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Fidelity and diagnostic species concepts in vegetation classification in the Rocky Mountains, northern Utah, USA

Antonín Kusbach, James N. Long, Helga Van Miegroet, and Leila M. Shultz

Abstract: The concepts of diagnostic species and fidelity have been used frequently in European phytosociology but rarely in North American vegetation classification. We developed a classification of the vegetation of a mountainous area of northern Utah and compared the diagnostic species approach with the indicator-species approach of habitat type classification *sensu* Daubenmire prevailing in the U.S. Interior West. A total of 157 forest and nonforested plots were described by vascular plants and basic environmental factors. Clustering with RandomForest classification and ordination reduced the original number of plots to 26 meaningful vegetation units. Of these 26 units, 22 were strong, having four or more faithful species. Four units were weak, having less than three faithful species. We identified species diagnostic of particular vegetation units that are potentially useful for recognition of these units in the field. We proposed vegetation types at the level of vegetation alliances and associations, and correlated them with environmental factors. We found our vegetation units to be more strongly associated with the underlying environment than major habitat types *sensu* Daubenmire. Our approach to classification has the potential to directly link vegetation with the physical environment and could be the basis for a substantial improvement of vegetation classification in the central Rocky Mountains.

Key words: vegetation alliance, vegetation association, faithful species, character species, differential species, diagnostic species, indicator species.

Résumé : On utilise fréquemment le concept des espèces diagnostiques et de fidélité chez les phytosociologues européens, mais rarement dans la classification nord-américaine de la végétation. Les auteurs ont développé une classification de la végétation d'une région montagneuse du nord de l'Utah, et ont comparé l'approche d'espèces diagnostiques avec celle des espèces indicatrices de la classification des types d'habitats *sensu* Daubenmire, prévalant dans la région intérieure occidentale aux États-Unis. Ils ont décrit 157 parcelles forestières et non forestières selon les plantes vasculaires et les facteurs environnementaux de base. Le regroupement avec la classification forestière aléatoire et l'ordination réduit le nombre original des parcelles à 26 unités de végétation significatives. De ces 26 unités, 22 sont robustes ayant quatre ou plus espèces fiables. Quatre unités s'avèrent faibles avec moins de trois espèces fiables. Ils ont ainsi identifié des espèces diagnostiques d'unités de végétation particulières comme potentiellement utiles pour reconnaître ces unités sur le terrain. Ils proposent des types de végétation à l'échelle d'alliances et d'associations végétales, les mettant en corrélation avec les facteurs environnementaux. Les auteurs ont constaté que leurs unités de végétation montrent une association plus robuste avec l'environnement sous-jacent que les types majeurs d'habitats *sensu* Daubenmire. Ils considèrent que leur approche pour la classification a le potentiel le relier directement la végétation avec l'environnement physique et pourrait servir de base pour une amélioration substantielle de la classification de la végétation du centre des montagnes Rocheuses.

Mots-clés : alliance végétale, association végétale, espèces fiables, espèces caractéristiques, espèces différentielles, espèces diagnostiques, espèces indicatrices.

[Traduit par la Rédaction]

Introduction

"Without classification there can be no science of vegetation" - R.F. Daubenmire

As a distinctive landscape feature, vegetation has been a fundamental component of land classifications (Daubenmire 1989). Recently, vegetation classification has been emphasized as a communication tool in ecological research and in the application of ecological information in planning, monitoring, conservation, and management (Jennings et al. 2009).

In the U.S. Interior West, early land classifications such as the concept of potential natural vegetation (Küchler 1969) and habitat type (HT) (Daubenmire 1952) were based on species composition occurring in potential climax communities. In the habitat and community type (CT) classification (Pfister and Arno 1980), HTs were based on total species composition, combining frequent (constant) and dominant species, which were considered HT indicators (indicator species *sensu* Daubenmire). For example, criteria of 5% of canopy cover for well represented species and 1% of canopy cover for

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scarce species were used in classification keys of conifer HTs for each indicator species and at least 25% constancy and 5% of canopy cover in classification of aspen plant communities (e.g., Pfister and Arno 1980; Mueggler 1988). This abundance/dominance-based approach stresses focal species in target vegetation units based on certain cover and constancy thresholds, regardless of their presence in other vegetation units and thus regardless of a species' real "discriminating" value. The indicator species-based HT classification, while quantitative, was intuitive, not really statistical, and did not reveal within- and out-of-unit species relationships (Barkman 1989; Chytrý et al. 2002a; Willner et al. 2009).

A statistical approach, associated with the concepts of fidelity and diagnostic species (Whittaker 1962; Westhoff and van der Maarel 1973; Jennings et al. 2008, 2009), is a promising alternative. Fidelity is a measure of species concentration in vegetation units (Chytrý et al. 2002a). Its statistical form is based on species' frequencies observed within a vegetation unit compared with expected frequencies if the species' distributions were random, i.e., also taking out-of-unit species (within a total data set) occurrence into consideration (Barkman 1989; Chytrý et al. 2002a; Willner et al. 2009). Fidelity accounts for the relationship between the number of vegetation samples (relevés) containing focal species in a vegetation unit and the number of such relevés in the total data set. It is better done by using correlation measures and statistical tests rather than by just comparing constancy values. A traditional constancy measure of species frequency in vegetation units does not evaluate frequency in the context of regional vegetation, i.e., outside a target vegetation unit. A fidelity approach is more appropriate for identification of vegetation units and classification schemes than traditional measures because no frequency thresholds for focal species are defined for fidelity measures (e.g., Chytrý et al. 2002a; Willner et al. 2009).

The use of fidelity relative to focal species, especially when associated with environmental factors or disturbances, may enhance power to identify habitats. Consequently, these diagnostic species may signify habitats better than indicator species *sensu* Daubenmire. Some applications of the diagnostic species concept are stricter (e.g., European), constrained to character species (i.e., species restricted to a single vegetation unit for which they are characteristic), and differential species (i.e., species occurring in a few vegetation units that they can discriminate as a group) (Mueller-Dombois and Ellenberg 1974; Chytrý et al. 2002a). Alternatively, some approaches apply a looser interpretation, including constant (i.e., the most frequent) and dominant species (species with high cover) to the set of faithful (character and differential) species giving the "characteristic species combination" of the vegetation type (Westhoff and van der Maarel 1973; Brohman and Bryant 2005; Winthers et al. 2005; FGDC 2008; Jennings et al. 2008, 2009).

A combined fidelity and diagnostic species approach may increase the general validity of vegetation types in large phytosociological databases representing broad taxonomic units such as orders or classes, and also in smaller data sets representing geographically small but ecologically diverse areas (Chytrý et al. 2002a; De Cáceres and Legendre 2009; De Cáceres et al. 2010).

There are two steps in determination of vegetation types,

although there is no standard for this determination (De Cáceres and Wiser 2011): (1) to distinguish meaningful (i.e., interpretable) groups of species within the original data set, thereby apportioning and aggregating a large number of relevés into a smaller number of meaningful vegetation units; and (2) to identify diagnostic species within these vegetation units. While the concepts of diagnostic species, fidelity, and faithful species have frequently been used in European phytosociology to characterize vegetation types, such classification is scarcely practiced in North America. The recently proposed U.S. National Vegetation Classification (Jennings et al. 2008, 2009) is close to the European approach but has not yet been applied to the central Rocky Mountains.

Our objectives were to (*i*) develop a quantitative classification of vegetation in the Rocky Mountains of northern Utah; and (*ii*) examine the descriptive power of species diagnostic of particular vegetation units and their usefulness for recognition of these units. We compared our approach with the traditional and extensively applied HT and CT type classifications in the Intermountain West (e.g., Mauk and Henderson 1984; Mueggler 1988). By using an alternative approach to the HT classification, we hoped to gain a better understanding of vegetation patterns, particularly the distribution of species assemblages in the study area.

Materials and methods

Study area

The study area covered ~16 000 ha and consisted of two parts: (1) Franklin Basin, a montane–subalpine area, approximately 15 000 ha in size, situated between the Bear River Range and the Wasatch Range in the central Rocky Mountains on the Utah and Idaho border; and (2) the T.W. Daniel Experimental Forest (TWDEF), approximately 1000 ha in size, situated on the high ridge-plateau of the Wasatch Range (10 km to the southeast of the Franklin Basin) (Fig. 1).

The terrain is mountainous, rocky, and steep with occasional flat to gently sloping high ridge-plateaus. Elevation ranges from 2050 to 3060 m across the two study sites. The highest area of the Bear River Range was glaciated during the Pleistocene as manifested by features like moraines, U-shaped valleys, erratics, and irregular glacial deposits (Young 1939; Degraff 1976). The study area is mostly built from calcareous sedimentary rocks (limestone, dolomite) with interlayered quartzite, and from Tertiary sediments (grit, conglomerate, and siltstone of Wasatch Formation) at the TWDEF site. The soils are formed in residuum, colluvium, alluvium, glacial till, and outwash, and occur on diverse landforms such as cliffs, moraines, karst valleys, slopes, landslides, plains, valleys, depressions, ravines, and wetlands (Schoeneberger et al. 2002).

