dickmann (1982) to be common on both unburned clear-cut and burned areas of the Grayling Subdistrict. Bocetti (1994) found that while young jack pine plantations in the Grayling Subdistrict tended to contain significantly less coverage of ground flora than wildfire areas, ground flora was similar in composition between burns and plantations. The persistence of ground flora species following heavy disturbance is likely due to the high frequency of clonal and perennial plants in the region (Spies and Barnes 1985; Barnes 1989). The successful application of the ecological species group approach to old-growth treefall gap forests (Pregitzer and Barnes 1982; Spies and Barnes 1985; Smith 1995), formerly logged forests (Archambault et al. 1989; Host and Pregitzer 1991), and our work in heavily burned and planted areas, confirms the usefulness of the ecological species group approach across a large range of disturbance regimes. Additionally, a multi-factor approach, including physical site factors as well as ecological species groups, is invaluable whenever vegetation composition may be affected by disturbance.

The site-species relationships of the ecological species group members in our study agreed with those of the species described in general references of Michigan flora (Voss 1972, 1984, 1997; Barnes and Wagner 1981) and in studies of ground flora in ecosystems dominated by jack pine in this region (Beaufait and Brown 1962). The species groups developed in this study, however, should not be extrapolated to landscape ecosystems other than those in the Grayling Subdistrict (8.2; Albert et al. 1986). The indicator value of ecological species groups varies across different regions of climate and physiography (Pregitzer and Barnes 1982), and thus plant community assemblages are likely to changes across or near climatic and physiographic boundaries. For example, ecological species groups developed for upland ecosystems in two areas of Upper Michigan within a 40-mile radius (Pregitzer and Barnes 1982; Simpson et al. 1990) exhibited very different composition and site relationships because they are found in areas characterized by very different macroclimate and physiography. Similarly, the site-species relationships for many of the plants included in our ecological species groups were described by Spies and Barnes (1985) for northern hardwood-hemlock ecosystems of Upper Michigan and by Archambault et al. (1989) for oak ecosystems in southeastern Lower Michigan, but these species occur in very different plant communities and often represent different site conditions. Likewise, our species groups are not applicable to dry, sandy, jack pine-dominated ecosystems on the Lake Huron lake plain (the Standish Subdistrict (7.1) of the Arenac District (7); Albert et al. 1986), although it lies just to the east of our study area. Based on field observations and sampling, strong differences in regional climate (moderated by Lake Huron) markedly affect the specific assemblages in this landscape. For example, frost-sensitive oak species (white oak (*Quercus alba* L.), northern pin oak, and to a much lesser extent black oak (*Q. velutina* Lamb.)) commonly dominate the ground flora, reflecting the lack of frost during the growing season that is prevalent in the more continental climate of the Grayling Subdistrict (Kashian et al. (in press)). Finally, while the species groups may be usable at ecosystem scales contained within landforms (i.e., ecosystem types), they are likely most effective in landform-level ecosystems rather than landscape ecosystems at other scales. Development of the groups presented in this study was completed using data stratified at the landform scale, and the groups therefore incorporate ground flora associations that reflect all the physical site variation of the ecosystem types contained with landscape-level ecosystems. As a result, the species groups may not be as effective at delineating ecosystem types.

In addition to their development specifically for dry, sandy ecosystems in the Grayling Subdistrict dominated by jack pine, the species groups presented here were developed using only data from ecosystems formerly or currently occupied by the Kirtland's warbler. In the classical sense, ecological species groups are usually developed for a contiguous land area using data from the entire spectrum of ecosystems contained within it (Barnes 1984) rather than a set of selected ecosystems. The groups may then be utilized in facilitating and expediting the identification of ecosystems for field mapping exercises. In fact, field testing of ecological species groups in mapping ecosystems serves as the ultimate validation of the groups themselves. In contrast, our sampling regime was limited by those landform-level ecosystems occupied by the Kirtland's warbler, with little or no mapping objective. As a result, our species groups represent a narrower range of ecosystems than would otherwise be studied, and have been validated only by quantitative, rather than field-based, analyses. Nevertheless, the range of site conditions included in our sampling regime likely spans the entire range of upland ecosystems dominated by jack pine, and thus represents an useful experimental application of the ecological species group approach within a single forest cover type (*sensu* Archambault et al. 1989).

Management implications

Information about site conditions provided by species groups may be used in part to determine upon which landforms jack pine will grow the slowest and thus will be occupied for long durations by the warbler (Kashian et al. (in press); Walker et al. (in press)). For example, the *Rubus* group is useful in distinguishing sandy, infertile sites that are influenced by the water table during the growing season. Although water-table-influenced outwash plains are rarely occupied by the warbler, their root-restricting water table slows jack pine height growth and thus extends the duration of warbler occupancy. The *Fragaria* group distinguishes the most productive sites dominated by jack pine and occupied by the warbler. These sites are characterized by moderately infertile, fine-sand soil textures and large amounts of fine-textured banding, are most often located on ice-contact terrain or banded outwash plain landforms, and typically have fast-growing jack pines and short duration of warbler occupancy. Similarly, the *Maianthemum* and *Crataegus* groups also distinguish productive sites with fine sand textures and infertile soils. These sites are also found on ice-contact terrain and banded outwash plain landforms that include moderate-to-fast-growing jack pines and short duration of warbler occupancy. The *Vaccinium* and *Gaultheria* groups are the most widespread of the eight groups and are found on a wide range of soil water and fertility, and are useful in distinguishing widely occurring sites. The presence of these groups coupled with the absence of moderately moist or moderately fertile species groups typically indicates relatively poor height growth conditions for jack pine and long duration of warbler occupancy. Finally, the *Danthonia* and *Solidago* groups distinguish very dry sites with coarse, very infertile soils. These sites are typically on outwash channels and unbanded outwash plains that include slow-growing jack pines and long warbler occupancy (Kashian et al. (in press); Walker et al. (in press)).

Ecological species groups reflect the total site complex, and in conjunction with climate, physiography, and soil, they are useful in distinguishing landscape ecosystems at multiple scales. The approach is also applicable to ecosystems characterized by a wide range of disturbance regimes. Although the potentially large number of ground flora species present may intimidate the investigator attempting to utilize vegetation for ecosystem classification, often only a few key species or groups of species are needed to distinguish sites and thus may be quite useful and hence efficient in differentiating and mapping ecosystems in the field. Ecosystems are best distinguished by employing a multifactor approach, requiring an understanding of site factors as well as biota, all operating together as a cohesive ecological system. As such, ecological species groups are vital in their role of classifying ecosystems, whether the objective is preservation, conservation, or management of forests or wildlife.

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