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Adjacency arrangement effects on plant diversity and composition in woodland patches

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To understand "adjacency arrangement" (configuration of a patch and its adjoining elements) as a basic unit of landscape pattern, we studied 30 woodland patches (*Populus tremuloides)* in Alberta, Canada, with adjacent vegetation varying from 0% shrubland (100% grassland) to 100% shrubland (0% grassland). We evaluated (1) how important adjacency effects are relative to resource availability and disturbance in affecting plant species richness and composition in the woodland understory, and (2) which species and species groups change in abundance and presence with increasing percent shrubland in the adjacency arrangement. We found that, in addition to topography and previous grazing, adjacency arrangement is a major significant variable affecting the vegetation composition of woodland patches. Along a gradient from 0% to 100% adjacent shrubland, the species composition in woodland patches changed from an abundance of weedy and introduced plants to an abundance of moist-environment plants, the proportion of native species and perennials increased linearly, the number of "shrubland species" increased linearly, "grassland species" decreased linearly, and total species richness remained constant. Woodland vegetation did not differ significantly where adjacent shrubland was to the east or to the west of the wooded patch, nor between patches which did or did not experience a change in the adjacent shrubland in the recent past. We conclude that adjacency arrangement is an easily measured, highly promising concept for ecological understanding, as well as for land planning, design, conservation and management.

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A widely accepted premise in landscape ecology is that the spatial arrangement or juxtaposition of adjacent elements (e.g. local ecosystems or land uses) in a heterogeneous landscape has a major effect on the species and processes (Risser et al. 1984, Turner 1987, 1989, Wiens et al. 1993, Wiens 1995, Klopatek and Gardner 1999). To date, researchers have focused on habitat composition (the percentage of each habitat type within a landscape, Romme and Knight 1982, Robbins et al. 1989, Ihse 1995) and the effect of patch size and patch shape on species richness (Mac-Arthur and Wilson 1967, Forman et al. 1976, Galli et al. 1976, Hardt and Forman 1989, Gutzwiller and Anderson 1992, Vickery and Hunter 1994, Freemark et al. 1995). Also, studies of interpatch distance, habitat interspersion, and landscape connectivity have been used to understand interaction among, and movement between landscape elements (Hanski 1982, Saunders and Ingram 1987, Lawton and Woodroffe 1991, Taylor et al. 1993, Fahrig and Merriam 1994, Hanski and Gilpin 1997). Even though these studies use many assays for measuring characteristics of landscape structure, the challenge remains to measure and differentiate the explicit spatial arrangement of elements in the landscape and understand its ecological importance (Gustafson 1998).

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This study is directed at understanding the effect of adjacent elements on a patch. We refer to "adjacency arrangement" as the spatial configuration of a patch (or corridor) and its adjoining landscape elements (local ecosystems, habitats or land covers). Further, we expect that the diversity of adjacent habitats, as well as their spatial arrangement, should affect the ecological characteristics in a target patch. Since there is no generally accepted method for measuring adjacency effects (the ecological effects of adjacency arrangements), we propose to use the percent common border between a patch and each of its adjacent elements as an independent variable or index for evaluating adjacency effects. In this study the target patch is woodland and the two adjacent elements present are shrubland and grassland. The adjacency arrangement varies from 100% shrubland surrounding a woodland patch to 100% grassland surrounding the patch (Fig. 1).

One approach towards understanding adjacency effects is to compare edges of a patch that borders different adjacent elements. For example, a study of forest fragments in human dominated areas of upstate New York found that forest edges adjacent to residential areas have higher plant species richness than forest edges adjacent to fields (Moran 1984). Similarly, tree mortality is higher in forest edges adjacent to pasture than in those adjacent to young secondary forest in Brazil (Mesquita et al. 1999), and rodent damage in macadamia orchards in Australia is higher in the edge adjacent to forest than in the edge adjacent to grassland (White et al. 1997).

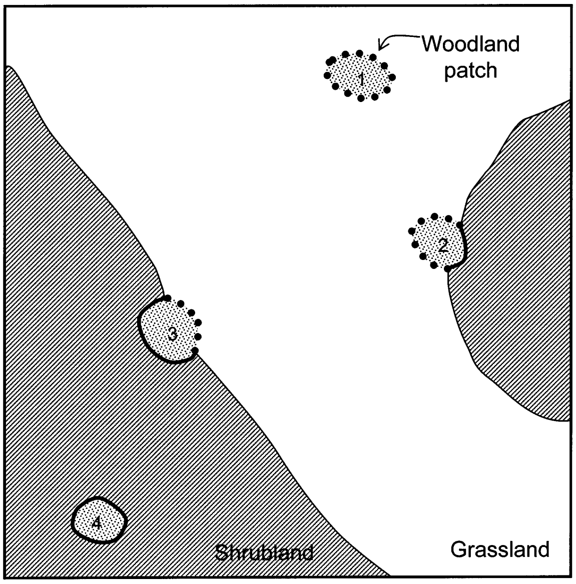

Fig. 1. Landscape mosaic and adjacency arrangements. Thick dotted line = perimeter shared by the aspen patch and the adjacent grassland; thick solid line = perimeter shared by the aspen patch and the adjacent shrubland. (1), (2), (3), and (4) are aspen woodlands with 0%, 30%, 60% and 100% adjacent shrubland respectively.

Another approach towards understanding adjacency effects correlates ecological characteristics of the target patch with indices of the adjacent habitat composition (Webb et al. 1984, Freemark and Collins 1989, Metzger 1997, Bastin and Thomas 1999). For example, the similarity between the adjacent habitat and the patch is a good predictor for vegetation composition of forest fragments in Britain (Bastin and Thomas 1999). Also, heathland patches in Britain with woodland in the adjacent matrix show higher invertebrate diversity than patches with grassland or bare ground in the adjacent matrix (Webb et al. 1984).