Over half of the study area is occupied by forest ecosystems including Engelmann spruce (*Picea engelmannii*, PIEN), subalpine fir (*Abies lasiocarpa*, ABLA), Douglas-fir (*Pseudotsuga menziesii*, PSME), aspen (*Populus tremuloides*, POTR), and woodland ecosystems including mountain mahogany (*Cercocarpus ledifolius*, CELE) and Rocky Mountain juniper (*Juniperus scopulorum*, JUSC). Substantial changes in fire regimes, often in combination with timber harvest and grazing, have led to dramatic changes in the structure and the age–class distribution of forest stands. In many places, 100-

Fig. 1. The study area on the border between Utah–Idaho, USA, with subareas; digits represent numbers of sample plots.
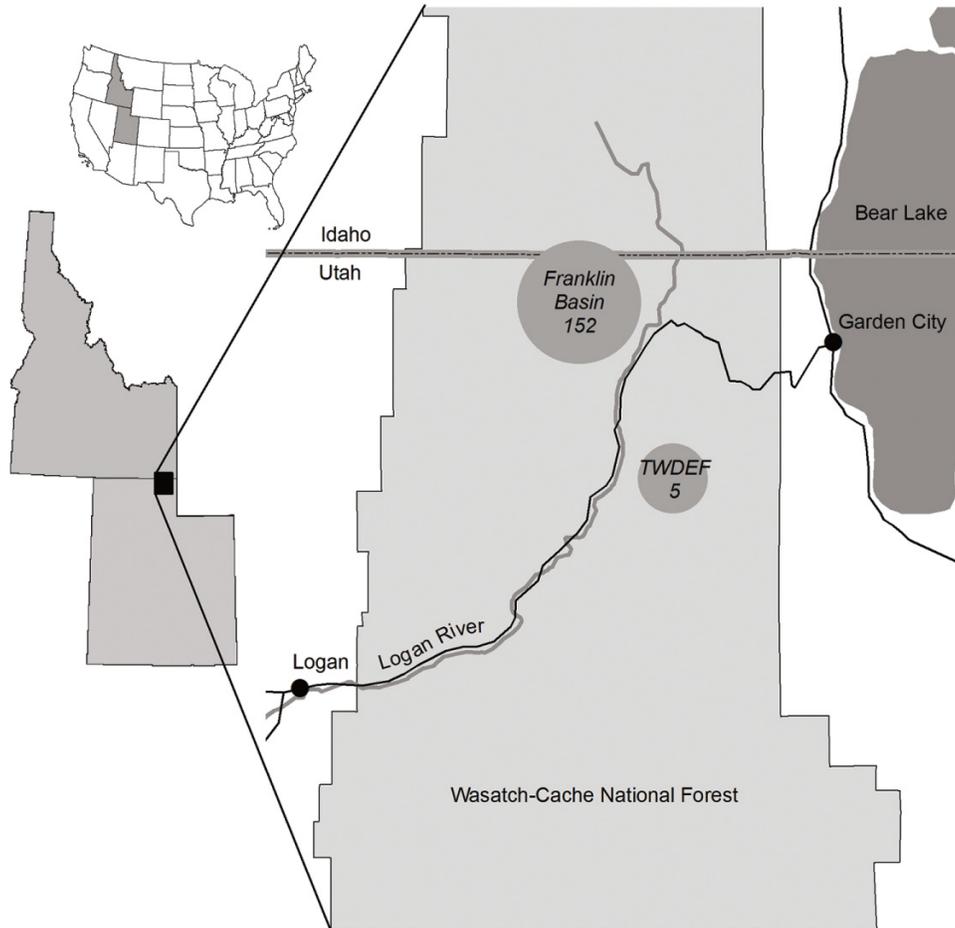
to 160-year-old stands are now predominant (Long 1994). Forests in the study area are thus characterized by mid- and late-seral stages where forest understory is usually well developed (Pfister and Arno 1980). Nonforested ecosystems include riparian strips and wetlands (*Salix* spp.), low shrublands (*Artemisia* spp.), tall-forb meadows, and sparse vegetation on talus and rock outcrops, which may represent either stable or seral communities.

Data collection

We collected vegetation samples (relevés) in 157 plots across the study area in the summers (late May–August) of 2006 and 2007. Sampling followed the *Existing Vegetation Classification and Mapping Technical Guide* (Brohman and Bryant 2005) and *Terrestrial Ecological Unit Inventory Technical Guide* (Winthers et al. 2005).

After field reconnaissance, we sampled vegetation across a broad range of the physical environment to capture as much environmental variation as possible. In an effort to minimize the major influence of historical factors such as fires and logging, and stress the impact of the physical environment on vegetation, we focused on mature, late-successional, and relatively stable plant communities. In the case of forest vegetation, this condition was characterized by advance regeneration of potential climax tree species (Pfister and Arno 1980; Pojar et al. 1987). We sampled stands reasonably uniform in physiognomy, floristic composition, and environ-

ment (Jennings et al. 2009). We tried to avoid ecotones, i.e., habitats in transition, where important environmental factors merge; as well as degraded or atypical stands. A stratified (based on vegetation physiognomy) preferential (subjective selection) sampling design was used with sample plot size of 1000 m² for forest and 100 m² for nonforested ecosystems and three replicates were considered the minimum for sampling a preliminary vegetation unit (Podani 2000; Brohman and Bryant 2005; Jennings et al. 2009). The plots were usually circular, but the shape was adjusted according to the character of habitat, e.g., linear for riparian vegetation. In each sample plot, we tallied all vascular plant species and their abundances (canopy cover percentage for forest trees and ground cover percentage for forest and nonforested shrubs and understory). Nomenclature followed the United States Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) (USDA NRCS 2011), Shultz et al. (2010) and Shultz (2009) delimitation for Utah.

To characterize important environmental factors we described each sample plot in terms of relatively static physiographic attributes, i.e., elevation, slope aspect, slope gradient, topographic position, and slope shape (Lotspeich 1980); slowly changing soil attributes, i.e., O and A horizon thickness, humus form (Green et al. 1993), pH, nutrient pools; and attributes such as nutrient supply rates describing relatively fast processes (Table 1). One soil pit was dug in each sample plot to the unweathered parent material or permanent

Table 1. List of parameters determined for each sampling plot.

Factor	Abbreviation	Units/values
Elevation	elev	m
Topographic position	topos	1, crest, shoulder; 2, back slope; 3, foot slope; 4, flat (<5%); 5, toeslope; 6, depression
Slope gradient	sl	%
Slope aspect	av	aspect values 0–1 (Roberts and Cooper 1989)
Parent material	parmat	1, quartzite; 2, Wasatch formation; 3, till; 4, limestone or dolomite; 5, colluvium; 6, alluvium
Soil O horizon depth	Ohor	cm
Soil A horizon depth	Ahor	cm
Humus form	hum	values 1–17; e.g., 1, fibrimor; 10, mormoder; 14, rhizomull; 17, no humus (Green et al. 1993)
Soil depth	sdepth	cm
Coarse rock fragment content	RF	% volumetric
Soil water table	wtable	1, up to 30 cm depth; 2, 30–80 cm; 3, 80–150 cm; 4, no water table
Soil mottles	mottles	1, up to 30 cm depth; 2, 30–80 cm; 3, 80–150 cm; 4, no mottles
Soil color value	cvalue	1–7 according to Munsell notation
Soil pH	pH	1–14 pH scale
Calcium carbonate content	$CaCO_3$	%
Total nitrogen	Nox	%
Total carbon	Cox	%
Carbon nitrogen ratio	C.N	NA
Mineralizable nitrogen DNAI	Nmin_d	$\mu g \cdot 10\ cm^{-2} \cdot 6\ weeks^{-1}$
Ammonium DNAI	NH4_d	$\mu g \cdot 10\ cm^{-2} \cdot 6\ weeks^{-1}$
Calcium DNAI	Ca_d	$\mu g \cdot 10\ cm^{-2} \cdot 6\ weeks^{-1}$
Magnesium DNAI	Mg_d	$\mu g \cdot 10\ cm^{-2} \cdot 6\ weeks^{-1}$
Potassium DNAI	K_d	$\mu g \cdot 10\ cm^{-2} \cdot 6\ weeks^{-1}$
Phosphorus DNAI	P_d	$\mu g \cdot 10\ cm^{-2} \cdot 6\ weeks^{-1}$
Iron DNAI	Fe_d	$\mu g \cdot 10\ cm^{-2} \cdot 6\ weeks^{-1}$
Manganese DNAI	Mn_d	$\mu g \cdot 10\ cm^{-2} \cdot 6\ weeks^{-1}$
Mineralizable nitrogen SNAI	Nmin_s	mg/kg
Ammonium SNAI	NH4_s	mg/kg
Calcium SNAI	Ca_s	mg/kg
Magnesium SNAI	Mg_s	mg/kg
Potassium SNAI	K_s	mg/kg
Phosphorus SNAI	P_s	mg/kg
Iron SNAI	Fe_s	mg/kg
Manganese SNAI	Mn_s	mg/kg

Note: Dynamic nutrient availability index (DNAI) is indicated by "*d*" and static nutrient availability index (SNAI) is indicated by "*s*" in abbreviations. NA, not applicable.

water table, and described following practices and terminology of the *National Cooperative Soil Survey* (Soil Survey Staff 1999, 2006; Schoeneberger et al. 2002).

