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How Well Do U.S. Forest Service Terrestrial Ecosystem Surveys Correspond with Measured Vegetation Properties?

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Reliable estimates of species composition that forest sites are capable of supporting – specific to ecosystem mapping units across landscapes – are useful for many purposes in forest science and management. Like forestry agencies in numerous countries, the U.S. Forest Service has invested in ecological land classification (termed terrestrial ecosystem survey [TES] in the study region of Arizona) that includes ecosystem-explicit species lists taken to be estimated potential natural vegetation (PNV). Using multivariate community analyses, PNV in the TES was compared to measured species composition on 66 sites representing among the least-disturbed vegetation (considered this study's measured PNV) spanning 11 ecosystem types on a *Pinus ponderosa* P. & C. Lawson landscape in northern Arizona, USA. Agreement between the TES PNV and measured species composition was lowest for forbs and shrubs (compared to graminoids), and species composition differed significantly between the TES and this study for at least one plant lifeform in 73% of ecosystems. Reasons for differences between the TES and this study are difficult to resolve, but in some cases appear to result from identification of different species pools in the region. This study suggests that the TES is a useful starting point in understanding vegetation-environment relationships, but further work is needed to refine species lists and more thoroughly account for the influences of fire, grazing, and climate that can influence both PNV and current vegetation. Refining and updating ecosystem-specific species lists may benefit existing forest site classifications and could be planned for when new site classifications are developed, especially with changing climates.

Keywords ecosystem classification, *Pinus ponderosa*, potential natural vegetation, reference conditions, understory
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1 Introduction

Ecological forest site classification has a long history in forest science and management. In Finland, for instance, Cajander (1926) was among the first to depict interrelationships among topography, soils, and vegetation that formed repeatable ecological units mappable across the landscape. Tonteri et al. (1990) subsequently applied and refined Cajander's methods for classifying Finnish boreal forest sites based on soils and understory vegetation. Similarly, work in Michigan by Barnes et al. (1982) helped to popularize ecological site classification in the USA. The U.S. Forest Service, Natural Resources Conservation Service, and other agencies have invested and continue investing substantial resources to develop these systems (McMahon et al. 2001). The Forest Service, for example, has termed its site classification program the terrestrial ecosystem survey (TES) in region 3 (Arizona and New Mexico), and surveys have been developed since the 1980s for this region's national forests (U.S. Forest Service 1986, Robbie 1992, Ganey and Benoit 2002). Site classifications have many potential uses. The TES has been used, for instance, by Ganey and Benoit (2002) for identifying potential habitat for *Strix occidentalis lucida* (Mexican spotted owl), understanding spatial variation in soil seed banks for assessing plant regeneration potential (Abella et al. 2007), and estimating the historical density of *Pinus ponderosa* P. & C. Lawson (ponderosa pine) trees as a benchmark for understanding forest change (Abella and Denton 2009, Bell et al. 2009).

Ecological site classification usually includes late-successional vegetation in the development of the classification for the vegetation component (Nolet et al. 1995). The use of this late-successional vegetation is one of the greatest uncertainties in the development and application of ecological site classifications. This vegetation is typically considered to be in long-term equilibrium with environmental site factors (topography and soils) and is often termed potential natural vegetation (PNV) as in the TES (Miller et al. 1995). The concept of PNV has been extensively debated and much confusion surrounds its use (e.g., Küchler 1964, Härdtle 1995, Moravec 1998, Zerbe 1998). Using observations in central European ecosystems, Härdtle (1995) sought to clarify principles of PNV, which he defined as a theoretical state of vegetation in equilibrium with the site conditions taken as the basis for PNV construction. If some disturbance (e.g., mining) essentially permanently alters site capability, then PNV changes. However, if a disturbance (e.g., nutrient enrichment) is considered to have only transient effects and not alter long-term site capability, then PNV remains the same. Temporal dynamics are by definition not part of PNV because the concept of PNV focuses on the vegetation that a site is capable of supporting at a given time, rather than changes in vegetation through time. However, as climates change through time, PNV can change because site capability can differ in different climatic regimes. Moravec (1998) and Zerbe (1998) also highlighted the differences among PNV, reconstructed natural vegetation, and actual vegetation based on observations in forets of the Czech Republic, Germany, and elsewhere. These authors noted that reconstructed natural vegetation is often considered to be historical vegetation, prior to intensive human manipulation, which differs from PNV. Anthropogenic severe disturbances alter PNV by changing site capability, whereas reconstructed natural vegetation remains the same. Actual vegetation is the present-day vegetation, which can be similar to PNV or reconstructed vegetation, but often is not due to a variety of influences.

Understory vegetation typically is the focus of PNV for ecological site classification, as, for example, some forests consist of a single tree species (such as *Pinus ponderosa* forests of the western USA) but contain an array of understory communities distributed according to variation in site factors (Härdtle 1995). A reliable species list of PNV for different ecosystem units made available as part of site classification could have many uses. For example, the species list could be useful in revegetation projects of disturbed sites by helping managers match species adapted to the environments of specific ecosystem types. Species lists also could be helpful in land condition or management effectiveness assessments, where actual vegetation is compared to the PNV a site is capable of supporting. However, the utility of PNV for these and other purposes can hinge upon the construction and reliability of the PNV species list.

In *Pinus ponderosa* forests of the western USA, much attention is currently being given to tree thinning and prescribed burning for reducing hazardous fuels that have accumulated during over a century of fire exclusion and rehabilitating sites burned by severe wildfire (Allen et al. 2002). The reference conditions of historical tree structure (density and spatial arrangement) prior to fire exclusion in the late 1800s have enabled a detailed understanding of change in forest structure (Fulé et al. 1997). Dead wood persists in the semi-arid climate of *P. ponderosa* forests, preserving the record of past tree structure. In contrast, like in other ecosystems where herbaceous vegetation is abundant, understanding reconstructed natural (historical) vegetation of forest understories is challenging. Detailed quantitative and place-based historical documents of the species composition of understories prior to widespread human settlement, livestock grazing, logging, and fire exclusion are not available. Other techniques for reconstructing historical understories, such as soil phytolith analysis, have been applied on a limited basis in *P. ponderosa* forests (Kerns et al. 2001). Phytolith and the closely related packrat midden analyses are constrained by the specialized expertise needed, their expense, and not all (or even most) species are preserved as fossils (Piperno 2006), making them difficult to use in forest management planning. Given these difficulties in reconstructing historical vegetation, PNV may provide a useful reference measure of the vegetation that current sites are capable of supporting that can be compared to the actual vegetation of degraded sites and historical vegetation where it can be reconstructed. Open areas with low tree canopy cover, often near old-growth trees and free from acute disturbance (e.g., harvesting disturbance, wildfire), are considered in *P. ponderosa* forests to best express PNV (Laughlin et al. 2006), recognizing that fire exclusion and livestock grazing could influence species composition.

Species lists of PNV, by ecosystem type, are available in the TES, but there are no known published comparisons of the TES PNV with landscape-scale vegetation assessments. Using multivariate community analyses, the TES PNV on a *Pinus ponderosa* landscape was compared to measured plant community composition of 66 mapping units spanning 11 ecosystem types replicated across the landscape. The specific objectives of this study were to: 1) evaluate the correspondence between the TES and measured vegetation of this study among plant lifeforms (graminoids, forbs, and shrubs); 2) compare the correspondence among ecosystem types representing a gradient of xeric, nutrient-poor to moist, nutrient-rich ecosystems; 3) determine the congruence in species richness estimated by the TES and this study; and 4) develop an updated species list and provide suggestions for how factors such as fire exclusion, grazing, and climate change could be considered in PNV development. Results illustrate several considerations about PNV and factors affecting PNV, and provide comparative data for other regions, such as European biomes, where PNV is used in forest research and management.

2 Material and Methods

2.1 Study Area

This study occurred within a 100,000-ha area of the northern half of the Coconino National Forest and the southern half of the Northern Arizona University Centennial Forest surrounding the city of Flagstaff in northern Arizona, USA. The corners of the study area were: southwest, 35°04’N, 111°53’W; northwest, 35°29’N, 111°51’W; northeast, 35°23’N, 111°31’W; and southeast, 35°01’N, 111°23’W. Study sites ranged in elevation from 1,921–2,564 m. Precipitation primarily occurs in winter as snow (ca. 50%) and as July–September summer monsoonal storms. Most of the landscape is without substantial slope gradient (<10%), but cinder cones, ravines, and low hills of greater slope gradient punctuate the undulating topography. Major soil subgroups (U.S. classification system) include Typic and Udic Argiborolls, Typic and Mollic Eutroboralfs, Typic Ustorthents, and Vitrandic Ustochrepts (Miller et al. 1995).