We focus on two questions in this study:

1) How important is the adjacency arrangement relative to measures of resource availability and disturbance in affecting species richness and/or composition in a woodland patch?
2) Which species and species groups increase or decrease in their abundance and presence with increasing percent shrubland (or grassland) in the adjacency arrangement?

We also gather evidence for two additional questions:

3) Does the location of the adjacent shrubland (e.g. to the east or west of the woodland patch) affect the species composition in the woodland?
4) Does the species composition in woodland patches with a stable adjacency arrangement differ from the species composition in patches where the adjacent land cover had been altered in the recent past?

We examine these questions using aspen woodland patches (*Populus tremuloides*) in a grassland and shrubland matrix of southern Alberta, Canada. The arrangement of adjacent shrubland and grassland may affect plant composition in a woodland patch because the adjacent shrubland and grassland affect specific ecological mechanisms, especially resource distributions, dispersal, and disturbances. These mechanisms in turn will interact with a species' life history traits to define each species' competitive advantage and resultant spatial distribution (Grime 1979, Bazzaz 1996, see also Hersperger 2000 for a discussion and evaluation of potential mechanisms in the study area). A range of variables is included to estimate the relative importance of resource availability (elevation, slope, soil texture, soil moisture, and soil pH), and disturbance (old sheep grazing, old cattle grazing, recent cattle grazing, and current cattle grazing).

A general west-to-east airflow characterizes the region (Atmospheric Environment Service 1993) in which the study is located, and we expect that these westerly winds affect seed dispersal, disturbance regimes, and microclimate. Thus we hypothesize that the effect of the adjacent element differs if the shrubland element is located east or west of the target patch. Therefore we compare aspen woodlands with adjacent shrubland to the east versus woodlands with shrubland to the west.

We are also interested in the effect of stability or persistence of the adjacency arrangement. The shrubland adjoining several woodlands in our study area was removed and replaced by grassland (as a ranch improvement strategy) during the period 6 to 17 years preceding our measurements. We hypothesize that these changes in adjacency arrangements were followed by changes in the understory woodland vegetation, and that today's understory vegetation reflects the current adjacency arrangement, rather than that preceding the shrubland/grassland alteration.

Methods

Study site description

The study area is a 35 × 5 km section of the aspen parkland in the foothills of the Rocky Mountains of Alberta, Canada (lat. 50°10′00″ N, long. 114°00′00″ W). It is located 30 km west of the town of Nanton, 80 km south of Calgary, and 110 km north of the United States border on the western slope and the crest of the first north-south ridge east of Chain Lakes at an altitude of 1300–1450 m.

The plant cover in this part of the aspen parkland study area is strikingly patchy with clearly delineated aspen woodlands surrounded by a matrix of mostly lightly grazed natural grassland. An aspen woodland typically consists of one clone of *Populus tremuloides* and ranges from 0.05 to 0.8 ha in size. In many areas, willow shrubland (*Salix* spp.) on ridges, slopes, and valleys adds to the distinct vegetation mosaic. Infrequent *Populus balsamifera* clones, sloughs, ranch houses and rural roads are also present. The aspen trees are 8–20 m high and measure 10–20 cm dbh. Most tree trunks are even aged and grow close together. The edge trees are usually as high as the trees in the patch interior. The patch interior is characterized by a lot of light because the crown cover averages approximately 45%. Since no aspen grow in the adjacent grassland and shrubland, the patch border towards grassland and shrubland is sharp. Almost all woodland patches contain at least a few scattered standing dead willow shrubs. Broadleaf herbs, grasses, and shrubs generally < 1 m high and tolerant of dappled shade are typical in the understory of the aspen woodlands.

Willow shrubland dominated by *Salix bebbiana* is a distinctive community to this part of the aspen parkland. *S. bebbiana* is a shrub or occasionally a small tree with several thick stems (5–20 cm diameter) and often many dead branches growing up to ca. 5 m high (typical height 3-4 m) forming extensive thickets. Occasional individuals of the tree *Pinus contorta* or *Picea glauca* are present. Since only the crowns of a few larger willows touch, the light environment (and the microclimate) in the shrubland interior is very heterogeneous. Areas between shrubs (often 2–7 m^2 in size) can be completely exposed to sunlight whereas areas near willow trunks are much darker and somewhat sheltered. Rather little wind penetrates the shrubland. The shrubland understory is generally lush (often ca 1 m high) and resembles the aspen patch understory, though the shrubland plant cover is more heterogeneous.

Fescue-oat grass (*Festuca scabrella)* communities dominate the grassland. In the early part of the 20th century, before extensive cattle grazing, *Festuca scabrella* grew almost to the exclusion of other grasses in the expansive areas of the aspen parkland (Moss 1955), with Parry oat grass (*Danthonia parryi*) being the second most abundant grass species. Today, however, *Danthonia parryi* and the introduced *Phleum pratense* dominate large areas, because cattle-grazing has been modifying the grassland composition (Moss and Campbell 1947). Many forbs and low shrub species grow among the grasses, such as the forbs *Agoseris glauca*, *Aster laevis*, *Dodecatheon conjugens*, *Galium boreale*, *Geranium viscosissimum*, and *Lupinus sericeus*, and the shrubs *Potentilla fruticosa* and *Rosa woodsii*. The last big fire most likely swept through the study area in 1910 (Nanton and District Historical Society 1975).