One composite soil sample (0–30 cm) was collected from a pedon face in each plot, air dried, and sieved (<2 mm), and the fine fraction was analyzed for texture using the feel-method (Thien 1979). pH (1:1 soil in water) was determined using a Corning pH analyzer. $CaCO_3$ content (Loeppert and Suarez 1996) and total C and N concentrations were determined using LECO CN analyzer (LECO Corp., St. Joseph, Mich., USA). A static-absolute nutrient availability index (SNAI), i.e., cation pool "snapshot", was determined by soil extraction with 1 mol/L HN_4Cl at pH 7.0 using a mechanical vacuum extractor (Holmgren et al. 1977) and cation analysis of the extractant was determined using an inductively coupled plasma spectrophotometer (ICP) (Iris Advantage, Thermo Electron, Madison, Wis., USA). Extractable P (PO_4) was determined by the Olsen P method (Olsen et al. 1954) using a spectrophotometer (Spectronic 20 Genesys, Thermo Electron, Madison, Wis., USA). Total mineralizable nitrogen was deter-

mined using 7-day anaerobic incubation and extraction with 2 mol/L KCl (Keeney and Bremmer 1966) followed by NH_4 analysis (Lachat Quickchem 8000, Loveland, Colo., USA).

To determine a dynamic-relative nutrient availability index (DNAI) (Qian and Schoenau 2002), plant root simulators (PRS-probes; Western Ag Innovations, Inc., Saskatoon, Sask., Canada), consisting of anion and cation exchange membranes, were buried vertically in the mineral soil at each site for 6 weeks (during September and November) and then sent to Western Ag Innovations for chemical analysis of major cations and anions (Table 1).

Data analysis

Vegetation analysis followed the *Existing Vegetation Classification and Mapping Technical Guide* (Brohman and Bryant 2005), the *National Vegetation Classification Standard* (FGDC 2008), and *Standards for Associations and Alliances of the U.S. National Vegetation Classification* (Jennings et al. 2009). We ran an analysis of the 157 relevés representing 324 species (supplementary material, Table S1[1]).

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[1]Supplementary data are available with the article through the journal Web site (http://nrcresearchpress.com/doi/suppl/10.1139/b2012-033).

There were four steps in the vegetation analysis: (1) partitioning of the data set into meaningful vegetation units (classes); (2) association of the vegetation units with the physical environment; (3) characterization of the vegetation units based on diagnostic, i.e., faithful, constant, and dominant species (a looser interpretation); and (4) comparison of major HTs and CTs in the study area with the vegetation units. In the first step, we used agglomerative and divisive methods of partitioning. The agglomerative approach involved Ward's hierarchical clustering combined with Euclidean and Sørensen distance, and Flexible beta linkage method with Sørensen distance (Bray and Curtis 1957; Ward 1963). We used the Ward/Euclidean and Flexible beta/Sørensen combination to maximize defensibility (distance measures are compatible with the clustering methods, e.g., McCune et al. 2002) despite the criticism of Euclidean distance in analysis of community data (e.g., Legendre and Legendre 1998). Percentage cover was standardized by both the logarithmic and square root transformations to equalize common and rare species. The divisive approach was represented by modified TWINSPAN, which prevents unsubstantiated division of homogeneous clusters (Roleček et al. 2009). For raw data, we applied three measures of within-cluster heterogeneity: Whittaker's beta (Whittaker 1960); total inertia (Greenacre 2000), and chord distance (Orlóci 1967), and we used three cut-levels for pseudospecies (0, 5, 25). We removed rare species (just one occurrence in the entire data set) before partitioning the data set.

Using both the agglomerative and divisive approaches, nine alternative partitioning methods were assessed by OptimClass. This method evaluates data set partitioning based on the greatest number of faithful species (OptimClass I; Tichý et al. 2010). In OptimClass, for each partitioning method, the total number of faithful species was calculated by Fisher's exact test as a measure of species-to-unit fidelity for presence–absence data (Chytrý et al. 2002a). The best partitioning solution was chosen as a compromise between statistical assessment represented by Fisher's exact test, represented by the total number of faithful species, and ecological feasibility represented by meaningful, i.e., interpretable, vegetation units (Chytrý et al. 2002a).

The more relevés in a vegetation unit the better that unit may be characterized. For our data set, we expected greater descriptive power of diagnostic species inside larger vegetation units than in small units (less than three relevés), where there was a greater probability of faithful species presence solely by chance. Therefore, when appropriate, we opted for larger vegetation units. We removed "small-member clusters", i.e., vegetation units represented just by one and two relevés within the best partitioning solution, because small units created at high hierarchical levels are considered outliers (McCune et al. 2002; Jennings et al. 2009; Tichý et al. 2010).

In the second step, we attempted to characterize the vegetation units by environmental factors.

We used RandomForest classification (RF) (Breiman 2001) of the physical environment represented by external explanatory factors and unconstrained-free nonmetric multidimensional scaling (NMS) of species data sets suggested by RF. External environmental factors were chosen in the RF variable importance analysis as the most influential of 34 environmental factors (Table 1), affecting plant species distribution and particularly species composition of the vegetation units in the study area (Kusbach 2010a). Prior to the NMS ordination, we deleted rare species with just one occurrence. We checked the data sets' properties (Whittaker's beta diversity, common vs. rare species numbers), and then we standardized species (columns in the data set matrix) by the binary relativization with respect to median to equalize, to some extent, common and rare species and emphasize optimal parts of a species range (McCune et al. 2002). A relationship between common and rare species was checked by dominance curves (Peck 2010). Relative Sørensen distance was used in the ordination to (i) emphasize proportion of species in relevés rather than abundances and again, favor rare species with potential indicative values over common ones; and (ii) avoid the double-zero problem (Legendre and Legendre 1998). We dropped moderate and strong outliers (species and sample plots with standard deviation >2.3 McCune et al. 2002). Environmental factors with | skewness | >1 were transformed to be close to multivariate normality, and the data set was checked for outliers using a cutoff of 2.0 standard deviations from the grand mean (McCune et al. 2002; Peck 2010). A Monte Carlo randomization test with 250 permutations was performed to test the significance of the NMS ordination (McCune and Mefford 2011). Relevés without environmental data were removed from the RF and ordination.

We visualized the vegetation units and their relationship with important external factors in the NMS ordination space. The relative position of the units was assessed by Euclidean and Sørensen distance between unit centroids calculated from ordination scores in a type-to-type similarity matrix. Then, close vegetation units were combined.

In the third step, we used fidelity calculations to determine faithful species with the expectation that this method should help evaluate the validity of vegetation types. We used phi coefficient of association (Sokal and Rohlf 1995) because (i) it is independent of the size (the number of relevés) of the data set and little affected by the size of the vegetation unit (Chytrý et al. 2002a); and (ii) as a correlation-based measure, it is advantageous for determining the ecological preference of a given species among a set of alternative vegetation units (De Cáceres and Legendre 2009).

The phi coefficient value ranges from –1 to +1 (–100% to +100% for the phi times 100) with a positive value indicating the species-unit co-occurrence is more often than expected by chance only. We calculated the phi coefficient with presence–absence data after standardization of the units' size (to minimize possible effects of unequal-sized units) and adjustment of weight tending to equalize common and rare species (Tichý and Chytrý 2006; Willner et al. 2009). We tested the statistical significance of the positive phi coefficient by Fisher's exact test with $p < 0.05$ (Chytrý et al. 2002a).

There is no fixed threshold for the phi coefficient of faithful species. We set a data set-specific threshold of phi $\geq 35\%$ (Willner et al. 2009) to distinguish faithful species from the rest of species with significant yet low phi values. A higher threshold would be too restrictive, producing vegetation units with less than three faithful species. Conversely, a lower threshold would produce large units with unnecessarily high numbers of faithful species with limited diagnostic power in this geographically small data set. Diagnostic species were

categorized based on the following thresholds: faithful species, phi ≥ 35%; constant species, constancy (frequency) ≥ 60% (Mueller-Dombois and Ellenberg 1974); and dominant species, cover ≥ 5%. This relatively low cover value was chosen so as to include open-canopy woodland and high elevation open-canopy conifer forests. Character species were all faithful species occurring in only a single vegetation unit, to which they are highly faithful.

The relationship among vegetation units and validity of each unit was based on number of faithful species and the mean positive fidelity calculated as a simple mean of significant non-negative fidelity values. We also calculated species richness as the number of species within a vegetation unit and an indicator of local (alpha) species diversity (e.g., Whittaker 1972; McCune et al. 2002; Colwell et al. 2004). This diversity measure should be considered with caution because it is influenced by the number of relevés (Gotelli and Colwell 2001; Colwell et al. 2004). We considered strong, i.e., well-characterized, units as those with four or more faithful species or mean positive fidelity of 40% or more. Weak, i.e., poorly characterized, units were those with few or no faithful species and mean positive fidelity <40%, (Chytrý et al. 2002a).

We proposed vegetation types as species assemblages at the floristic level of vegetation alliances and associations (Grossman et al. 1998; FGDC 2008; Jennings et al. 2008, 2009). Alliances emerged from compilations of species: (i) whose "fidelity niche" spans more than one unit, i.e., which are differential (within the same hierarchical level, e.g., De Cáceres et al. 2010); and (ii) such as constant trees and shrubs (FGDC 2008; Jennings et al. 2009). Associations were suggested by arrays of character species. In the case of weak (poorly characterized) vegetation units, the most constant and dominant species were considered as diagnostic, faithful species were by definition lacking. We did not consider annuals and invasive species in the characterization of vegetation types.

In the fourth step, we compared our vegetation units with major HTs and CTs in the study area. These HTs were keyed out from current HT and CT classifications (Mauk and Henderson 1984; Mueggler 1988) and visualized in the same NMS ordination space.

JUICE software version 7.0.65. (Tichý 2002) and PC-ORD 6 (McCune and Mefford 2011) were used in the partitioning analysis. Diagnostic species within vegetation units were analyzed using JUICE. PC-ORD 6 was used for NMS ordination and R software version 2.7.2. (http://www.r-project.org/) was used for RF analysis.