Forests are predominately pure *Pinus ponderosa*, but *Quercus gambelii* Nutt. (Gambel oak) occurs with *P. ponderosa* in some areas and small stands (generally <20 ha) of *Populus tremuloides* Michx. (trembling aspen) also are present (Hanks et al. 1983). Graminoids are the dominant understory plants, often including *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (blue grama), *Carex geophila* Mackenzie (White Mountain sedge), *Elymus elymoides* (Raf.) Swezey (squirreltail), *Festuca arizonica* Vasey (Arizona fescue), and *Muhlenbergia montana* (Nutt.) A.S. Hitchc. (mountain muhly). Five fire-history studies in the area, summarized in Van Horne and Fulé (2006), reported mean fire intervals of 2–5 years prior to the late 1800s. During the 1900s, however, the study area was subject to a policy of fire exclusion, and the frequent fires were suppressed as they were on other western U.S. forestlands (Covington et al. 1994). Densities of *P. ponderosa* trees escalated during this period, increasing, for example, by 11-fold from 66/ha in 1883 to 739/ha in 1994 at Camp Navajo in the western part of the study area (Fulé et al. 1997). Livestock grazing, primarily by cattle and sheep, began in earnest in the late 1800s and continues with lower stocking levels to the present (Clary 1975, Bakker and Moore 2007). Herbivory by *Cervus elaphus nelsoni* (Rocky Mountain elk) and other ungulates also occurs (Huffman and Moore 2003).

2.2 Data Collection

The TES of the Coconino National Forest, reported in Miller et al. (1995) and online at http://alic.arid.arizona.edu/tes/tes.html, covered the study area with a minimum mapping unit of 16 ha. Using a map of the TES in a geographic information system, six mapping units were randomly selected for sampling in each of 11 ecosystem types for this study (Table 1). These ecosystems are predominant in *Pinus ponderosa* forests of the study area, encompass a range of soil parent materials including basalt, benmorite, limestone, and volcanic cinders, and include four soil orders (Mollisols, Alfisols, Entisols, and Inceptisols). At a random coordinate within each mapping unit, a 0.05-ha (20 m × 25 m) plot was measured in the nearest open area (except for the aspen and park ecosystems) with no visual evidence of recent disturbance. Disturbances such as off-road vehicle imprints, slash piles, tree harvesting (e.g., landings for logging equipment), and wildfires were avoided. The remnant open patches that

Table 1. Properties of ecosystem types sampled in *Pinus ponderosa* forests of northern Arizona, USA. Ecosystems are arranged in general order from xeric, nutrient-poor, to moist, nutrient-rich.

Ecosystem[a]	Precip.[b]	Soil parent material	Soil great group	Texture[c]	Features
558: Black cinder	50–60	Basaltic cinders/ash	Ustochrepts/Ustorthents	Sand	Dry, gravelly, volcanic cinders
513: Red cinder	46–56	Basaltic cinders	Ustochrepts/Ustorthents	Sandy loam	Dry, gravelly, volcanic cinders
523: Clay basalt	46–56	Basalt	Eutroboralfs/Argiborolls	Clay loam	Clay subsoils, large surface cracks
500: Xeric limestone	46–56	Limestone/sandstone	Eutroboralfs/Ustochrepts	Sandy loam	Climatically dry; neutral pH
536: Mesic limestone	50–60	Limestone/sandstone	Eutroboralfs/Ustochrepts	Sandy loam	Climatically moist; pH = 6.1
570: Submesic benmorite	50–60	Benmorite	Eutroboralfs	Loam	Clayey, often shallow subsoils
551: Mixed igneous	50–60	Mixed igneous	Eutroboralfs/Argiborolls	Loam	Surrounding San Francisco Peaks
585: Rocky basalt	50–60	Basalt/cinders	Eutroboralfs/Argiborolls	Loam	Rocky; clay loam subsoils
582: Mesic basalt	50–60	Basalt/cinders	Argiborolls/Eutroboralfs	Silt loam	Variable; high productivity
611: Aspen	60–68	Andesite	Argiborolls	Loam	Deep, N–rich soils; productive
55: Park	50–60	Basalt/cinders	Argiborolls	Clay loam	Treeless basins; deep soils

[a] Numerical code assigned by the terrestrial ecosystem survey (Miller et al. 1995) and the descriptive name assigned by this study.
[b] Range of average annual precipitation (in cm) within ecosystems (Miller et al. 1995).
[c] 0–15 cm soil layer; data from Abella and Covington (2006).

were sampled were usually near groups of old trees, largely free of 1900s tree encroachment, and were readily identified using a three-class categorization (old tree, remnant opening, and young tree) of patch types widely employed in previous research in these forests (e.g., Kerns et al. 2001). In aspen and park ecosystems, the opening criterion was not applied because tree cover was continuous in aspen; and park ecosystems do not contain trees (Abella and Covington 2006).

In each plot within 15, 1-m^2 subplots centered at 0.5, 5, 12.5, 20, and 24.5 m along the bottom, middle, and top axes of the 25-m sides of plots, the areal percent cover of each plant species rooted in each subplot was visually categorized. Cover categories were 0.1, 0.25, 0.5, and 1% up to 1% cover, 1% intervals to 10% cover, and 5% intervals above 10% cover. The whole 0.05-ha plot was also surveyed for species not already occurring in subplots, and these species were assigned a cover of 0.1%. Data were collected from May–September 2003. Plants not able to be readily identified in the field were collected, pressed, and keyed to species if possible. Of 271 total taxa, 264 (97%) were identified to species and 7 (3%) were definitively identified only to genus.

2.3 Data Analysis

Data collected by this study were compared to the PNV data in the TES. The TES data consisted of the percent canopy cover of the predominant plant species (up to 38 species in the ecosystems examined) categorized into graminoid, forb, and shrub lifeforms (Miller et al. 1995). The percent cover classes constituted ‘present’ (only one or a few individuals), ‘trace’ (< 0.1% cover), 0.1% intervals to 0.5% cover, 1% intervals to 10% cover, and 5% intervals for ≥ 10% cover. Few details were provided on sampling methods for the TES, but generally, species lists were derived by integrating plot surveys and knowledge of the local flora by the TES developers (U.S. Forest Service 1986, Miller et al. 1995).

Several procedures were used to standardize the TES and this study’s data for analysis. Only taxa distinguished to the species level, representing > 90% of the entries, were included in both the TES and plot data generated by this study. The ‘present’ cover category in the TES was assigned a 0.01% cover and ‘trace’ was assigned 0.05% cover for analysis. Nomenclature and plant lifeform classifications were standardized to NRCS (2010). The number of species given in the TES manual varied by lifeform and ecosystem type, ranging from 4 (red cinder ecosystem) to 12 (clay basalt) for graminoids, 1 (black cinder) to 15 (mesic limestone and park) for forbs, and 0 (park) to 7 (clay basalt and xeric limestone) for shrubs. In this study’s data set all species were available, rather than just the predominant species as in the TES. Including all species in this study’s compositional data, however, could influence comparisons with composition derived from the fixed number of species in the TES. All of the species in this study’s plot data would contribute some cover value, “diluting” the cover contributed by the predominant species when cover was relativized to a fixed amount (often 100% as in this study) for multivariate compositional analyses. To overcome this challenge, this study’s plot data were standardized to include the same number of predominant species (though their identities could differ) by lifeform/ecosystem type as were included in the TES. Since this procedure captured over 90% of the total cover of all species on plots, in practice the data were similar for quantifying community composition when the predominant only and all species were included. This is analogous to the observation that rare species contribute little to community similarity indices and multivariate community analyses (McCune and Grace 2002). Since raw cover can be measured differently in different studies and to ensure that species composition, rather than total plant cover, guided the analyses (McCune and Grace 2002), relative cover was calculated from the species data. This measure was calculated for each TES ecosystem and individual plot by growth form and overall (all lifeforms combined) as: the proportion of the total cover summed for all species that an individual species contributed, × 100 to total 100% for all species.