Patch selection

The aspen woodlands of this study were selected in June 1998. All 126 aspen patches present were identified in 1982 aerial photographs (scale approximately 1:20 000) for potential study, and each patch was examined in the field. Aspen patches were excluded if they: (1) consisted of *Populus balsamifera*, (2) appeared to consist of more than one aspen clone, (3) were < 30m long or < 20m wide, (4) had $< 10\%$ crown cover, (5) were protected by topography from westerly winds, or (6) contained a creek or area of standing water. All patches selected are oval or round in shape. The aspen crown, or aspen sucker ≥ 5 cm diameter, defines the border of a patch. Patches which were < 5 m from another aspen patch, and patches where the adjacent shrubland or grassland was < 10 m wide, were excluded.

From the remaining 65 patches, four were randomly selected in eight adjacency classes (four woodlands per class, 32 woodlands totally). The classes are differentiated by percent shrubland in the adjacency arrangements and by location of the shrubland (east or west of an aspen patch). Later two of the woodlands were excluded based on their isolated location 3 km west of the other 30 patches and their plant dissimilarity evident in the results of initial principal component analyses (PCA's, Hamilton 1992). Thus the data set for the study contains 30 woodland patches (Hersperger 2000).

Vegetation sampling

In July 1998, we compiled a species list of grasses, forbs, shrubs, and trees for each patch (Hersperger 2000). The nomenclature follows Moss (1955). We sampled the smaller patches (<0.505 ha) for 60 minutes and the larger ones (≥ 0.505 ha) for 75 minutes (preliminary sampling by patch size showed that very few species could be found after these time periods). During the first 15 minutes we walked a zigzag route in the interior. The next 15 minutes we walked slowly around the entire edge. For the remaining time (30 min for smaller patches, 45 min for larger patches), we focused on special micro-sites (e.g. open areas, dark areas, moist areas, and old willow trunks). In addition to presence/absence, we also recorded the abundance of each species in each of the 30 patches in six abundance classes: 1 (<5 individuals), 2 ($<1\%$ estimated cover), 3 (1–5% cover), 4 (5–25% cover), 5 (25–50% cover), and 6 ($>50\%$ cover).

In order to classify the habitat affinities of plant species in the woodland understory, we sampled 13 large, patch-sized plots (approximately 30×40 m or 0.12 ha) in shrubland, and also 13 plots in grassland. For purpose of analysis here, we define "shrubland species" as species more abundant (statistically) in shrubland than in grassland. Similarly, "grassland species" are species more abundant in grassland than in shrubland.

Information on the following functional attributes of all species was compiled: origin (native, introduced), life form (woody, herbaceous), life cycle (annual, perennial), fruit type (fleshy fruit, dry fruit) and presence of vegetative reproduction (yes, no). The data were collected from Moss (1955) and Tannas (1997a, b), as well as various monographs on individual plant groups, and personal communications with William Romme, Harry Archibold, and Werner Wilms.

Environmental variables

The following environmental variables were measured in July and August 1998: slope, elevation, soil pH, soil moisture, soil texture, grazing intensity, and stability of the adjacency arrangement. The slope (%) was measured with a clinometer and then classified into four categories: relatively flat (0–5%), gradual slope (5–10%), moderate slope (10–15%), and steep slope ($>20\%$). Elevation of patches was measured with a GPS instrument with vertical accuracy of 1.0 m (manufacturer specification) (real-time differential Ashtech Reliance SCA #SW00274). Soil texture, moisture, and pH were measured for two stratified randomly located samples per patch (one in each half of the patch). We determined the soil texture with the "Simplified guide to field assessment of soil texture for mineral soils" (Landon 1988). The patches were classified according to a progressive decrease in clay content: 1 (clay): both samples clay; 2 (clay/clay loam): one sample clay, one sample clay loam; 3 (clay loam): both samples clay loam or one sample clay loam and one sample silty clay loam; 4 (clay loam/loam): one sample clay loam and one sample loam (see soil textural triangle in the "Soil survey manual", Soil Survey Division 1993). We measured soil pH and moisture in the field at approx. 5–15 cm below the organic layer with the Kelway Soil Acidity and Moisture Tester, Model HB-2 (Kel Iinstruments Co. Inc). All soil moisture measurements were taken August 7–13 to reduce variation.

We assessed the impact of cattle grazing with nine indicators, i.e. presence of: current ($<$a few days) trails, current patties (feces), current trampling, recent ($>$a few days, $<$a few months) trails, recent patties, recent trampling, old ($>$a few months) trails, old patties, and old trampling. The impact level for each indicator was estimated in three classes: none (0), few (1), and many (2). The nine cattle grazing indicators were aggregated into three variables: current cattle grazing (impact level of current trails + current patties + current trampling); recent cattle grazing (impact level of recent trails + recent patties + recent trampling); and old cattle grazing (impact level of old trails + old patties + old trampling). The potential values for the three variables ranged from 0 to 6 [3 (variables) × 2 (maximum value for the impact level)]. Cattle grazing impact values for the 30 woodland patches ranged from zero to four.

We learned from the local rancher that three woodland patches had been grazed by sheep between 1982 and 1992 to improve the rangeland quality, specifically to control aspen regeneration and willow growth. Thus in the analysis old sheep grazing is an ordinal variable ($0 =$ no sheep grazing, $1 =$ sheep grazing occurred).