Results

Partitioning the data set

After deleting outliers, 150 relevés and 268 species were left in the analysis. Using OptimClass, we chose the partitioning based on Ward/Euclidean/square root transformation from the nine alternative solutions because it retained (i) a high total number of faithful species (395) and (ii) 32 ecologically easy interpretable units. In contrast, the Ward/Sørensen experimental solution provided the highest number of faithful species (403) but also detailed clustering representing 48 smaller vegetation units that were difficult to interpret

(Fig. 2). The flexible beta and modified TWINSPAN solutions did not produce as many faithful species as Ward/Euclidean clustering (e.g., Brown 2006). More general solutions resulted in lower numbers of faithful species and larger units, which were difficult to interpret.

We were aware (i) that the 32-vegetation unit solution, even though readily interpretable, may be problematic, because it could produce constancy and fidelity values with low reliability for small vegetation units; (ii) the high total number of faithful species can overfit the analysis; and (iii) use of Euclidean distance is generally not recommended for community data analyses.

Environmental associations

RandomForests (RF) classification identified those environmental factors most strongly associated with the vegetation units. In the case of the entire data set including all vegetation units, i.e., forest and nonforested communities, "out-of-bag" estimate of error as a measure of misclassification was 40%. The confusion matrix of the RF indicated the highest misclassification between some forest and nonforested communities, and conifers and aspen communities. This suggested that those communities were close in measured environmental factors and were distinguished by other than these factors, e.g., disturbance or microclimate. For example, there was considerable similarity in environmental factors between physiognomically different vegetation units such as conifers and aspen suggesting potential successional stages of aspen units. Therefore, we split the data set into conifer (including juniper and mahogany woodland), aspen, and nonforested units and performed RF and NMS ordination independently to identify the most important environmental factors for each subset.

Although the results of RF analysis varied from run to run, the ranking of variable importance (mean decrease accuracy) was quite stable for solutions with four variables randomly used at each split (mtry function in R) and number of trees 500–5000 used to grow a "forest" in the machine-learning process (ntree function in R) (Liaw and Wiener 2002). For the conifer data set, out-of-bag estimate of error was 23% for these important factors (mean decrease accuracy in parentheses): elevation (2.21), mottles (1.94), parent material (1.92), magnesium concentration (SNAI) (1.83), C/N ratio (1.79), coarse rock fragment content (1.77), and total nitrogen (1.73). For the nonforested units, the misclassification was 26% for calcium (2.1) and potassium (1.85) concentrations, coarse rock fragment content (1.98), elevation (1.92), parent material (1.91), water table (1.85), calcium carbonates (1.85), and soil depth (1.84). For the aspen data set, the misclassification was 44% for: C/N ratio (1.98), elevation (1.98), soil depth (1.86), pH (1.68), ammonium supply rate (DNAI) (1.32), soil color (1.04), magnesium (1.04), and potassium (0.94) concentration. The confusion matrix of the RF indicated the highest rate of misclassification between aspen units 31, 32 and 29, 31. This misclassification suggested environmental similarity between these units and factors other than environmental, e.g., plant interactions (competition or mutualism) responsible for the split of these aspen units.

The conifer data set represented by 66 relevés and 252 species was as diverse as the nonforested data set (51 relevés and 248 species) assessed by beta diversity (7.2 and 8.6, re-

Fig. 2. Results of the OptimClass method, Fisher's exact test with $p < 0.05$. Each of nine curves represents one solution based on partitioning method, distance measure and species cover transformation for number of clusters/vegetation units from 2 to 100 (on the horizontal axis). The vertical axis represents the total number of faithful species in all clusters for the given partitioning. Both bold and dotted curves are two best solutions in terms of the highest number of faithful species. The dotted curve represents statistically the best (403 faithful species in 48 clusters) but worse interpretable solution. The bold curve represents a feasible solution with the highest number of faithful species (395) in 32 interpretable clusters.
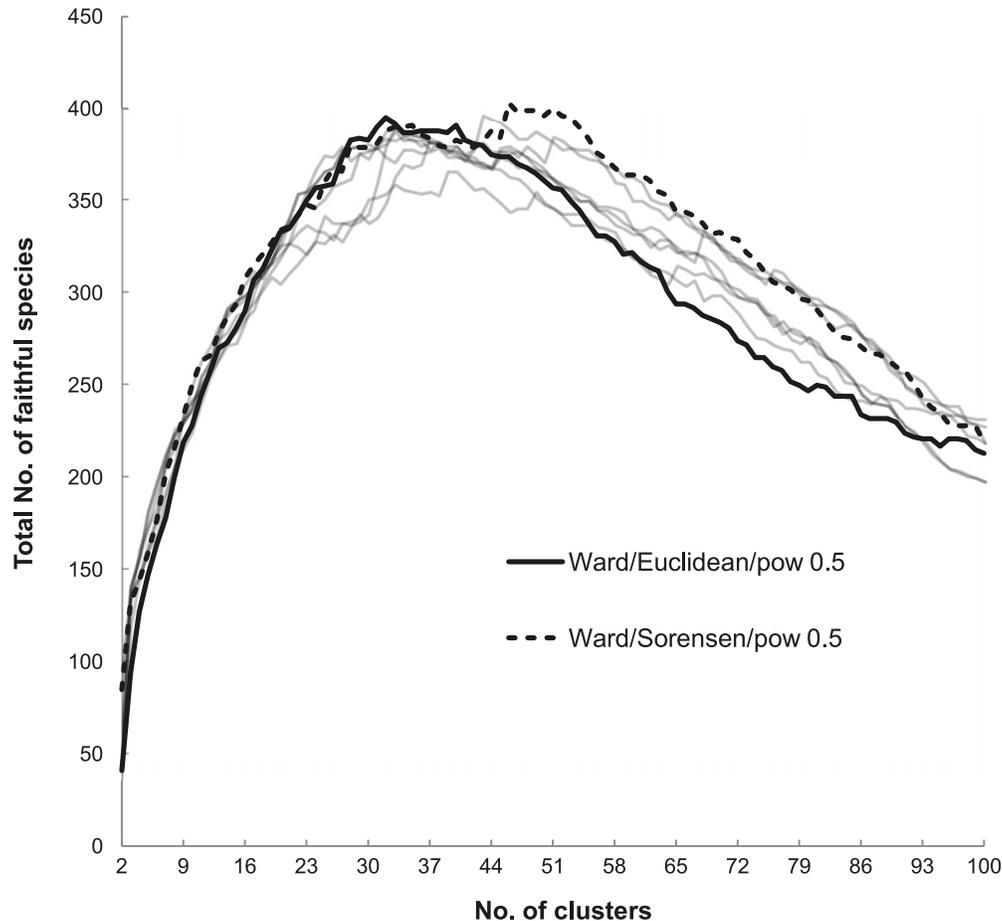
spectively), whereas the aspen data set (28 relevés and 136 species) was less diverse (3.2). All data sets included large numbers of rare species (those with appearance <5% of the data set relevés); conifers – 92 rare species (37%), nonforest – 100 (40%), and aspen 47 (35%). Therefore, it was important to account for them by standardization of the data sets before the ordination as detailed in the methods.

The NMS ordination displayed all vegetation units in ordination space for conifers, aspen, and nonforested communities in association with the most important environmental factors suggested by the RF analysis (Figs. 3–5). Binary relativization with respect to median showed the best results across the data sets in the NMS ordination. The dominance curves for all data sets were lined up, i.e., a difference between common and rare species was balanced. The ordination produced a meaningful distribution of relevés in the ordination space for this transformation.

For the conifer data set, the final solution after 108 iterations with the final stress 15.1 ($p = 0.004$) and instability 0.0 suggested two dimensions (gradients) explaining 75% (first axis 60%, second 15%) of the after-the-fact total amount of variation within the data set (Peck 2010). For the aspen units, the final solution after 59 iterations with the final stress

11.3 ($p = 0.004$) and instability 0.0 suggested three dimensions explaining 79% (first axis 50%, second 18%, and third 11%) of the total amount of variation within the data set. For the nonforested units, the final solution after 68 iterations with the final stress 17.3 ($p = 0.004$) and instability 0.0 suggested three dimensions explaining 79% (first axis 38%, second 24%, and third 17%) of the total amount of variation within the data set.