Species composition (using relative cover) was compared, separately by lifeform, between the TES and this study using the Sørensen index in a permutational multivariate analysis of variance (permanova) implemented in the software

XMATRIX and DISTLM (Anderson 2001, 2003, 2004). In the decade since its development, permanova has become widely used for analyzing community data sets such as those generated by this study (e.g., Marignani et al. 2008, Burrascano et al. 2009). Permanova is a non-parametric procedure free of the assumptions in traditional manova commonly not met by ecological community data (Reiss et al. 2010). Lifeforms were treated in separate models because two ecosystem types were dropped from the shrub lifeform: park ecosystems because no shrubs occurred in the plot data, nor were any reported in the TES (perfect match, hence no variation); and aspen ecosystems where shrubs were reported in the TES but none were detected in the plot data (perfect mismatch). The main effects of sampling source (i.e. TES versus plot data) and ecosystem type were not of interest, so only the interaction term of ecosystem type × data source was tested. Since these comparisons essentially involved comparing this study's plot data to a standard (the TES), which did not have an associated error (variability among mapping units was not reported in the TES), the TES data should not contribute to the 'error' variance. The denominator therefore was a plot (the individual 66 plots) within ecosystem type error term calculated only from the plot data. When the interaction was significant, the TES and this study's plot data were compared within ecosystem types using the above error term. P-values estimated by 999 permutations and Monte Carlo sampling of the pseudo-*F* distribution were similar, so the permuted P-values are reported.

Variation between the TES and this study was further examined using several techniques. Patterns in overall species composition, including all lifeforms combined and averaged by ecosystem type for the plot data, were displayed using two non-metric multidimensional scaling (NMS) ordinations in the 'autopilot, thorough' mode of the software PC-ORD (McCune and Mefford 1999). The first ordination employed compositional vectors to illustrate the relative amount of deviance by ecosystem type between the TES and this study. The second ordination included species as vectors that exhibited Pearson r^2 coefficients of 0.30 or above with community patterns. Sørensen similarities were computed between the TES and this study's plot data averaged by ecosystem type for each lifeform and for all lifeforms combined. Congruence in individual species between the TES and this study was calculated as the proportion of species that were the predominant species (standardized by the number of species given in the TES by lifeform and ecosystem) in both the TES and this study. Simple linear regressions were used to assess the relationship between the number of species (richness) reported in the TES with the measured total mean species/m^2 (averaged from 15, 1-m^2 subplots per plot) and 0.05 ha, averaged by ecosystem type. For this analysis, all of the species recorded on plots (rather than only the predominant species as in other analyses) were used to represent total richness.

3 Results

Only 3 of the 11 (27%) ecosystems did not have significant differences in species composition between the TES and this study for at least one lifeform based on the permanova (Table 2). The Sørensen similarity between the TES and plot data was greatest for graminoids but only averaged 39 ± 5% (± SE) among ecosystems, with graminoid species composition differing significantly for 8 of 11 (73%) ecosystems. Similarity for forbs averaged 12 ± 3% among ecosystems, and 9 of 11 (82%) ecosystems differed significantly. Shrubs exhibited the lowest similarity (11 ± 3%), but because shrubs occurred only sporadically, variability was high and only 3 of 10 ecosystems differed significantly (the 11th ecosystem, parks, contained no shrubs).

When species composition was averaged across all plots within ecosystems and compared to the TES, trends were similar to the permanova results. Similarity was greatest for graminoids and least for forbs and shrubs (Fig. 1). By ecosystem, the similarity of overall species composition between the TES and plot data exceeded 50% in only two ecosystems (mixed igneous and mesic basalt). Similarity was lowest in the black and red cinder, park, and aspen ecosystems.

Ordinations highlighted differences in overall species composition between the TES and this study. Vector lengths portrayed that deviance between the TES and this study was greatest for

Table 2. Summary of permutational multivariate analysis of variance results for comparing understory species composition by plant lifeform between the terrestrial ecosystem survey (TES) and this study's plot data for 11 ecosystem types of *Pinus ponderosa* forests of northern Arizona, USA. P-values in bold are < 0.05.

	Graminoids			Forbs			Shrubs		
Ecosystem	Sim. (%)[a]	Pseudo *F*	P	Sim. (%)	Pseudo *F*	P	Sim. (%)	Pseudo *F*	P
558: Black cinder	12±10	4.59	**0.001**	0±0	4.15	**0.001**	5±2	3.59	**0.002**
513: Red cinder	31±14	2.40	**0.031**	3±8	4.14	**0.001**	8±9	1.45	0.162
523: Clay basalt	50±3	6.88	**0.001**	8±2	4.64	**0.001**	0±0	3.32	**0.003**
500: Xeric limestone	59±7	3.42	**0.005**	2±1	4.79	**0.001**	26±39	1.18	0.304
536: Mesic limestone	35±15	1.35	0.217	18±10	1.77	**0.022**	13±10	2.10	**0.023**
551: Mixed igneous	54±15	3.09	**0.006**	21±21	1.57	**0.043**	17±13	1.81	0.086
570: Submesic benmorite	47±15	1.29	0.236	27±15	1.43	0.083	6±10	1.40	0.190
585: Rocky basalt	31±14	2.46	**0.023**	6±7	2.80	**0.001**	22±11	1.21	0.271
582: Mesic basalt	51±13	1.94	0.080	26±17	1.06	0.313	13±14	1.71	0.092
611: Aspen	44±16	2.32	**0.028**	19±8	3.37	**0.001**	0±0	–[b]	–
55: Park	20±15	8.51	**0.001**	7±6	4.39	**0.001**	–	–	–

[a] Sørensen similarity (mean ± SE of the mean) comparing species composition of the TES with this study's plot data.
[b] Shrubs were listed in the TES for aspen ecosystems but were not detected by this study; hence, there was a perfect mismatch. Shrubs were not detected in park ecosystems in either the TES or this study, so no statistics are reported.

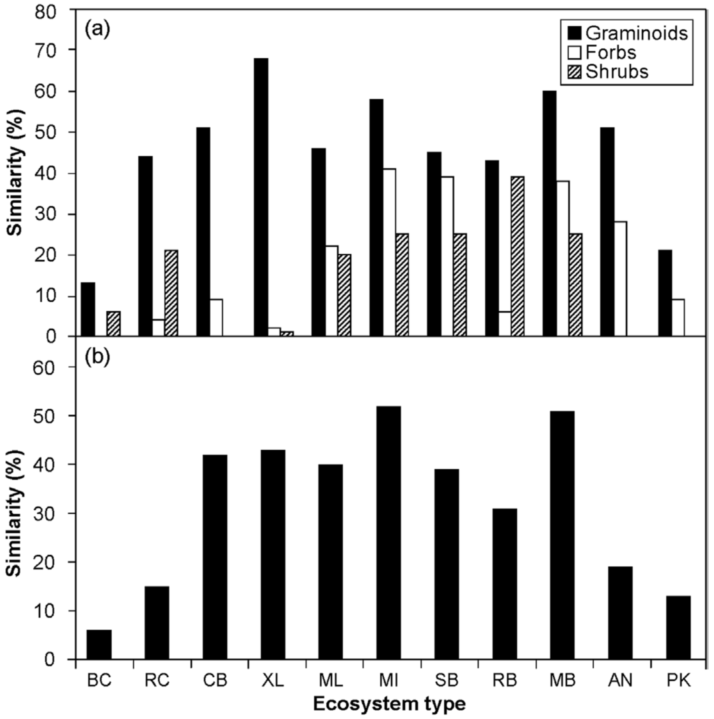

Fig. 1. Sørensen similarities of plant community composition a) by plant lifeform and b) overall between the terrestrial ecosystem survey (TES) and this study's plot data for 11 ecosystem types of *Pinus ponderosa* forests of northern Arizona, USA. There are no error bars because the TES did not report variability and species composition of the plots was averaged by ecosystem type, resulting in one similarity value per ecosystem. Abbreviations for ecosystems and their TES numerical designations are as follows: BC = black cinder (500), RC = red cinder (513), CB = clay basalt (523), XL = xeric limestone (500), ML = mesic limestone (536), MI = mixed igneous (551), SB = submesic benmorite (570), RB = rocky basalt (585), MB = mesic basalt (582), AN = aspen (611), and PK = park (55).