We used air photos for the years 1952, 1966, 1972, 1982, and 1992 (Alberta Environmental Protection 1952, 1966, 1972, 1982, 1992), and field measurements of 1998 to document the historic development of the adjacency arrangement for each woodland. During the period between 1982 and 1992 ranchers cut the shrubland adjacent to 10 patches. Since then, the shrubland adjacent to one patch grew back. Consequently, nine patches had in the past considerably more shrubland in the adjacency arrangement than they have today. In order to capture a potential effect of this previous adjacency arrangement, "stability" is introduced as an ordinal variable ($0 =$ patch has the same percent adjacent shrubland as before 1987 ± 5 years; $1 =$ patch had considerably higher percent adjacent shrubland before 1987 ± 5 years than today).

Data analysis

In order to examine the basic questions posed, we conduct a species-centered principal component analysis (PCA), followed by multiple least square regression on the factor scores (Jongman et al. 1995). The principal component factors are extracted by applying the "principal component factoring (pcf)" method on species abundance (Hamilton 1992). PCA is an ordination technique that applies a linear model in which the abundance of any species either increases or decreases with the value of each of the latent environmental variables. We use the straight-line model, rather than a unimodal response model such as correspondence analysis (Jongman et al. 1995), because (1) we assume that percent shrubland has a linear effect on number of shrubland and grassland species, and (2) the 30 patches are quite similar in their environmental characteristics, and therefore are expected to cover only a limited range on a bell-shaped response curve for most species. Based on the PCA "scree graph", the first four components in the PCA were retained (Hamilton 1992). They explain 35% of the combined variation.

The site scores resulting from the PCA on abundance data are regressed on the following 12 environmental variables: percent shrubland in the adjacency arrangement; area (log-transformed) of the woodland patch; slope; elevation; soil texture; soil pH; soil moisture; current cattle grazing; recent cattle grazing; old cattle grazing; old sheep grazing; and stability. A stepwise regression with automatic backward elimination (maximum P-value required to retain the variable = 0.05) is performed (Hamilton 1998).

The 141 plant species present in the 30 aspen woodlands are classified into "shrubland species" and "grassland species" with a one-way analysis of variance (ANOVA, Sokal and Rohlf 1995). Abundance data of 13 observations in grassland (patch-sized plots) and 13 observations in shrubland are used. Species are classified as shrubland species if (1) the model is significant at the 5% level, and (2) the mean abundance in shrubland exceeds the mean abundance in grassland. Similarly, species are classified as grassland species if (1) the model is significant at the 5% level, and (2) the mean abundance in grassland exceeds the mean abundance in shrubland. Based on the one-way ANOVA, 27 species are classified as shrubland species and 17 as grassland species (Table 1).

The ecological differences between grassland species and shrubland species are analyzed with functional characteristics (origin, life form, life cycle, fruit type, and vegetative reproduction). The analysis is performed with a Pearson chi-squared test for the independence of rows and columns (Agresti 1996) with significance level = 0.05. Shrubland and grassland species differ mostly in fruit type and growth form. A higher percentage of shrubland species than grassland species has fleshy fruits (a lower percentage has dry fruits, $P = 0.022$). A higher percentage of shrubland species than grassland species is woody (a lower percentage is herbaceous, $P = 0.033$). No significant differences are found in origin (native or introduced) and vegetative reproduction. All shrubland and grassland species are perennials. Interestingly, five of the six shrubs of the shrubland species have fleshy fruits. Consequently, shrub species with fleshy fruits are quite characteristic of shrubland species.

A bivariate ordinary least square regression is performed on increasing percent shrubland in the adjacency arrangement to analyze the change in (1) the number of shrubland and grassland species, and (2) the proportion of selected functional species groups (Hamilton 1992). The data set contains 30 observations (30 woodland patches). The number of shrubland and grassland species is further regressed on the subset of 12 woodlands with adjacent shrubland to the east, and the subset of 12 woodlands with adjacent shrubland to the west. All statistical analyses are performed in Stata 5.0 (Stata Statistical Software 5.0 1997).

Results

Relative importance of adjacency effects

A multiple regression of the site scores on the first PCA-axis (based on species abundance data as described above) on 12 environmental variables yields a significant coefficient only for old sheep grazing and slope (Table 2). These two variables combined explain 66% of the variation in factor one, the first axis in the ordination diagram (Fig. 2). Three patches with very low scores on factor one were the only patches in the study area subject to an intensive sheep-grazing regime in the late 1980s and early 1990s. Today the understory of these patches tends to be more grassland like, with few shrub species and generally low vegetation height. The relatively small differences among non-sheep-grazed woodlands (between -1 and $+1$ on the first axis, Fig. 2) apparently are related to the slope of the aspen woodland.

A multiple regression of the second PCA-axis on 12 environmental variables yields a significant coefficient for percent shrubland in the adjacency arrangement, old cattle grazing, and elevation (Table 2). These three environmental variables combined explain 62% of the variation in factor two. Indeed, vegetation composition in the woodland patches (as described by the site scores in the second PCA-axis) strongly correlates with percent shrubland in the adjacency arrangement ($P = 0.000$, adj. $R^2 = 0.36$ for a bivariate regression of the second PCA-axis on percent shrubland, Fig. 3).

A multiple regression of the third PCA-axis on the 12 environmental variables yields a significant coefficient

Table 1. Plants classified as "shrubland species" and as "grassland species". Species are ordered according to the P-value (ANOVA) used for classification. Frequency is the number of grassland plots or shrubland plots in which a species is present (13 samples). Median abundance is derived from the estimated abundance of a species (1 = lowest, 6 = highest) in each grassland plot or shrubland plot. Sixty-three species present in at least one shrubland plot and 70 species present in at least one grassland plot had p-values ≥0.05 and were therefore not classified as "shrubland species" ("grassland species" respectively).