The NMS ordination visualized a clear partitioning structure within all three data sets. Twelve of 14 conifer vegetation units were distinct in the ordination space. Their relationship with environmental factors (soil depth, mottles, and pH) especially along the first ordination axis suggesting a strong moisture gradient was significant based on loadings (linear and rank correlations of factors with ordination axes). Based on type-to-type similarity matrixes, the mean Euclidean and Sørensen distance between centroids was 1.34 and 0.2. We decided to join vegetation units 3 and 4 (Euclidean and Sørensen distance between centroids 0.28, 0.05), and 19 with 20 (0.21, 0.02) (Fig. 3). Four of five aspen units were distinct. Their relationship with environmental factors (elevation, C/N ratio, soil depth, and soil color) especially along the first ordination axis suggesting a strong climatic-fertility

Fig. 3. Nonmetric multidimensional scaling (NMS) ordination of the conifer data set visualizing 14 vegetation units (represented by centroids and Arabic numerals) with associated important environmental factors. Factors are defined in Table 1. Vegetation unit 6 was represented only by one relevé with available environmental factors.
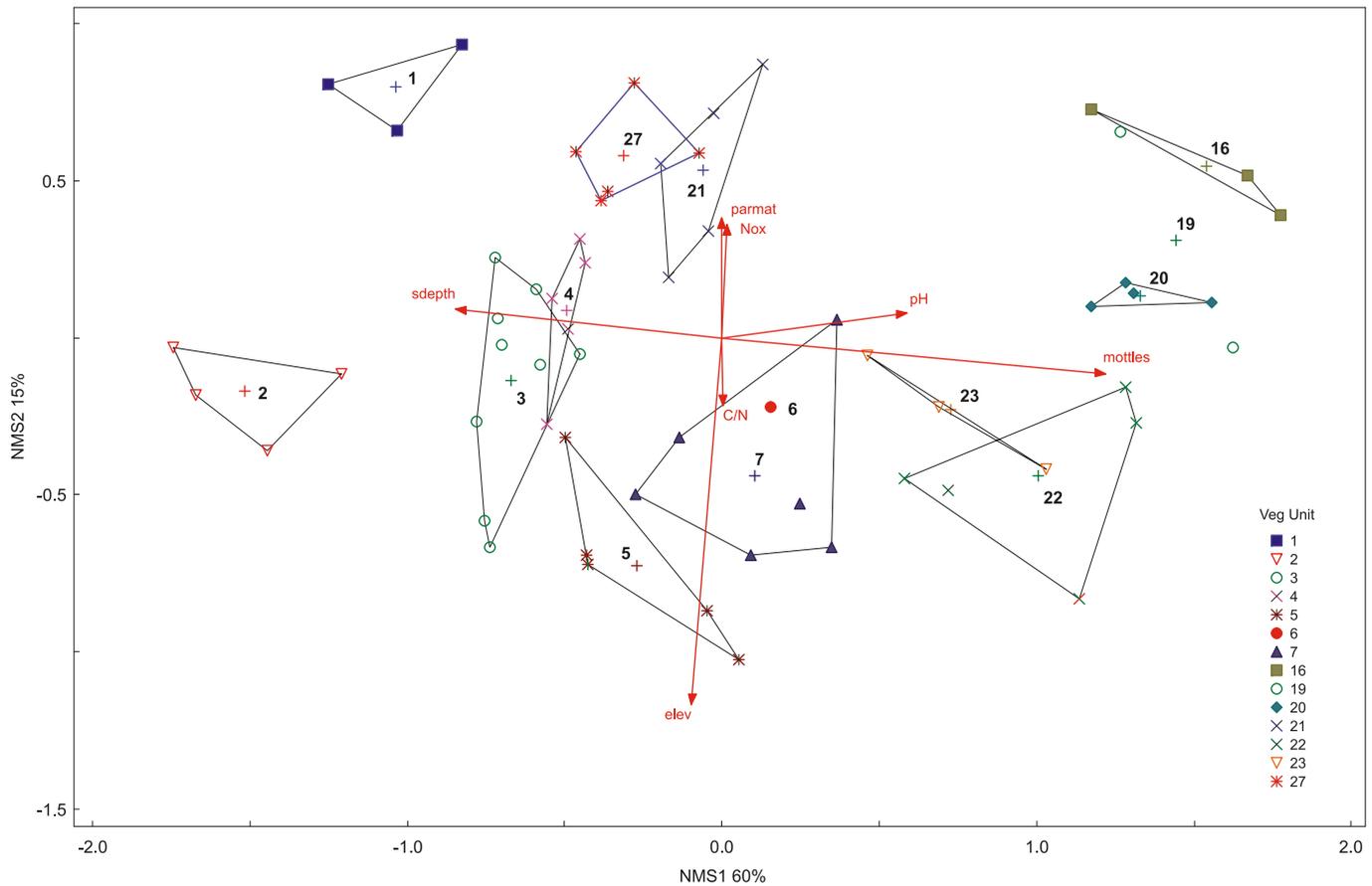
gradient was significant based on loadings. Based on type-to-type similarity matrixes, the mean Euclidean and Sørensen distance between centroids was 1.1 and 0.14. We decided to join vegetation units 31 and 32 (Euclidean and Sørensen distance 0.42, 0.01) (Fig. 4). This finding was consistent with the RF misclassification between these units.

Nine of 12 nonforested vegetation units were distinct in the ordination space. Their relationship with environmental factors (topographic position, soil depth, parmat, elevation, pH, potassium concentration, and phosphorus supply rate) was significant based on loadings. These units showed high predictability for environmental factors associated with three significant ordination axes suggestive of moisture, fertility, and climatic gradients. Based on type-to-type similarity matrixes, the mean Euclidean and Sørensen distance between centroids was 1.33 and 0.3. We decided to join the vegetation units 9, 11, and 12 (Euclidean distance 0.38, 0.45; and Sørensen distance 0.09, 0.09); and 24 with 26 (0.52, 0.08) (Fig. 5).

Based on RF and NMS ordination, 32 vegetation units were reduced to 26.

Characterization of vegetation units

The combined synoptic tables for conifer, aspen, and nonforested units (Table S2[1]) display numerical differences within and among the vegetation units. Species were sorted by decreasing fidelity at the phi coefficient positive threshold

value (phi $\geq$ 35) into diagonally arranged blocks (Tichý 2002). Fidelity values were complemented by constancy values. It is obvious that fidelity and constancy did not always match perfectly. Indeed, species with high fidelity did not inevitably have high constancy and species completely constant were not necessarily faithful. This was true for the majority of tree species and some widespread understory species such as *Symphoricarpos oreophilus* (SYOR), *Paxistima myrsinites* (PAMY), *Osmorhiza chilensis* (OSBE), *Pedicularis racemosa* (PERA), *Berberis repens* (BERE), *Thalictrum fendleri* (THFE), and *Ribes montigenum* (RIMO), mostly indicator species for major HTs in Mauk and Henderson (1984).

The strict diagonal blocks, unique for each vegetation unit, consist of character species. Additional blocks of faithful species lower in the synoptic table, which occur in a few vegetation units, represent differential species potentially useful to characterize alliances (Table S2[1]). This sorting helped to distinguish character and differential species and together with the analysis of the synoptic table (Table S3[1]), facilitated characterization of the vegetation units by diagnostic, i.e., faithful, constant, and dominant species (a looser interpretation). All forest and nonforested rangeland (shrubland, dwarfshrubland, herbaceous, and sparse vegetation) vegetation units were sorted into alliances and associations with a short description of the habitat (Appendix A) (Grossman et al. 1998; Lund 2006; FGDC 2008). Habitat characterization of the vegetation types was derived from the environmental as-

Fig. 4. Nonmetric multidimensional scaling (NMS) ordination of the aspen data set visualizing five vegetation units (represented by centroids and Arabic numerals) with associated important environmental factors. Factors are defined in Table 1.
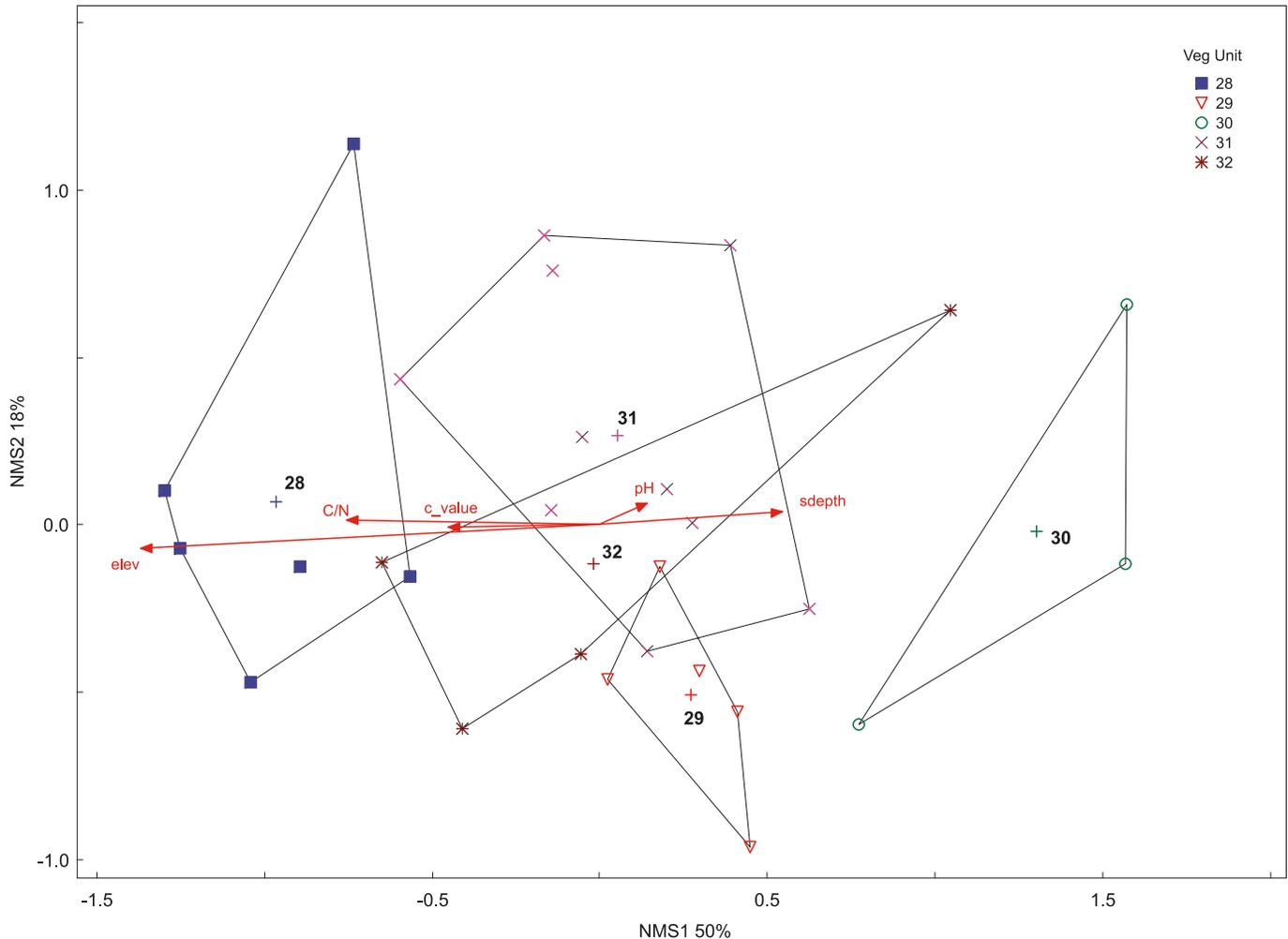
sociations and relative elevation stratification into lower montane (<ca. 2350 m), upper montane (2350–2650 m), subalpine (2650–2950 m), and alpine (>2950 m).