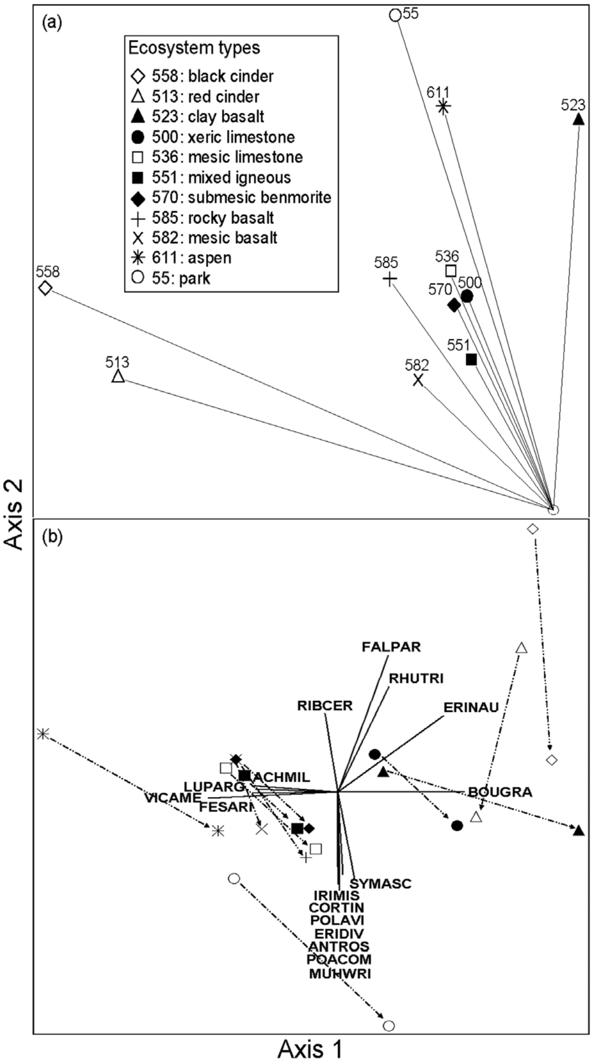

Fig. 2. Non-metric multidimensional scaling ordinations of a) deviance in species composition between the terrestrial ecosystem survey (TES) and this study's plot data and b) TES and plot data with species exhibiting r^2 values ≥ 0.30 shown as vectors, for 11 ecosystem types of *Pinus ponderosa* forests of northern Arizona, USA. In a), longer vectors indicate greater disparity, and in b) longer vectors between plots indicate greater disparity (arrows point to this study's samples) while longer vectors for species signifiy greater correlation coefficients. Species are abbreviated as: ACHMIL = *Achillea millefolium*, ANTROS = *Antennaria rosulata*, BOUGRA = *Bouteloua gracilis*, CORTIN = *Coreopsis tinctoria*, ERIDIV = *Erigeron divergens*, ERINAU = *Ericameria nauseosa*, FALPAR = *Fallugia paradoxa*, FESARI = *Festuca arizonica*, IRIMIS = *Iris missouriensis*, LUPARG = *Lupinus argenteus*, MUHWRI = *Muhlenbergia wrightii*, POACOM = *Poa compressa*, POLAVI = *Polygonum aviculare*, RHUTRI = *Rhus trilobata*, RIBCER = *Ribes cereum*, SYMASC = *Symphyotrichum ascendens*, and VICAME = *Vicia americana*.

the black cinder, park, red cinder, aspen, and clay basalt ecosystems, and least in the mixed igneous, basalt, benmorite, and limestone ecosystems (Fig. 2a). Species composition did group in both the TES and plot data, with related ecosystems such as the black and red cinder ecosystems grouping together (upper right corner of Fig. 2b). However, different species were correlated with the respective TES and plot groups for dry ecosystems. For example, *Bouteloua gracilis* was most closely associated with the xeric limestone, red and black cinder, and clay basalt ecosystems, whereas shrubs such as *Rhus trilobata* Nutt. (skunk-brush sumac) most closely corresponded with the TES data. For moister ecosystems such as the basalt ecosystems, species including *Festuca arizonica* and *Lupinus argenteus* Pursh (silver lupine) were correlated both with the TES and this study.

In examining the congruence of the presence/absence of individual species as the top dominants by ecosystem type, larger proportions of graminoids were congruent between the TES and this study than forbs and shrubs except for the black and red cinder ecosystems that had only ≤ 4 forbs and ≤ 6 shrubs in the TES (Fig. 3). The dry ecosystems and aspen had the lowest overall proportion of congruent species with less than 50%, while the moister basalt, benmorite, mixed

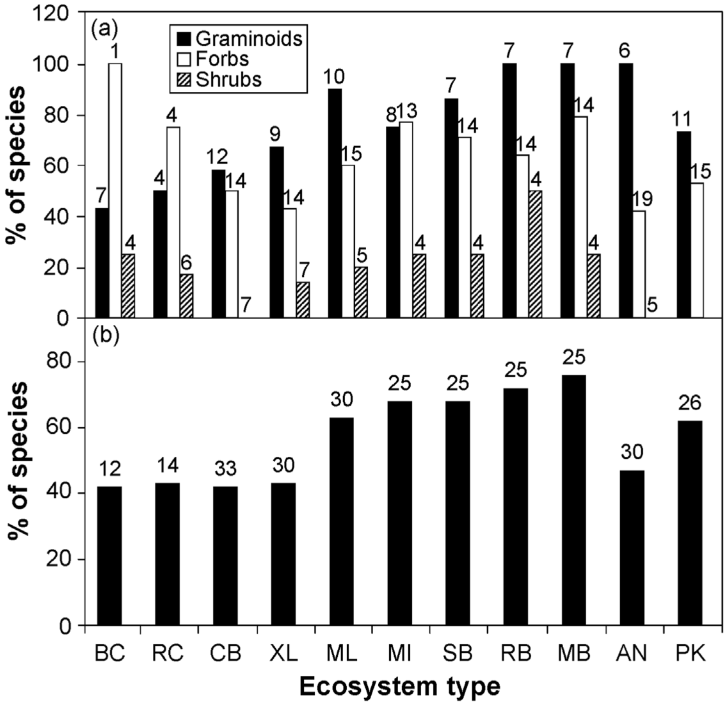

Fig. 3. The percent of species a) by lifeform and b) overall that were recorded as the predominant species in both the terrestrial ecosystem survey (TES) and this study's plot data for 11 ecosystem types of *Pinus ponderosa* forests of northern Arizona, USA. Numbers at the tops of bars are the actual numbers of species that were considered, representing the number of species listed in the TES by ecosystem. Abbreviations for ecosystems and their TES numerical designations are as follows: BC = black cinder (500), RC = red cinder (513), CB = clay basalt (523), XL = xeric limestone (500), ML = mesic limestone (536), MI = mixed igneous (551), SB = submesic benmorite (570), RB = rocky basalt (585), MB = mesic basalt (582), AN = aspen (611), and PK = park (55).

igneous, and mesic limestone ecosystems had the greatest.

A comparison of individual species, representing all species listed in the TES and the corresponding same number of the top species (in terms of relative cover) in this study, is provided in the Appendix. There were some patterns in the variation of individual species. In the graminoid category, for example, this study found a higher relative cover of the C_4 (warm season) *Bouteloua gracilis* than in the TES in all four ecosystems (all dry ecosystems) in which *Bouteloua* was a dominant species. *Elymus elymoides* (C_3, cool season) exhibited a greater relative cover in the TES than this study in all four dry ecosystems, but this trend reversed in the seven moist ecosystems where this study recorded greater relative cover than in the TES. *Festuca arizonica* (C_3) consistently exhibited a greater relative cover in the TES than this study. *Poa fendleriana* (Steud.) Vasey (mutton grass), another C_3 grass, was more dominant in the TES in 8 of the 10 ecosystems where it was recorded. *Muhlenbergia montana*, a C_4 grass, had greater relative cover in 8 of 11 (73%) ecosystems in this study compared to the TES.

Most forb species occupied fewer ecosystems than graminoids, but several of the more common species also exhibited patterns between the TES and this study (Appendix). For instance, *Achillea millefolium* L. (western yarrow) had greater relative cover in the TES than this study in all nine ecosystems in which it was a major species.