	P-value	Frequency		Median abundance	
		Grassland plots	Shrubland plots	Grassland plots	Shrubland plots
Shrubland species					
Amelanchier alnifolia	0.000	0	12	0	2
Arenaria laterifolia	0.000	0	9	0	1
Geranium richardsonii	0.000	3	13	0	2
Osmorhiza depauperata	0.000	0	12	0	2
Pyrola asarifolia	0.000	0	13	0	2
Ribes oxyacanthoides	0.000	1	12	0	2
Salix bebbiana	0.000	7	13	1	6
Sanicula marilandica	0.000	2	13	0	3
Symphoricarpos albus	0.000	5	13	0	3
Aster ciliolatus	0.001	7	13	2	3
Castilleja miniata	0.001	2	11	0	2
Delphinium glaucum	0.001	2	10	0	2
Disporum trachycarpum	0.001	0	8	0	1
Viola canadensis	0.001	1	9	0	2
Zizia aptera	0.001	5	12	0	2
Epilobium angustifolium	0.002	11	13	3	4
Heracleum lanatum	0.002	1	9	0	2
Viola adunca	0.002	2	9	0	1
Lonicera dioica	0.005	0	7	0	1
Geum macrophyllum	0.012	1	6	0	0
Lilium philadelphicum	0.013	4	10	0	1
Vaccinium scoparium	0.014	1	7	0	1
Elymus innovatus	0.020	4	9	0	2
Habenaria viridis	0.031	3	8	0	1
Thalictrum venulosum	0.033	11	13	2	2
Actaea rubra	0.036	0	4	0	0
Zigadenus elegans	0.036	9	13	1	2
Grassland species					
Erigeron speciosus	0.000	10	1	2	0
Gaillardia aristata	0.000	10	0	1	0
Sisyrinchium montanum	0.000	10	1	2	0
Agoseris glauca	0.001	12	11	3	2
Galium boreale	0.001	13	13	3	2
Lithospermum ruderale	0.001	10	5	2	0
Lupinus sericeus	0.001	12	10	3	1
Aster laevis	0.005	13	12	3	2
Geranium viscosissimum	0.006	11	7	2	1
Monarda fistulosa	0.008	8	2	2	0
Anemone multifida	0.017	7	2	1	0
Cirsium spp.	0.018	5	0	0	0
Thermopsis rhombifolia	0.018	5	0	0	0
Hedysarum sulphurescens	0.030	4	0	0	0
Potentilla arguta	0.030	7	2	1	0
Taraxacum officinale	0.036	12	13	3	2
Tragopogon dubius	0.042	4	0	0	0

for current grazing, elevation, and area (Table 2). These three variables combined explain 56% of the variation in factor three. A multiple regression of the fourth PCA-axis on the 12 environmental variables yields a significant coefficient for stability of an adjacency arrangement, which explains 13% of the variation in factor four. Four of the 12 variables in the PCA analysis (soil texture, soil moisture, soil pH, and recent grazing) were not significant in any of the ordination axes (Table 2).

In summary, the differences in understory vegetation composition among the 30 aspen woodland patches are primarily related to (1) previous grazing (old sheep grazing, old cattle grazing), (2) topography (slope, elevation), and (3) the adjacency effect.

Changes in species composition and diversity

The woodland patches with high values on the second PCA-axis (generally patches with little shrubland in the

Table 2. Significant regression coefficients of the first four principal-component-analysis (PCA) ordination axes regressed on 12 environmental variables. Maximum P-value required to retain the variable = 0.05. Adjusted-R^2 = explained variance adjusted for the complexity of the model (Hamilton 1992).

Axis	Variable	P-value	Adjusted-R^2
First PCA-axis	Old sheep grazing	0.000	0.66
	Slope	0.001	
Second PCA-axis	Adjacent shrubland	0.000	0.62
	Old cattle grazing	0.001	
	Elevation	0.001	
Third PCA-axis	Current cattle grazing	0.000	0.56
	Elevation	0.001	
	(Log)Area	0.001	
Fourth PCA-axis	Stability	0.027	0.13

adjacency arrangement) are characterized by an abundance of *Urtica dioica*, *Lappula* spp., *Descurainia richardsonii*, *Artemisia ludoviciana*, *Cirsium* spp., *Erigeron speciosus*, *Bromus inermis*, and *Thlapsi arvense* (Table 3). Most of these are weedy species, and *Thlapsi arvense* and *Artemisia ludoviciana* are introduced non-native species. *Cirsium* spp. and *Erigeron speciosus* are classified as grassland species (Table 1).

In contrast, the woodland patches with low values on the second PCA-axis (generally with much shrubland in the adjacency arrangement) are characterized by an abundance of *Zizia aptera*, *Antennaria pulcherrima*, *Hedysarum alpinum*, and *Smilacina stellata* (Table 3). *Zizia aptera* is classified as a shrubland species (Table 1). In the region, all four species generally grow in moist and open woods (*Antennaria pulcherrima*, *Hedysarum alpinum*, *Smilacina stellata*) or moist grassland (*Zizia aptera*) (Tannas 1997b).