Some species were present in many vegetation units, e.g., ABLA, PIEN, PSME, POTR, SYOR, THFE, OSBE, PAMY, and PERA. In contrast to these generalists, other species appeared to be habitat specialists, restricted to as few as two units, e.g., *Zigadenus elegans* (ZIEL), *Calochortus nuttallii* (CANU), and CELE. Abundant, nonfaithful species unsurprisingly are generalists. Interestingly, several tree species appeared in the majority of forest vegetation units and often coexisted, e.g., PIEN with ABLA and PSME or POTR with conifers (Figs. 6, 7; Tables S2[1], S3[1]).

Of the 26 vegetation units, 22 were strong (well-characterized) with four or more faithful species and mean positive fidelity of at least 40. Four units were weak (poorly characterized) with fewer than four faithful species and mean positive fidelity less than 40. The mean species richness of weak groups (72) is significantly greater than the richness of strong groups (54). Aspen units appeared to be somewhat weak except the unit associated with wet habitats (unit 15). Unit 14 was weak and unit 16 was close to the weakness limit (number of faithful species, 2; mean positive fidelity 40%) (Table S2[1]).

Comparison of the vegetation units with habitat and community types

We keyed out nine conifer HTs based on the HT classification in our conifer data set (Mauk and Henderson 1984). Two woodland units, mahogany (3) and juniper (11), are not included in this classification and stay in a level of series (tree indicator, Fig. 6). Two habitat types (1- ABLA/OSBE, 8- PIFL/BERE) were represented only by two relevés. Except a minor wet HT 6 (PIEN/*Equisetum arvense*, EQUAR), 10 (ABLA/*Senecio triangularis*, SETR), and major dry HT 7 (PSME/*Berberis repens*, BERE), all remaining major HTs (1, 2, 4, 5, 9) highly overlapped, suggesting similar associations with the important environmental factors. There was a weak coincidence of these major HTs with our vegetation types; instead, these HTs (especially 4, 5, and 9) showed a broad environmental span (Fig. 6).

There were 10 aspen CTs (Mueggler 1988) keyed out from 28 aspen relevés. Six of all CTs were represented just by one relevé and one CT by two relevés. While some single relevés of incidental CTs at the edges of the ordination space (5- POTR/VECA, 8- POTR-ABLA/SYOR/THFE, 9- POTR-ABLA/CAGE) can indicate environmental diversity within the aspen community, major CTs at the center (1- POTR/Tall Forb, 3- POTR-ABLA/THFE, 6- POTR/SYOR/Tall

Fig. 5. Nonmetric multidimensional scaling (NMS) ordination of the nonforested data set visualizing 12 vegetation units (represented by centroids and Arabic numerals) with associated important environmental factors. Factors are defined in Table 1. Vegetation unit 17 was represented only by one relevé with available environmental factors. Vegetation unit 25 is missing because no environmental data were measured.
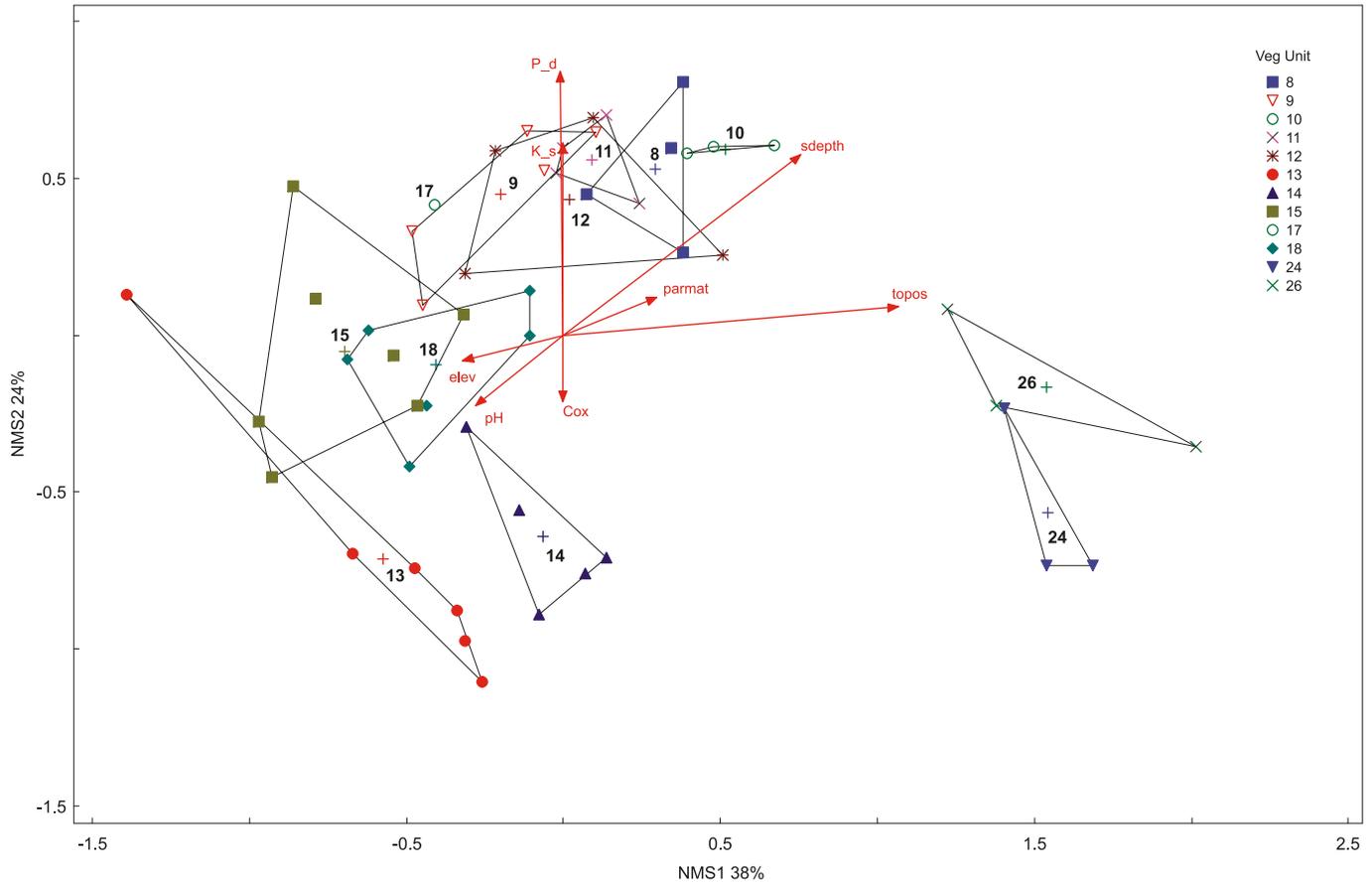
Forb) highly overlapped suggesting similar associations with the important environmental factors (Fig. 7). Except the wet incidental POTR/VECA CT, there was no coincidence of major CTs with our vegetation types and even bad coincidence of CTs with indicator species. Notice, e.g., extreme distances among 2- POTR-ABLA/THFE, 8- POTR-ABLA/SYOR/ THFE, and 7- POTR/SYOR/THFE and much smaller distances among relevant species (Fig. 7).

Discussion

Potential limitations of the classification

Both strong and weak vegetation units were associated with patterns that facilitate their explanation and interpretation. For example, based on habitat features (Appendix A), the strong units were associated with extreme environments such as wet, rocky, or calcareous sites. These units also had a high frequency of faithful species. The appearance of these faithful species associated with extreme environments, which we interpreted to be habitat specialists, appears to be tied to environmental factors such as soil moisture and pH; whereas, occurrence of habitat generalists may be explained by spatial and temporal factors, such as dispersal processes and patch dynamics (Pandit et al. 2009). In contrast, the weak vegetation units were associated with moderate environments such as well drained, nonskeletal sites on moderately deep soils;

these units had abundant common species. These units tend to have greater species richness, represented mostly by generalists and highly abundant species, and fewer specialists (Hájek et al. 2007). For example, the wet units 1, 2, 15, 25, and 26, and the dry calcareous units 5, 7, and 8 had the highest number of faithful species (putative specialists) and relatively low species richness. In contrast, the environmentally intermediate units 3, 9, 12, 14, 16, and 19 had few or no faithful species but higher species richness, mostly consisting of putative generalists (Appendix A).