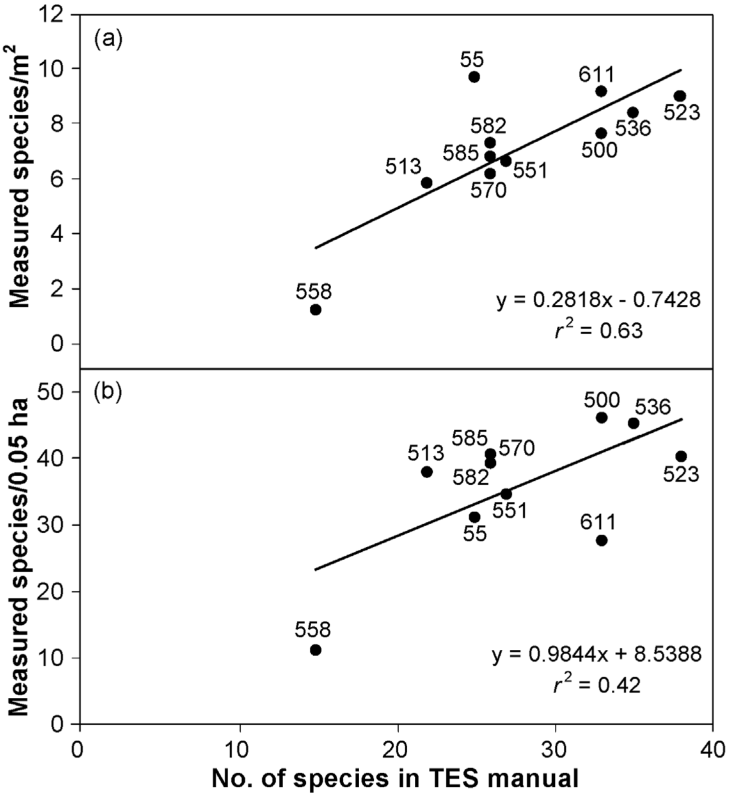

Fig. 4. Relationship between species richness given in the terrestrial ecosystem survey and this study's plot data for 11 ecosystem types of *Pinus ponderosa* forests of northern Arizona, USA.

Lupinus argenteus was more dominant in the clay basalt, xeric limestone, mesic limestone, and rocky basalt ecosystems in the TES than this study, but was notably greater in this study in the aspen ecosystem. The exotic biennial *Verbascum thapsus* L. (common mullein) was dominant in the TES in three ecosystems (black and red cinder and park), but was never among this study's dominants.

Shrubs were less prominent in this study than in the TES, and often a single species such as *Ceanothus fendleri* Gray (Fendler's buckbrush) had 100% or nearly 100% of the relative cover in ecosystems of this study (Appendix). Since more shrubs were reported in the TES, relative cover was better distributed among species in the TES. *Ceanothus fendleri* was consistent, at least on a presence/absence basis, between the TES and this study in five of six ecosystems where it occurred. Except in the limestone ecosystems, *Ericameria nauseosa* (Pallas ex Pursh) Nesom & Baird (rubber rabbitbrush) had higher relative cover in this study than the TES among seven ecosystems in which it occurred. In contrast, except in the xeric limestone where *Mahonia repens* (Lindl.) G. Don (creeping barberry) was a major species in this study but not reported in the TES, *Mahonia* had 20–80% relative cover in six ecosystems in the TES but was not among the prominent species in any of the ecosystems in this study. *Rhus trilobata* and *Ribes cereum* Douglas (wax currant) were consistently more prominent in the TES than this study, as was *Robinia neomexicana* Gray (New Mexico locust) in five of six ecosystems.

The relationship between the number of species listed in the TES and this study's species richness/m^2 was stronger than for richness/0.05 ha (Fig. 4).

This study's plot data reflected that richness relationships among ecosystems changed with spatial scale, whereas the TES did not address scale. In the plot data, aspen and park ecosystems had the highest richness/m^2, but the second and third lowest richness/0.05 ha.

4 Discussion

4.1 Individual Species

While species composition of graminoids (compared to forbs and shrubs) was most similar between the TES and this study, overall composition differed substantially and was driven by differences in individual species including some graminoids. For example, *Festuca arizonica* was more prominent in the TES than in this study, especially in dry ecosystems. This C_3 species is normally associated with sites higher in moisture and nutrients than the dry, nutrient-poor black cinder ecosystem (Abella and Covington 2006) where it had 12% relative cover in the TES. *Festuca arizonica* was absent from all six plots of this ecosystem in this study, and was not noted as present in a previous study on these soils (Hanks et al. 1983). The graminoid species comparisons collectively suggest that with the exception of the C_3 *E. elymoides* exhibiting greater relative cover in moist ecosystems in this study, C_3 graminoids were more prevalent in the TES than this study. Concurrently, C_4 species were generally more prevalent in this study. The greater predominance of C_3 graminoids in the TES also paralleled a greater richness and cover of shrubs in the TES than this study.

In comparing forbs, there were at least two species in the TES that were not detected on any plots in this study and are not documented as part of this region's flora. First, *Arctomecon californica* Torr. & Frém. (Las Vegas bearpoppy) had 2% relative cover in the clay basalt and 31% in the xeric limestone ecosystem in the TES (Appendix). However, *A. californica* is a low-elevation species of non-forested desert ecosystems, endemic to the eastern Mojave Desert more than 200 km west of the study area (Sheldon and Smith 1997). Second, *Erigeron melanocephalus* (A. Nelson) A. Nelson (blackhead fleabane) was listed in the xeric limestone ecosystem but is not reported in Arizona by NRCS (2010).

4.2 Influences on Species Composition

Given that species lists of the TES and this study differed, a question becomes which of the lists, if any, best represent PNV by ecosystem. The estimates of PNV could be influenced by a variety of factors, such as the methods used to estimate PNV and factors including fire, grazing, and others (e.g., N deposition, climate change). Estimates of PNV may be improved by experimentation in contemporary forests and reconstructing historical vegetation.

In comparing the development of PNV estimates between the TES and this study, the TES was constructed in the 1980s and early 1990s (Miller et al. 1995), while data for this study were collected in 2003. Although landscape-level dramatic shifts in species composition over the past 10–20 years have not been reported in the study area, the possibility that species composition has shifted in some ecosystems during this period cannot be dismissed. It is important to note that this analysis focused on species composition and not the absolute cover or biomass of plants, which is considered sensitive to variation in precipitation among years in *Pinus ponderosa* forests (e.g., Laughlin et al. 2006). At least in the short term, species composition can be remarkably similar from year to year in *P. ponderosa* forests in the study area, as was demonstrated by a permanent-plot study where Sørensen similarity averaged 94% between 2003 and 2004 in unmanipulated understory communities (Abella and Covington 2007). Data collection for the present study did follow the unusually dry year of 2002 with only 60% of long-term precipitation (Flagstaff Airport weather station, Western Regional Climate Center, Reno, NV). However, Laughlin et al. (2006) found that biomass was rebounding by 2003, and annual and biennial plants (e.g., *Erigeron divergens* Torr. & Gray [spreading fleabane]), anticipated to be especially sensitive to conditions for germination and establishment, were recorded as major species in the present study (Appendix).

Neither the TES nor this study were designed as exhaustive floristic inventories and instead had the objective of identifying characteristic species by ecosystem. However, some of the species composition differences could be related to scale: the TES is intended to represent the entire population of whole mapping units of an ecosystem, whereas this study's plot data were point samples within mapping units that characterized typical species encountered through sampling. This difference could be especially manifested for patchily distributed species (e.g., shrubs) and in ecosystems (e.g., black cinder) where vegetation was patchily distributed. For instance, four shrub species were listed in the TES for the black cinder ecosystem but only two were recorded in this study (Appendix). *Fallugia paradoxa* (D. Don) Endl. ex Torr. (Apache plume) had 88% relative cover and *Rhus trilobata* 6% in the TES but were not detected on plots in this ecosystem in this study. Christie's (2008) botanical inventory of the Sunset Crater volcanic area containing mapping units of the black cinder soils indicated that *F. paradoxa* was present on these soils but *R. trilobata* was not reported on these soils. On the other hand, there were several instances where this study detected shrubs that the TES did not report within an ecosystem. *Purshia tridentata* (Pursh) DC. (antelope bitterbrush), for example, had 61% relative cover in this study in the xeric limestone ecosystem but was not reported in the TES. Similarly, *Amelanchier utahensis* Koehne (Utah serviceberry) was detected by this study in the red cinder ecosystem but was absent from the TES. There also was at least one instance where a regional plant community study, Hanks et al. (1983), reported a major species in an ecosystem that neither the TES nor this study reported. Hanks et al. (1983) indicated that *Andropogon hallii* Hack. (sand bluestem) was an important graminiod (albeit patchily distributed and thus difficult to detect) of the black cinder ecosystem, consistent with observations during fieldwork for this study although plots did not fall on this species' locations. Combining the species lists of the TES and this study, in conjunction with using the available botanical and plant community inventories that are spatially explicit to at least generalized soil types (e.g., Hanks et al. 1983, Christie 2008), may provide the most comprehensive PNV species list.