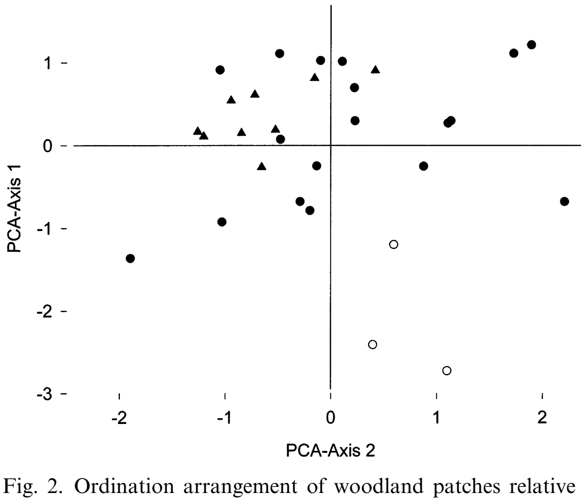

Fig. 2. Ordination arrangement of woodland patches relative to the first two principal-component-analysis axes. Triangles indicate adjacency arrangements in which shrubland cover was reduced in 1987 (± 5 years). Open circles indicate woodland patches that were grazed by sheep around 1990.

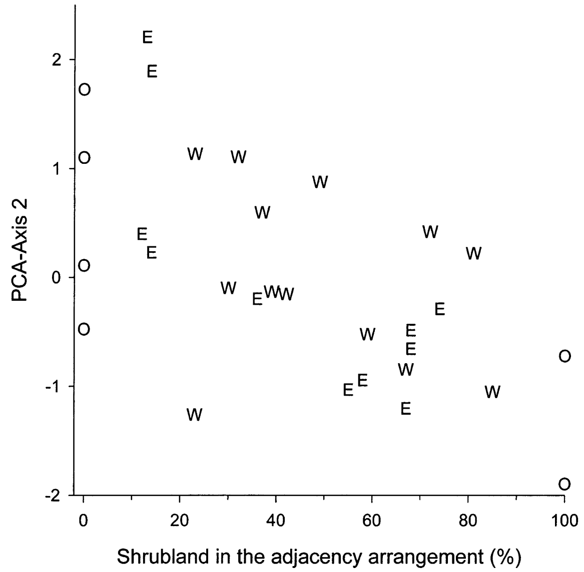

Fig. 3. Vegetation composition in woodland patches relative to amount and location of adjacent shrubland. Values (PCA-site scores) for vegetation composition in woodlands along the second principal-component-analysis axis are plotted against the percent of a patch perimeter shared with adjacent shrubland. E = patches with adjacent shrubland to the east; W = patches with adjacent shrubland to the west. O = patches with either 100% or 0% adjacent shrubland.

The number of shrubland species increases significantly with increasing percent shrubland in the adjacency arrangement (Fig. 4). In contrast, the number of grassland species decreases significantly. An increase from 0% adjacent shrubland to 100% shrubland results in a predicted gain of six shrubland species, whereas the same change in adjacent shrubland results in a predicted loss of four grassland species. The regression analysis predicts 10 grassland species and 16 shrubland species for woodlands surrounded entirely by grassland. In contrast, it predicts only six grassland species plus 22 shrubland species for woodlands surrounded entirely by shrubland.

We found in average 59.1 species per woodland (standard deviation = 6.1). Species richness, as the total number of plant species per woodland, does not change significantly with increasing percent shrubland. Indeed, total species richness is best explained by patch size and soil pH [based on a regression with stepwise backward exclusion, the only significant factors, patch size ($P = 0.000$) and soil pH ($P = 0.005$), explain 49% of the variation in species richness]. Not significant are the variables: percent shrubland in the adjacency arrangement; slope; elevation; soil texture; soil moisture; current cattle grazing; recent cattle grazing; old cattle grazing; old sheep grazing; and stability.

Patches with a large amount of adjoining shrubland have a high proportion of native species (low proportion of introduced species, $P = 0.012$, adj. $R^2 = 0.18$,

Table 3. Characteristic species for woodlands with a low percent adjacent shrubland and for woodlands with high percent adjacent grassland. Species with loadings >0.5 or <-0.5 on the second principal-component-analysis axis after varimax rotation (Hamilton 1998) are listed (loadings indicate the contribution of a species to the position of a patch on a PCA- axis). Species with a high positive loading are abundant in patches with a low percent shrubland in the adjacency arrangement. Species with a high negative loading are abundant in patches with a high percent shrubland in the adjacency arrangement.

	Species	Loading
Patches with a low percent adjacent shrubland	*Urtica dioica*	0.78
	Lappula spp.	0.69
	Descurainia richardsonii	0.68
	Artemisia ludoviciana	0.68
	Cirsium spp.	0.66
	Erigeron speciosus	0.57
	Bromus inermis	0.54
	Thlapsi arvense	0.54
Patches with a high percent adjacent shrubland	*Zizia aptera*	−0.77
	Antennaria pulcherrima	−0.75
	Hedysarum alpinum	−0.52
	Smilacina stellata	−0.51

coeff = ± 0.0006) and a high proportion of perennials (low proportion of annuals, $P=0.000$, adj. $R^2=0.36$, coeff = ± 0.0007). Correspondingly, patches with a large amount of adjoining grassland have a high proportion of introduced species and annuals. No significant relationships are found between the percent shrubland in the adjacency arrangement and herbaceous/woody species, species with fleshy/dry fruits, and species with and without vegetative reproduction.

In short, the regression analysis shows that the number of shrubland species, as well as the percent native species and perennials, in the aspen woodland understory is positively correlated with the percent shrubland in the adjacency arrangement. Analogously, the number of grassland species, the proportion of introduced species, and the proportion of annuals is negatively correlated with the percent shrubland. Therefore, percent of a patch perimeter adjoining a particular land-cover type, such as shrubland, appears to be a simple and promising measure of adjacency effects.