The four weak units may also reflect the challenge associated with sampling special habitats. In some cases it was difficult to avoid ecotones, such as riparian versus valley bottom transition (units 12, 19). Another example is a dry habitat of cliffs with interlayered benches (unit 10), resulting in a sample representing a mosaic of rocks and deeper soil.

Additionally, classification of environmentally intermediate aspen communities such as units 29, 31, and 32 (Fig. 4) is difficult using the fidelity and diagnostic species approach. Because of generally rich understory cover comprised of many generalists but few faithful species, ecotones between aspen units tend to be ambiguous. The considerable floristic variability of aspen units is consistent with a successional status that is not always clear (Mueggler 1988), and justifies exclusion of aspen communities from vegetation geo-climatic zonation (Kusbach 2010b). We suspect that a more detailed

Fig. 6. Nonmetric multidimensional scaling ordination of the conifer data set visualizing all habitat types (HTs) keyed out from the conifer data set (Mauk and Henderson 1984) represented by centroids and relevant indicator species with associated important environmental factors. *Osmorhiza chilensis* and *Pedicularis racemosa* removed as outliers before nonmetric multidimensional scaling ordination. Factors are defined in Table 1. Species are defined in Appendix A.
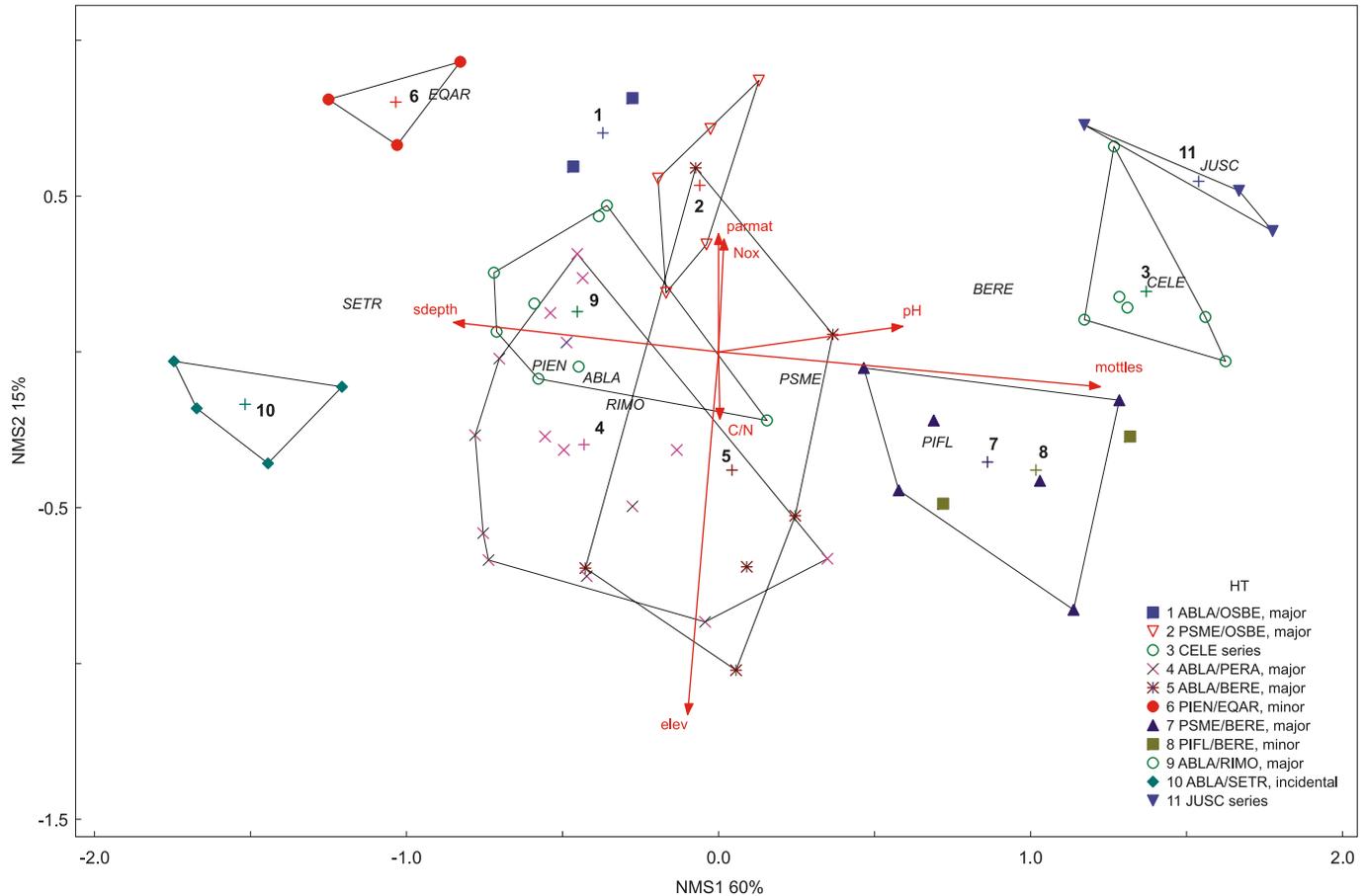
environmental description and sampling of aspen habitat (e.g., pH of soils or nutrient characteristics) might lead to better discrimination of aspen units.

Finally, data set size may overemphasize or strengthen the "validity" of vegetation units; some units appear to be strong in our data set but their status could change with spatial expansion of the sampling, likely resulting in an increasing number of species and potential expansion of environmental conditions (Chytrý et al. 2002*a*). Species listed as faithful should be interpreted with caution within the context of this study based on the potential of data set-specific fidelity (Chytrý et al. 2002*a*; Willner et al. 2009). The diagnostic species were derived for a relatively small geographic area but covered a broad spectrum of plant communities across great environmental complexity. We assumed that the local context of the species' diagnostic value would closely reflect regional patterns (Chytrý et al. 2002*b*; Willner et al. 2009).

## Potential value of the classification

Original partitioning with the OptimClass resulted in 32 vegetation units. Then, RF classification identified the most important environmental factors that resulted in split of the original data set into the conifer, aspen, and nonforest. Based on this explicit connection with the physical environment, ordinations (Figs. 3–5) of new data sets generally confirmed

the original partitioning, however, these ordinations suggested that several similar units could be reasonably combined.

Our vegetation classification revealed that major tree species such as Engelmann spruce, subalpine fir, Douglas-fir, limber pine, and aspen frequently co-occur as common species (generalists) (Appendix A, Tables S2[1] and S3[1]). This finding was consistent with vegetation geo-climatic zonation (Kusbach 2010*b*) but counter to the HT analytical process (e.g., Mauk and Henderson 1984) of a priori subjective selection of climax series based on one of the most shade-tolerant tree species, i.e., these series were not a result of an analysis (Spribille et al. 2001).

A real value of our classification is the grouping of species with high fidelity into vegetation types. A vegetation type characterized by faithful, either character or differential, species will certainly have more descriptive power than habitat types indicated by just two plant species where the first is ubiquitous (e.g., tree generalist) and the second is abundant. We propose that faithful species more so than common species (generalists) more closely reflect the combined influence of the underlying environment and disturbances on compositional similarities or differences of the vegetation as a whole (Spribille et al. 2001; Kusbach 2010*c*). Compared to the traditional, abundance/dominance-based approach, identification