The anthropogenic disruption of fire regimes – by excluding surface fires typically occurring at least once every < 10 years since the late 1800s in the study area (Van Horne and Fulé 2006) – adds uncertainty to PNV determinations. Since frequent fire is a natural part of the site environment, it could be argued that possible fire influences should be considered in PNV. However, except for small areas of prescribed fire or wildland fire use, the landscape does not experience frequent surface fire and uncertainty in responses to fire (and in particular ecosystem-specific responses) complicate incorporation of fire influences.

The TES did not specifically address the potential influences of fire and this study sampled the fire-excluded landscape. When surface fire is reintroduced to contemporary ecosystems, considered a different situation than historical re-occurring fire, effects on species composition have been relatively subtle (Abella 2004). Laughlin et al. (2004), for example, found that annual and biennial forbs were positively correlated with burned areas two years after a wildland fire use fire burned a northern Arizona *Pinus ponderosa* forest, but perennial plant composition showed little response to burning. The timing of fires, which primarily occurred in summer historically in the study area (Fulé et al. 1997) but now in fall or spring as prescribed burns, also could influence fire effects. C_3 and C_4 grasses, because of the different seasonal timing of their growth, could be affected differently based on burn timing (Howe 1995). These factors are important considerations for PNV measurement and highlight that multiple PNV types could exist within an ecosystem depending on the presence, absence, and nature of fire.

Grazing is another factor influencing vegetation on this landscape, and by definition, unless soil properties have been severely affected by grazing, PNV should be free from the influences of grazing by non-indigenous animals (Härdtle 1995). Therefore, the ability of this study to reflect PNV partly depends on the range condition class of the plant communities sampled (Clary 1975). Most of the sample sites were in the best range condition class for this region, considered to be the bunchgrass stage (Appendix; Clary 1975). This should not be interpreted to mean that these sites had not been affected in some way by grazing, as the generalized condition classes are not intended to reflect species such as rare forbs or shrubs (Clary 1975). Some sites, especially the treeless basins of the park ecosystems that often contain watering tanks and are areas where livestock congregate, were in lower condition classes such as the sod-forming grass, prostrate perennial forb, and short-lived half-shrub stages of Clary (1975). The study area also was subjected to heavy livestock grazing in the late 1800s and early 1900s (Clary 1975), and grazing at lower livestock densities and by large populations of *Cervus elaphus nelsoni* continues (Huffman and Moore 2003). This subspecies was introduced to the area in the early 1900s when *Cervus elaphus merriami* (Merriam's elk) became extinct (Truett 1996). Huffman and Moore (2003) found that *Cervus* heavily browsed the shrub *Ceanothus fendleri*, further suggesting that shrubs warrant additional attention in future research of PNV. Since grazing exclusion studies address vegetation dynamics in the absence of grazing but potentially after thresholds already had been passed with the formation of alternative stable vegetation types, studies of historical vegetation combined with exclusion studies (Bakker and Moore 2007) may be especially useful for estimating PNV.

Several other factors, such as altered tree structure, exotic species, N deposition, and climate could have influenced vegetation. The spatial pattern of trees affects the fine-scale distribution of understory plants in *Pinus ponderosa* forests (Naumberg and DeWald 1999). Logging of large trees and increases in the density of small-diameter trees have altered tree patterns (Covington et al. 1994). It is less clear, however, if or how these alterations influenced the species composition of mapping units at the landscape scale – the focus of the TES and this study. Exotic species can be part of PNV if the species are naturalized, and there were 10 exotics in the TES and this study's list of predominant species (Appendix). Some of the exotics, such as the perennial grass *Poa pratensis* L. (Kentucky blue grass), have been seeded for revegetation and forage production (Lavin and Springfield 1955). Additional factors, such as N deposition and climate change, need to be accounted for with their possible influences on PNV, which is intended to reflect site capabilities in the climatic conditions at the time of PNV construction.

To improve PNV estimates, experiments could be conducted in contemporary ecosystems to evaluate vegetation development under low tree density and summer frequent-fire regimes typical of the long-term evolutionary environment of the sites and species of this landscape (Covington et al. 1994, Laughlin et al. 2006). Vegetation developed under these regimes conceivably would represent PNV under a natural disturbance regime within contemporary conditions. However, where fire cannot be reintroduced or is not able to occur at the natural season of fire, PNV could be taken to be the mature vegetation that develops in thinned forests. Maintaining the current high-density *Pinus ponderosa* forests is not sustainable as they will eventually be burned by wildfire as has already widely occurred (Covington et al. 1994, Allen et al. 2002). More complex assessments also could help refine PNV, such as propagule-introduction experiments across different ecosystem types to determine plant habitat suitability in changing climates. For example, in the warmer and drier climate projected for the American Southwest (Seager et al. 2007), some species currently occupying a variety of ecosystem types may retract to just the moist ecosystems at this latitude. Climate change is a potentially important but little understood factor in the development of PNV. Given due consideration to climate change, efforts to reconstruct historical vegetation are also valuable for providing a baseline PNV against which future changes in PNV can be evaluated.

4.3 Historical Vegetation

Information on historical understory vegetation is limited, but some studies do permit comparisons with the TES and this study. Historical documents such as Vasey (1888), Britton (1889), and Rusby (1889) provided lists of species encountered within the study area, near the beginning of the fire exclusion period. These documents provide evidence that, at least on a presence basis, some of the species of the TES and this study were present historically. Kerns et al. (2001) reconstructed past vegetation, which could represent older vegetation (even of different climatic periods) than the settlement period of the late 1800s, at one site of the mesic basalt ecosystem using phytolith and carbon isotope analysis. Phytoliths are useful for detecting species that form them, and isotope analysis can help differentiate the relative abundance of C_3 versus C_4 species. Kerns et al. (2001) concluded that C_4 grasses were more widely distributed but less abundant at the site, and that species in the C_3 genera *Bromus* and *Koeleria* were more common. The TES and this study found that *Bromus* species were sparse across ecosystems, with the exception that *Bromus ciliatus* L. (fringed brome) had 44% relative cover in aspen ecosystems of the TES and was detected by this study in that ecosystem (Appendix). *Koeleria macrantha* (Ledeb.) J.A. Schultes (Junegrass) was important in the TES and among the top species in four ecosystems of the present study. Further research could attempt to more extensively estimate historical species composition, by ecosystem type, which could help understand how flora evolved with fire and prior to intensive anthropogenic land use.

5 Conclusion

This study supports several ideas for developing reliable estimates of ecosystem-specific plant community data in a forest site classification framework. First, the TES was useful for identifying species-poor and species-rich ecosystems, although the effects of spatial scale on species richness need to be addressed. Second, the data highlighted modifications that could be considered for the TES PNV species list. In particular, species not part of the regional species pool should be removed from the TES (at least *Arctomecon californica* and probably *Erigeron melanocephalus*). The data also suggest that some species could be added to species lists of some ecosystems, such as including a greater variety of forbs for the black cinder ecosystem. Third, including more detailed information in TES publications about how PNV estimates were formulated would be helpful. Since online resources are now more fully developed than when the TES was published, databases with spatially explicit vegetation plot data could be made available with the TES. Fourth, species composition of the TES and this study differed, but the data sets could be viewed as complementary that represent hypotheses about PNV. By definition, PNV is dynamic as site or atmospheric conditions change (Küchler 1964), so current hypothesized PNV could be tested with changing environments and updated. Fifth, hypothesized PNV can be further evaluated by more extensive field sampling, additional studies of historical vegetation (e.g., Kerns et al. 2001), and experiments in contemporary forests. For example, prescribed fire could be applied to multiple ecosystem units and ecosystem-specific compositional changes evaluated. Sixth, multiple types of plant community information may be useful, including historical vegetation prior to extensive anthropogenic disruption of ecosystems, PNV with and without a frequent-fire regime, and current actual vegetation. These data can further enhance the value of forest site classification and have many potential applications such as in monitoring forest conditions and treatment effects in reference to baseline conditions, understanding vegetation-environment relationships for mapping resources, and formulating ecosystem-specific management prescriptions.