Stability of adjacency arrangement and location of adjacent shrubland

Nine of the 30 aspen woodlands had some adjacent shrubland converted to grassland between 1982 and 1992, creating a new adjacency arrangement that remained during this study (see Methods). Based on the first three PCA-axes, stability of an adjacency arrangement is not significant in explaining vegetation composition in woodland patches (Table 2). On the fourth PCA-axis stability explains only 13% of the variation. These PCA results suggest that the understory of the nine woodlands with the altered adjacency arrangement differs little from the understory of the 21 woodlands without change in the adjacency arrangement. In other words, before the conversion of shrubland into grassland the nine woods probably had more shrubland species and fewer grassland species (Fig. 4), as well as a higher abundance of the shrubland species and lower abundance of the grassland species than at present. Over the 11 ± 5 years since the disturbance, the vegetation in the nine woodlands has apparently adjusted to the new adjacency arrangement.

On the PCA-ordination axes, the mean score of woodlands with shrubland to the east does not differ significantly from that for woodlands with shrubland to the west (t-test on all four ordination axes was never significant at the 5% level). The mix of "E" and "W" in Fig. 3 illustrates this pattern for the second PCA-axis. In addition, out of four relationships between species groups (grassland species/shrubland species) and percent adjacent shrubland (for patches with shrubland to the east/patches with shrubland to the west), only the relationship between the number of shrubland species and percent adjacent shrubland for patches with shrubland to the east is statistically significant at the 5% level. In short, PCA and the analysis of species groups show only minor differences among the patches with shrubland to the east versus shrubland to the west.

Discussion

The analyses suggest that woodland species composition changes along the gradient from no adjacent shrubland to 100% adjacent shrubland, from many weedy, introduced species and common grassland species to more shrubland species and species typically found in moist environments (Table 3). More specifically, weedy species, introduced species, and species of disturbed areas are mostly found in aspen patches with low percent adjacent shrubland and heavy grazing in the past. Species characteristic of moist open woods and moist grassland grow predominately in patches with a high percent shrubland in the adjacency arrangement, low grazing in the past, and higher elevation.

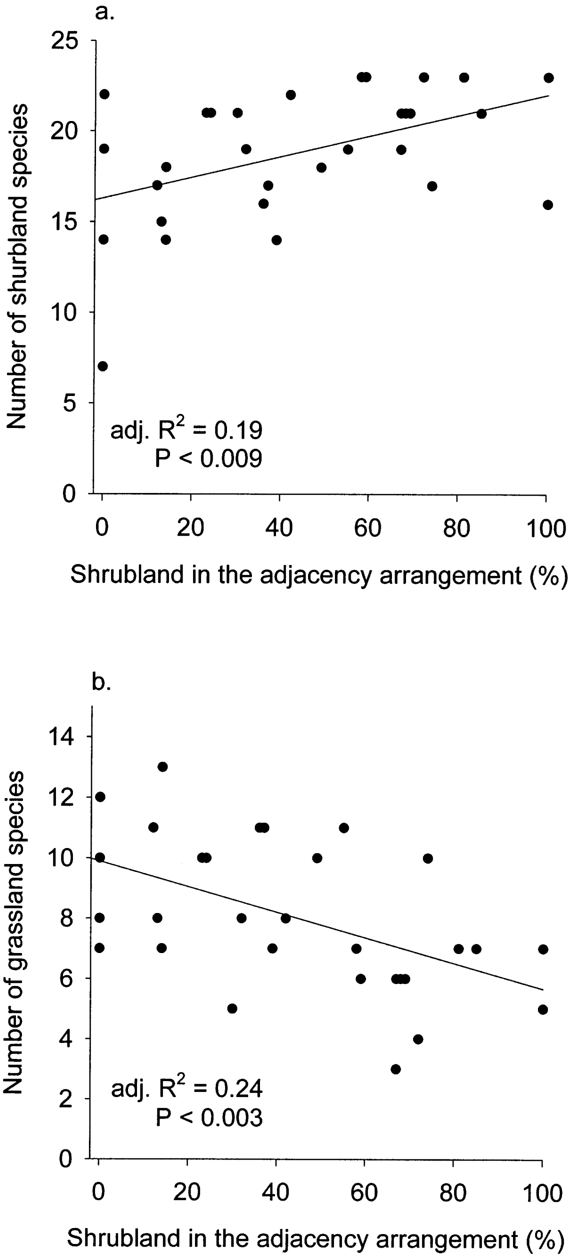

Fig. 4. Plant species richness in woodland patches related to the percent of a patch perimeter shared with adjacent shrubland. Only plants classified as (a) shrubland species and (b) grassland species are included (Table 1).

As expected, topography and disturbance history (grazing here) also affect the species composition in aspen patches. The first three PCA-axes are all partially explained by grazing indicators: old sheep grazing on the first axis, old cattle grazing on the second axis, and current cattle grazing on the third axis (Table 2). Sheep grazing affects the species composition severely (Fig. 2). This is not surprising since sheep grazing has been implemented (and considered effective) as a vegetation management tool (Adams et al. 1992).

Slope and elevation are the most important resource-related factors for explaining understory species composition in the aspen woodlands (Table 2). Aspen woodlands at higher elevation are expected to experience slightly cooler air and soil temperature, a shorter vegetation growth period, and more precipitation. Aspen woodlands on steeper slopes are expected to experience lower solar exposure and more nutrient leaching. Interestingly, neither soil texture, soil pH, nor soil moisture contributes significantly to the explanation of the species composition in the aspen woodlands (Table 2). Soil moisture seems to vary within aspen woodlands as much as among aspen woodlands, though sampling of this variable was limited.