Fig. 7. Nonmetric multidimensional scaling ordination of the aspen data set visualizing all community types (CTs) keyed out from the aspen data set (Mueggler 1988) represented by centroids and relevant indicator species with associated important environmental factors. Factors are defined in Table 1. Species are defined in Appendix A. TF, Tall Forb (Mueggler 1988).
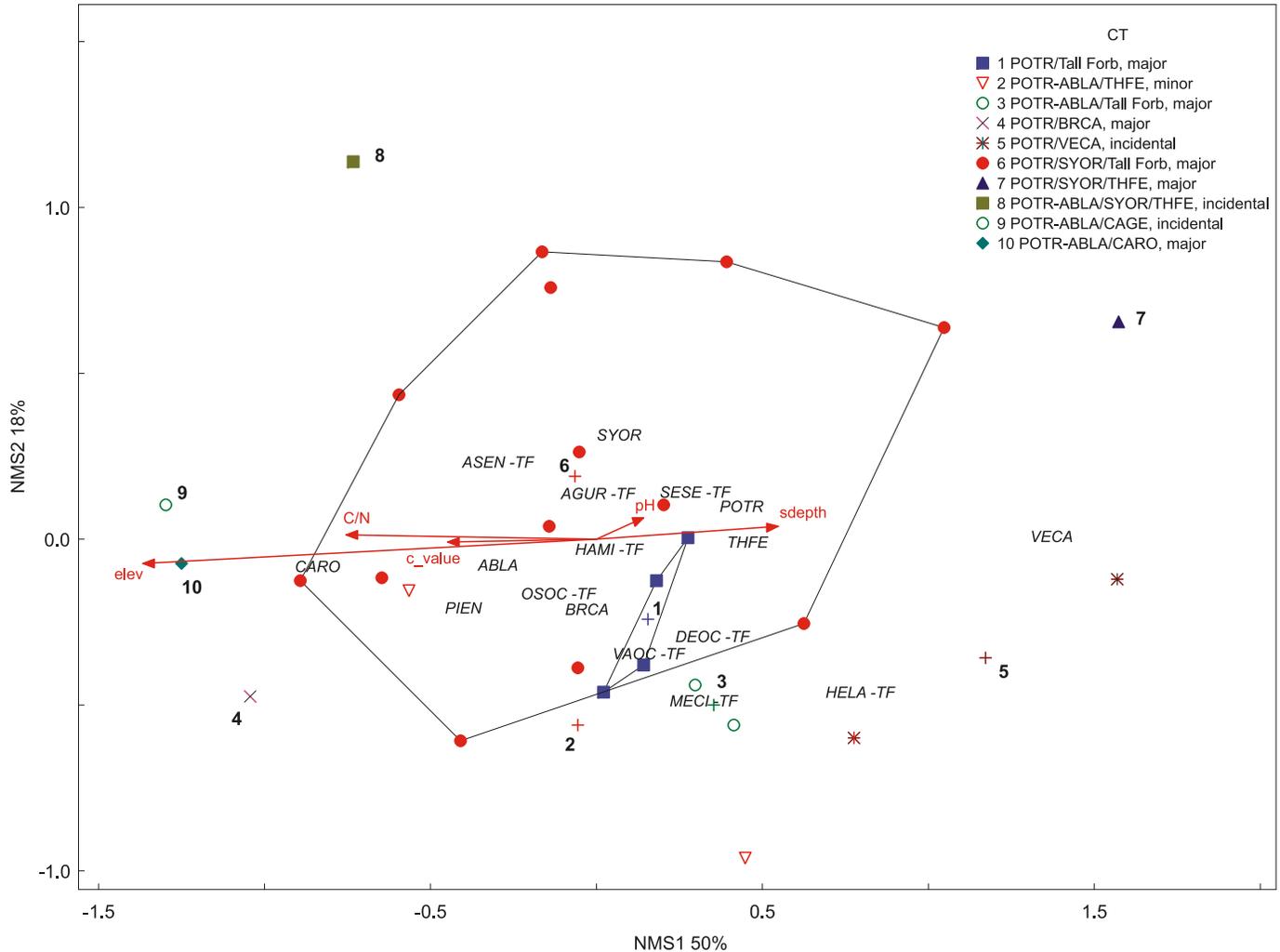
of faithful species calculated by phi coefficient appears to have great promise for recognition and mapping of vegetation types in the field. It should facilitate more accurate ecological interpretation and prediction especially in ecologically heterogeneous areas (Petřík and Bruelheide 2006; Willner et al. 2009). The weak vegetation units have broad similarities, e.g., high species richness, association with moderate environment, and similar disturbance history. These patterns are intriguing and merit further study.

The understory indicator species of the major conifer forest HTs within the study area (e.g., BERE, OSBE, PERA, SYOR, THFE, and RIMO) did not solely occur within one HT (Appendix C-1 in Mauk and Henderson 1984). These indicator species are not even restricted to a single series; they occurred in HTs of PSME, PIEN, and ABLA series and also throughout these series. The indicator species of the major HTs are in fact generalists lacking real descriptive power and different from our faithful species. This result is consistent with the disparity between floristic associations and habitat types found by Spribille et al. (2001). Consequently, indicator species *sensu* Daubenmire, at least for the major HTs and CTs in the study area, failed in discriminating between envi-

ronmental conditions, i.e., their link with the underlying environment is limited (Figs. 6, 7).

Summary and conclusions

Using the concept of diagnostic species (looser interpretation) and fidelity, we developed a vegetation classification of our floristically and environmentally complex study area in the Rocky Mountains of northern Utah. Based on cluster analysis, RF classification, and NMS ordination of a community data set, we identified 26 vegetation units. For each species, fidelity and constancy was calculated. Diagnostic, i.e., faithful, constant, and dominant species were then determined for each vegetation unit at the floristic level of alliances and associations.

We compared our vegetation classification with the forest habitat type classification for the study area. We suggest that (*i*) for a relatively small but ecologically diverse area, our vegetation classification was more comprehensive, reflecting existing vegetation of a broader range of ecosystems (forest, woodland, riparian, nonforested); (*ii*) a priori delimitation of vegetation units via a primary stratification by tree species is

ill-advised; and (*iii*) our vegetation units based on diagnostic species had more descriptive power, were more strongly associated with their underlying physical environment and disturbances than the major relevant habitat and community types, as represented by indicator species *sensu* Daubenmire.

Our approach to classification based on fidelity and diagnostic species concepts has the potential to directly link vegetation with the physical environment. This approach could therefore be the basis for a substantial improvement of vegetation classification in the central Rocky Mountains.

Acknowledgments

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Appendix A

Table A1. Forest and nonforested vegetation units, proposed alliances, associations and vegetation type habitat description.

Unit	Alliance	Association	Vegetation type	Habitat[a]
1	*Abies lasiocarpa*	*Equisetum arvense*	ABLA-PIEN-SABO/EQAR	Riparian alluvia
	Picea engelmannii			
	Salix boothii			Photo S1
2	*Abies lasiocarpa*	*Zigadenus elegans*	ABLA-PIEN-SABO/ZIEL	Wetlands
	Picea engelmannii			
	Salix boothii			Photo S2
3	*Abies lasiocarpa*	*Poa bolanderi*	ABLA-PIEN/POBO	Subalpine mesic slopes/undulating plateaus
	Picea engelmannii			Photo S3
4	*Abies lasiocarpa*	*Rubus parviflorus*	ABLA-PIEN-PSME/RUPA	High elevation shady skeletal slopes
	Picea engelmannii			
	Pseudotsuga menziesii			
5	*Abies lasiocarpa*	*Anemone multifida*	ABLA-PIEN-PIFL/ANMU	Subalpine rocky calcareous slopes/flats
	Picea engelmannii			Sparse vegetation
	Pinus flexilis			Photo S4 a, b
6	*Abies lasiocarpa*	*Juncus parryi*	ABLA-PIEN-PIFL/JUPA	Subalpine quartzite talus
	Picea engelmannii			Sparse vegetation
7	*Juniperus scopulorum*	*Calochortus nuttallii*	JUSC/CANU	Lower elevation dry skeletal slopes
	Artemisia tridentata			Photo S5
8	*Cercocarpus ledifolius*	*Petradoria pumila*	CELE/PEPU	Dry calcareous slopes, rocks and cliffs
	Artemisia tridentata			Photo S6 a, b
9	*Pseudotsuga menziesii*	*Smilacina racemosa*	PSME-ABLA/SMRA	Lower elevation shady slopes
	Abies lasiocarpa			Photo S7
10	*Pseudotsuga menziesii*	*Linanthastrum nuttallii*	PSME-PIFL/LINU	Subalpine sunny calcareous slopes
	Pinus flexilis			Photo S8 a, b
11	*Pseudotsuga menziesii*	*Stipa lattermanii*	PSME-PIFL/STLA	High elevation sunny calcareous slopes
	Pinus flexilis			Photo S9
12	*Abies lasiocarpa*	*Lathyrus lanszwertii*	ABLA-POTR/LALA	Undulating moraines, moderate (quartzite) slopes
	Populus tremuloides			
	Pseudotsuga menziesii			
	Picea engelmannii			Photo S10
13	*Populus tremuloides*	*Helianthella uniflora*	POTR-ABLA-PIEN/HEUN	Undulating moraines, moderate (quartzite) slopes
	Abies lasiocarpa			
	Picea engelmannii			Photo S11
14	*Populus tremuloides*	Tall forbs: *Rudbeckia occidentalis* RUOC	POTR-ABLA/Tall Forb	Rich toes, moderate slopes
	Abies lasiocarpa	*Delphinium occidentale* DEOC, *Senecio serra*		
		SESE, *Valeriana occidentalis* VAOC		Photo S12
15	*Populus tremuloides*	*Veratrum californicum*	POTR/VECA	Wet valley bottoms, toe-slopes
				Photo S14
16	*Populus tremuloides*	*Berberis repens*	POTR-ABLA/BERE	Undulating moraines, moderate slopes
	Abies lasiocarpa			Photo S13
17	*Artemisia spiciformis*	*Elymus cinereus*	ARSP-SYOR/ELCI	Lower elevation valley bottoms/ slopes
	Symphoricarpos oreophilus			Photo S15

Table A1 (*concluded*).

Unit	Alliance	Association	Vegetation type	Habitat[a]
18	*Stipa nelsonii*	*Ranunculus adoneus*	STNE/RAAD	Subalpine depressions/colluvial outwashes
				Photo S16
19	*Artemisia spiciformis*	*Elymus lanceolatus*	ARSP-SYOR/ELLA	High elevation valley bottoms/ slopes
	Symphoricarpos oreophilus			Photo S17 a, b
20	*Penstemon leonardii*	*Linum kingii*	PELE/LIKI	Subalpine-alpine sunny skeletal slopes
				Shallow soils, Photo S18
21	*Ivesia gordonii*	*Juncus parryi*	IVGO/JUPA	Quartzite talus and rocks, sparse vegetation
				Photo S19
22	*Ivesia gordonii*	*Monardella odoratissima*	IVGO/MOOD	Subalpine talus and rocks, shallow soils
				Photo S20
23	*Comandra umbellata*	*Wyethia amplexicaulis*	COUM/WYAM	Low elevation undulating moraines
				Photo S21
24	*Comandra umbellata*	*Calochortus nuttallii*	COUM/CANU	Lower elevation dry rocky slopes
				Photo S22
25	*Salix drummondiana*	*Cornus sericea*	SADR/COSE	Riparian alluvia
	Salix boothii			Photo S23
26	*Salix drummondiana*	*Salix wolfii*	SADR/SAWO	Wetlands
	Salix boothii			Photo S24 a, b

[a]Photos S1–S24 are available online in the supplementary material.