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Appendix. Relative cover (%, summing to 100% for all species within lifeforms of an ecosystem type) of species in the terrestrial ecosystem survey (TES) and the present study (PS) for 11 ecosystem types of *Pinus ponderosa* forests of northern Arizona, USA. The same number of species in each lifeform as was provided in the TES are provided for the PS, so absences (denoted by –) indicate that a species did not occur in the ecosystem type or was not among the top species (in terms of relative cover) in the PS. Exotic species following NRCS (2010) are signified with asterisks. Abbreviations for ecosystems and their TES numerical designations are as follows: BC = black cinder (500), RC = red cinder (513), CB = clay basalt (523), XL = xeric limestone (500), ML = mesic limestone (536), MI = mixed igneous (551), SB = submesic benmorite (570), RB = rocky basalt (585), MB = mesic basalt (582), AN = aspen (611), and PK = park (55).

	558: BC		513: RC		523: CB		500: XL		536: ML		551: MI		570: SB		585: RB		582: MB		611: AN		55: PK	
	TES	PS	TES	PS	TES	PS	TES	PS	TES	PS	TES	PS	TES	PS	TES	PS	TES	PS	TES	PS	TES	PS
Graminoids																						
Aristida arizonica	–	0.1	–	6.8	–	–	–	–	–	0.9	–	–	–	–	–	–	–	–	–	–	–	–
Aristida purpurea	–	–	–	–	–	0.1	–	2.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Blepharoneuron tricholepis	24.4	–	–	–	0.8	0.0	0.9	–	3.4	2.5	2.3	–	8.7	2.4	8.7	6.2	8.7	1.8	–	–	0.1	–
Bothriochloa barbinodis	12.2	–	33.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bouteloua curtipendula	–	–	–	–	0.8	–	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bouteloua gracilis	2.4	81.8	33.3	41.6	42.2	76.6	44.2	60.4	–	4.7	–	0.6	–	–	–	–	–	–	–	–	1.4	7.4
Bouteloua simplex	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.1
Bromus anomalus	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–
Bromus ciliatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	44.4	2.8	–	–
*Bromus japonicus**	–	–	–	–	–	0.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*Bromus tectorum**	–	–	–	–	–	0.5	–	0.5	–	–	–	–	–	0.9	–	–	–	–	–	–	–	–
Carex geophila	–	–	–	–	–	0.0	–	–	–	2.6	–	9.2	–	7.3	–	15.9	–	20.0	–	7.5	–	2.3
Carex occidentalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4
Elymus elymoides	12.2	3.8	16.7	10.3	8.4	5.0	8.8	5.9	1.7	14.3	4.6	6.7	4.3	11.2	4.3	13.2	4.3	19.0	4.4	12.0	0.1	2.6
Elymus trachycaulus	–	–	–	–	0.1	–	–	0.4	–	0.8	–	–	–	–	–	–	–	–	–	–	0.1	–
Festuca arizonica	12.2	–	–	–	8.4	–	8.8	5.6	33.8	26.6	46.4	27.7	43.3	18.5	43.3	15.9	43.3	29.6	44.4	39.7	28.1	–
Hordeum jubatum	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Koeleria macrantha	–	–	16.7	–	8.4	0.5	0.4	0.7	33.8	–	4.6	–	8.7	–	8.7	–	8.7	0.2	2.2	–	–	2.2
Lycurus phleoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–
Monroa squarrosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1
Muhlenbergia minutissima	–	7.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2
Muhlenbergia montana	24.4	6.9	–	35.7	4.2	0.7	8.8	21.1	10.1	29.6	23.2	51.8	8.7	47.0	8.7	29.8	8.7	12.4	2.2	5.8	14.0	–
Muhlenbergia rigens	–	–	–	–	–	–	–	–	–	1.2	–	–	–	–	–	–	–	–	–	–	–	–
Muhlenbergia wrightii	–	–	–	–	0.4	5.7	–	–	0.2	–	–	1.0	–	–	–	–	–	–	–	–	7.0	60.0
Pascopyrum smithii	–	–	–	–	–	8.5	–	–	–	0.6	–	–	–	–	–	–	–	–	–	–	0.1	6.2
*Poa compressa**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.3
Poa fendleriana	–	–	–	5.6	25.3	2.2	26.5	2.8	10.1	5.2	13.9	1.9	26.0	10.8	26.0	7.9	26.0	15.2	–	5.8	7.0	–
*Poa pratensis**	–	–	–	–	0.4	–	0.4	–	0.2	11.0	0.2	0.8	0.4	–	0.4	3.8	0.4	–	2.2	26.4	42.1	12.2

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Schedonnardus paniculatus	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Schizachyrium scoparium	12.2	–	–	–	–	–	–	–	3.4	–	4.6	–	–	–	–	–	–	–	–	–	–	–
Sporobolus interruptus	–	–	–	–	0.4	–	–	–	3.4	–	–	–	–	1.9	–	7.4	–	1.8	–	–	–	–
Vulpia octoflora	–	–	–	–	–	–	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Forbs																						
Achillea millefolium	–	–	–	–	2.4	–	15.3	–	37.6	12.7	50.2	–	49.9	10.4	49.9	–	49.9	4.6	14.7	3.8	12.2	4.0
Agoseris glauca	–	–	–	–	–	–	–	–	–	–	–	2.4	–	–	–	–	–	–	–	–	–	–
Allium geyeri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	12.2	–
Antennaria marginata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.6	–	–	–	–
Antennaria parvifolia	–	–	–	–	–	–	–	–	–	5.0	–	2.2	–	2.6	–	17.0	–	–	–	1.4	–	–
Antennaria rosulata	–	–	–	–	24.3	0.7	0.8	–	6.3	8.2	5.0	3.6	5.0	–	5.0	–	5.0	–	3.7	–	2.4	7.3
Aquilegia canadensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.7	–	–	–
Arabis fendleri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.7
Arctomecon californica	–	–	–	–	2.4	–	30.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Arenaria fendleri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.0
Argentina anserina	–	–	–	–	–	–	–	–	0.1	–	0.5	–	0.5	–	0.5	–	0.5	–	–	–	2.4	–
Artemisia carruthii	–	–	–	–	–	1.3	–	–	–	3.5	–	2.2	–	2.7	–	6.4	–	2.7	–	1.1	–	0.8
Artemisia dracunculus	–	–	–	17.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Artemisia frigida	–	–	–	–	2.4	–	0.8	–	0.6	–	0.5	–	0.5	–	0.5	–	0.5	–	7.4	–	2.4	–
Artemisia ludoviciana	–	–	25.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.2	–
Asclepias subverticillata	–	–	–	–	–	1.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Astragalus humistratus	–	–	–	–	–	–	–	–	–	–	–	–	–	2.6	–	–	–	2.7	–	0.5	–	–
Bahia dissecta	–	–	–	42.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Calochortus nuttallii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–
Campanula rotundifolia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–
Castilleja occidentalis	–	–	–	–	–	–	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetopappa ericoides	–	–	–	–	–	–	–	6.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chamaesyce serpyllifolia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.5
Chenopodium graveolens	–	78.6	–	4.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cirsium wheeleri	–	–	–	–	–	–	–	–	–	13.4	–	6.8	–	13.8	–	9.8	–	8.6	–	0.4	–	–
Comandra umbellata	–	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Convolvulus arvensis	–	–	–	–	–	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coreopsis tinctoria	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.9
Cryptantha cinerea	–	–	–	–	–	–	–	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–
Cryptantha setosissima	–	–	–	3.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eriogonum alatum	–	–	–	–	–	–	–	3.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–