The data show no difference in vegetation composition among patches with shrubland to the east and patches with shrubland to the west. When we initially hypothesized the directionality of adjacency effects, we assumed that (1) wind is the most important directional process in this part of the aspen parkland, and (2) regional westerly winds dominate. During the two summers of fieldwork we observed that easterly and southeasterly winds seemed to be as common as westerly winds. Furthermore, upon entering an aspen patch even from the adjacent grassland, wind tends to die within a short distance. Since these observations seem to contradict our assumptions, we neither reject nor accept the hypothesis that directionality of adjacency arrangements matters, but will leave the question open to further investigation.

The understory of the woodlands with altered adjacency arrangements (patches with currently less adjacent shrubland than in 1987 ± 5 years) differs little from the understory of woodlands with stable adjacencies. This indicates that the understory in the aspen patches has adjusted to the new adjacency arrangement over the past 11 ± 5 years. The colonization by species more typical for the patches with lower percent shrubland in the adjacency arrangement (weedy and introduced species) and changes in abundance of perennials are expected to account for most of the adjustment.

We are convinced that the observed patterns of species distributions within aspen patches are caused by the interplay of many ecological mechanisms. Specifically, we expect that the adjacent grassland and shrubland affect resource distribution, disturbance, and seed dispersal within the aspen patches which in turn affect species distribution (Bazzaz 1996, Hersperger 2000).

Spatial indices have been a challenging but well discussed topic to landscape ecologists (Turner and Gardner 1990, Turner et al. 1991, Klopatek and Gardner 1999). As far as we know, there is no existing index of spatial configuration that addresses adjacency arrangements. Perhaps the ones which measure patch shape are closest to it. These indices are based on patch characteristics such as length of axes, area, perimeter,

perimeter and area, or area and length and they describe aspects of patch shape such as form, elongation, circularity, and compactness (Forman 1995, Gustafson 1998). Even though these indices focus merely on the patch shape, there is a lot of evidence that the shape affects movement and flows between the adjacent landscape elements and the patch (Forman 1995).

Other indices characterize broad landscape patterns based on patch characteristics. Such patch-based measures of landscape patterns include size, number, and density of patches (Forman 1995). These characteristics are sometimes reported as a statistical summary, such as mean, median, variance, and frequency distribution of all the patches (Baskent and Jordan 1995). However, these measures and indices are less useful for understanding adjacency arrangements since they aggregate information of the entire landscape. The same holds true for interspersion and contagion indices that measure the extent to which patch types are interspersed (O'Neill et al. 1988, Gustafson 1998).

Much useful information is gained, though, by reporting the frequency of specific classes of adjacency arrangements within a landscape. This rather simple measure is especially promising in combination with the proposed index for evaluating adjacency effects. Knowing the frequency of the important adjacency arrangements (as defined by the percent common border a patch shares with each of its adjacent elements) and the relevant adjacency effects tells one already a great deal about a landscape. The two measures might work well in combination with indices that examine the spatial relationship among multiple patches in a neighbourhood. Such indices are, for example, isolation, accessibility of a patch, dispersion of patches, and nearest neighbour probabilities (Forman 1995).

Instead of indices of spatial configuration, several investigators have used the habitat composition within a certain radius of the target patch to estimate adjacency effects (Webb et al. 1984, Metzger 1997, Bastin and Thomas 1999, Wolff et al. 2002). Even though habitat composition has proven a successful predictor in several studies, the choice of the radius remains somehow arbitrary. Furthermore, few studies report precisely how the radius was chosen.

This study tested the proposed adjacency arrangement index on roundish patches with smooth (not convoluted) borders. Since we sometimes find other shapes and borders, two issues need further discussion: Is the index appropriate also for elongated patches and is it appropriate for patches with convoluted borders? We expect that the actual location of the adjacent elements is much more important for an elongated patch than for a round one. For example, in an adjacency arrangement with 10% of adjacent element (A) and 90% of adjacent element (B) it might matter if the 10% of element (A) are located on the far end or near the centre of the elongated patch. We hypothesise that the adjacency effect is larger if the element (A) is located on the far end than if it is located near the center. The rather narrow end of the elongated patch is certainly more exposed to ecological effects exerted by the adjacent elements. Indeed, in extreme cases the narrow end might be considered a peninsula and experience peninsula effects (Forman 1995).

A convoluted patch border most likely is no issue if the entire border is evenly convoluted. However, if convolution is associated with only one adjacent element (e.g. the border to the adjacent element (A) is always convoluted, the border to the adjacent element (B) is never convoluted) one would expect that the length of the convoluted border is not an accurate measure for adjacency effects. In that case the index needs to be adjusted for the additional length of border due to convolution.

Whereas this study indicates that adjacency effects are an important factor for understanding the ecology of landscapes, there is a growing effort of incorporating spatial relationships into land-use planning (Hersperger 1994, Forman and Collinge 1995, Forman and Hersperger 1996, Klopatek and Gardner 1999, Forman 2000). The need for considering landscape configuration has been clearly recognized in bird conservation (Freemark and Collins 1989, Freemark et al. 1995) and road ecology (Forman and Hersperger 1996, Forman and Alexander 1998). Landscape ecology provides an understanding of the interactions between organisms and the environment at the scale of landscapes, which is at the scale of effective planning interventions. More experimental studies on the effects of explicit spatial arrangements on biological diversity and ecosystem processes could greatly enhance the planning, sustainable use, and management of our landscapes.

Conclusion

Adjacency arrangement emerges as a leading explanatory variable for the understory vegetation in woodlands, among an array of resource related, disturbance related, and spatial variables. Indeed, plant composition changes gradually along the gradient of increasing shrubland in the adjacency arrangement. We suggest that spatial relationships, and specifically adjacency effects, should become an integral part of vegetation models, together with factors of resource availability and disturbance.

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