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Erigeron colomexicanus	–	–	–	4.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Erigeron divergens	–	–	–	–	–	39.9	–	5.7	–	4.5	–	–	–	3.6	–	5.4	–	17.8	–	–	–	47.6
Erigeron flagellaris	–	–	–	–	–	–	0.8	–	–	–	–	–	–	–	–	–	–	–	–	2.5	–	2.6
Erigeron formosissimus	–	–	–	–	–	–	–	–	–	9.4	–	–	–	5.1	–	8.7	–	–	–	4.9	–	–
Eriogonum jamesii	–	–	–	–	2.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Erigeron melanocephalus	–	–	–	–	–	–	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eriogonum racemosum	–	–	–	–	2.4	7.7	–	12.2	0.6	–	0.5	–	0.5	–	0.5	–	0.5	–	–	–	2.4	–
Erigeron speciosus	–	–	–	–	2.4	–	0.8	–	0.6	–	0.5	–	0.5	–	0.5	–	0.5	–	–	–	1.2	–
Fragaria vesca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.7	–	–	–
Fragaria virginiana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–
Gaura coccinea	–	–	–	5.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Geranium caespitosum	–	–	25.0	–	–	–	–	–	0.6	2.5	0.5	–	0.5	–	0.5	–	0.5	–	1.8	–	1.2	–
Geranium richardsonii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.8	–	–	–
Gutierrezia sarothrae	–	–	25.0	4.7	2.4	10.9	0.8	6.3	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–
Helianthus annuus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–
Heliomeris longifolia	–	–	–	–	–	15.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Heliomeris multiflora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.2	–	0.2	–	–
Heterotheca villosa	–	–	–	–	–	–	–	–	–	1.9	–	–	–	–	–	–	–	–	–	–	–	–
Hieracium fendleri	–	–	–	–	–	–	–	–	–	–	–	–	–	3.6	–	–	–	–	–	–	–	–
Hymenopappus filifolius	–	–	–	–	–	–	–	5.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hymenoxys hoopesii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.4	–	–	–
Hymenoxys richardsonii	–	–	–	–	2.4	4.4	0.8	12.6	–	–	–	1.7	–	–	–	–	–	–	–	–	–	–
Iris missouriensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12.2	4.9
Lathyrus lanszwertii	–	–	–	–	–	–	–	–	0.6	–	0.5	–	0.5	–	0.5	–	0.5	–	18.4	17.2	–	–
Lepidium densiflorum	–	–	–	–	–	0.9	–	–	–	2.2	–	–	–	–	–	–	–	–	–	–	–	–
Linum australe	–	–	–	–	–	–	–	6.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lotus wrightii	–	–	–	–	2.4	–	0.8	3.3	0.6	–	0.5	1.8	0.5	3.0	0.5	–	0.5	–	–	–	–	–
Lupinus argenteus	–	–	–	–	48.5	–	45.8	–	50.1	8.8	40.2	44.3	39.9	28.2	39.9	6.1	39.9	31.9	3.7	44.9	12.2	–
Lupinus kingii	–	–	–	6.8	–	0.7	–	5.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Maianthemum stellatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.7	–	–	–
Mertensia ciliata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.7	–	–	–
Nama dichotomum	–	10.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oenothera flava	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.7
Oenothera pubescens	–	–	–	–	–	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–	–	–
Oxytropis lambertii	–	–	–	–	2.4	–	–	–	–	–	–	8.6	–	–	–	–	–	4.9	–	–	1.2	–
Packera multilobata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.4	–	3.3	–	–	–	–

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Pedicularis centranthera	–	–	–	–	–	–	–	2.3	–	–	–	–	–	6.9	–	–	–	–	–	–	–	–
Penstemon barbatus	–	–	–	–	–	–	–	3.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Penstemon linarioides	–	–	–	–	2.4	1.7	–	6.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Penstemon virgatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.9	–	–	–	–	–	–
Phacelia sericea	–	11.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phlox gracilis	–	–	–	–	–	–	–	11.3	–	2.6	–	–	–	–	–	–	–	–	–	–	–	–
Phlox speciosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6.4	–	3.2	–	–	–	–
Plantago argyraea	–	–	–	–	–	–	–	9.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*Polygonum aviculare**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.5
Polygonum douglasii	–	–	–	–	–	1.1	–	–	–	2.1	–	–	–	–	–	–	–	4.4	–	–	–	1.2
Potentilla crinita	–	–	–	–	–	–	–	–	–	–	–	–	–	2.5	–	3.9	–	–	–	–	–	–
Potentilla hippiana	–	–	–	–	–	–	–	–	–	–	–	11.7	–	–	–	–	–	–	–	–	–	–
Potentilla subviscosa	–	–	–	–	–	–	–	–	–	–	–	2.0	–	9.6	–	–	–	2.8	–	–	–	–
Pseudostellaria jamesiana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.6	–	–
Pseudocymopterus montanus	–	–	–	–	–	–	–	–	–	3.2	–	–	–	–	–	–	–	–	–	1.1	–	–
Psoralidium lanceolatum	–	–	–	6.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pterospora andromedea	–	–	–	–	0.5	–	0.8	–	0.6	–	0.5	–	0.5	–	0.5	–	0.5	–	–	–	–	–
Pteridium aquilinum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.4	–	–	–
Senecio actinella	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14.0	–	–	–	–	–	–
*Sisymbrium altissimum**	–	–	–	–	–	9.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Solidago velutina	–	–	–	–	–	–	–	–	–	5.4	–	8.9	–	–	–	–	–	–	–	–	–	–
Symphyotrichum ascendens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.4
Symphyotrichum falcatum	–	–	–	4.5	–	–	–	–	–	–	–	–	–	5.4	–	4.1	–	–	–	–	–	–
*Taraxacum laevigatum**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.7	–	–
*Taraxacum officinale**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9.5	24.3	–
Thalictrum fendleri	–	–	–	–	–	–	–	–	0.1	–	0.1	–	0.1	–	0.1	–	0.1	–	11.0	0.3	–	–
*Tragopogon dubius**	–	–	–	–	–	1.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Trifolium longipes	–	–	–	–	–	–	–	–	–	9.3	–	–	–	–	–	–	–	–	–	0.8	–	–
*Verbascum thapsus**	100	–	25.0	–	–	–	0.8	–	0.6	–	–	–	1.0	–	1.0	–	0.1	–	–	–	12.2	–
Vicia americana	–	–	–	–	–	–	–	–	0.1	3.4	0.5	2.1	0.1	–	0.1	7.9	1.0	5.2	3.7	9.9	–	–
Viola canadensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.7	–	–	–

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Shrubs																						
Amelanchier utahensis	–	–	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Artemisia frigida	–	–	–	–	–	3.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Brickellia californica	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ceanothus fendleri	–	–	–	–	3.7	–	–	–	20.0	100	25.0	98.9	25.0	28.4	25.0	14.4	25.0	100	–	–	–	–
Cercocarpus montanus	–	–	–	–	3.7	–	4.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cylindropuntia whipplei	–	–	–	–	18.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ericameria nauseosa	5.9	99.3	19.9	98.1	–	96.8	79.9	2.1	20.0	–	–	1.1	–	70.9	–	–	–	–	–	–	–	–
Escobaria vivipara	–	–	–	–	–	0.1	–	13.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Fallugia paradoxa	88.0	–	66.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mahonia fremontii	–	–	–	–	18.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mahonia repens	–	–	–	–	–	–	–	16.9	20.0	–	25.0	–	25.0	–	25.0	–	25.0	–	80.0	–	–	–
Opuntia engelmannii	–	–	–	–	18.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Opuntia fragilis	–	–	–	–	–	–	–	6.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Opuntia macrorhiza	–	–	–	–	–	–	4.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Opuntia polyacantha	–	–	–	–	18.5	–	4.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Paxistima myrsinites	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8.0	–	–	–
Purshia stansburiana	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Purshia tridentata	–	0.6	–	–	–	–	–	60.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhus trilobata	5.9	–	13.3	1.3	18.5	–	4.0	–	20.0	–	–	–	–	–	–	–	–	–	–	–	–	–
Ribes cereum	0.3	–	–	–	–	–	4.0	–	–	–	25.0	–	25.0	–	25.0	–	25.0	–	4.0	–	–	–
Robinia neomexicana	–	–	–	–	–	–	–	–	20.0	–	25.0	–	25.0	–	25.0	77.3	25.0	–	4.0	–	–	–
Rosa woodsii	–	–	–	–	–	–	–	–	–	–	–	–	–	0.7	–	8.3	–	–	–	–	–	–
Symphoricarpos oreophilus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.0	–	–	–
Yucca elata	–	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–