



# Relationships of exotic plant communities with native vegetation, environmental factors, disturbance, and landscape ecosystems of *Pinus ponderosa* forests, USA

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## ABSTRACT

Invasions by exotic plant species can threaten forest ecosystems in numerous ways. Theories on relationships of exotic species invasions with native vegetation, resource availability, and disturbance could assist in managing exotic plants by identifying parts of the landscape and ecological conditions most susceptible to invasion. However, generality of these theories is complicated by considerable variation among landscapes and ecology of individual species. We assessed hypotheses on relationships of exotic plant communities with native vegetation, environmental (soil, topographic, and climate), and disturbance (roads and grazing) variables using data from 66 plots within a 110,000-ha *Pinus ponderosa* forest landscape in northern Arizona, USA. We further assessed exotic plant relationships with ecosystem classification, which has a long history of use in forest ecology and management but has been underutilized for understanding exotic species distributions. Plots contained a total of 251 native and 20 exotic plant species. As hypothesized for distributional studies, native and exotic species were positively correlated, but the correlation varied with scale for species richness ( $m^2$ ,  $r = 0.65$ ;  $500 m^2$ ,  $r = 0.41$ ) and was weaker for cover ( $r = 0.32$ ). Multiple regression, including native vegetation and environmental variables, accounted for similar amounts of variation in exotic species richness (50% of variation) and cover (51%). Disturbance variables only entered regression models when native vegetation was excluded from models. Exotic species richness  $m^{-2}$ , cover, and community composition were strongly related to the ecosystem classification. For example, mean exotic cover ranged from <0.1% in ecosystems with volcanic cinder soils to 7% in ecosystems containing *Populus tremuloides*. As hypothesized, moist ecosystems were generally most invaded. However, also considering factors such as past management of the ecosystems and literature on the introduction histories (e.g., intentional seeding for range improvement) of the species, we hypothesize that the ecosystem classification integrated co-varying environmental, disturbance, and management variables related to exotic plant communities. Ecosystem classification was a useful framework for understanding distributions of exotic plant communities across the landscape.

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## 1. Introduction

Exotic plant species can impact human–environment forested systems in numerous ways, such as by replacing high-quality native forage on rangelands, ‘engineering’ novel fire regimes through fuel production, reducing indigenous biodiversity, and interfering with tree regeneration (Chornesky et al., 2005). Recognizing the threat that exotic species pose to indigenous ecosystems, many countries have created legal mandates for managing exotic species. In 1999, for example, Executive Order 13112 by the U.S. government established the National Invasive Species

Council which seeks to promote management strategies for exotic species on U.S. federal lands (Clinton, 1999). As a participating agency, the U.S. Forest Service (2004) issued guidelines for managing exotic species on its lands. These guidelines emphasized prevention (limiting invasions from occurring), early detection of new infestations, strategically managing priority exotic species and parts of the landscape, and restoration to strengthen indigenous ecosystems. Knowledge of the relationships of exotics with indigenous vegetation and disturbance, and the distribution and abundance of exotics across landscapes, is fundamental to meeting these guidelines. Ecological theories provide some general expectations regarding these relationships and distributions, but in order to make management decisions, further work is needed to understand reliability of these theories and to relate exotic species

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distributions to spatial maps (e.g., ecosystem classification) available for some forestlands. Some of the key general principles related to exotic species distributions advanced by invasion ecology are that native and exotic species richness are positively correlated at the landscape scale and invasibility increases when moisture, nutrients, or disturbance increase.

A general postulate from landscape sampling studies is that native plant species richness and cover are positively correlated with exotic richness and cover, suggesting that environments favorable for native species also are favorable for exotic species (Stohlgren et al., 1999; Gilbert and Lechowicz, 2005; Fornwalt et al., 2010). These favorable environments often are nutrient-rich and productive. However, some studies have not reported positive correlations between native and exotic species (e.g., Vilà et al., 2007; Hejda et al., 2009) or have found that for richness, results vary with spatial scale (e.g., Keeley et al., 2003). Moreover, a competing theory predicts that moist, nutrient-rich sites with high productivity would have lower species richness because a few dominant species usurp the resources and competitively exclude other species (Levine et al., 2004). This could reduce an ecosystem's invasibility by exotic species.

Invasibility is considered related to resource availability and disturbance, but the relative strength of relationships of environmental variables and disturbance with exotic species is not fully understood and can vary among landscapes and exotic species (Lockwood et al., 2009; Mortensen et al., 2009). The intermediate disturbance hypothesis predicts that total species richness peaks at intermediate levels of disturbance (Huston, 1979). Specifically for exotic species, however, high disturbance levels may promote high richness and abundance of exotic species through a variety of mechanisms, including disturbance effects on native vegetation (Eschtruth and Battles, 2009). Similar to environmental variables, the importance of disturbance variables to species invasions appears to vary among landscapes and species (Fowler et al., 2008; Eschtruth and Battles, 2009; Fornwalt et al., 2010). This variation complicates efforts to develop general theories and practical strategies for exotic species mapping and management, underscoring a use for multifactor studies that examine several factors potentially related to landscape-scale distributions of exotic species communities. Data sets including native and exotic plant community composition, disturbance variables, and environmental variables (with soil properties) at the landscape scale are rare but necessary for evaluating reliability of predictions regarding exotic species community distributions (Bashkin et al., 2003; Keeley et al., 2003; Gilbert and Lechowicz, 2005).

Ecosystem classification could be a valuable tool for integrating often co-varying factors such as environment and disturbance that affect exotic species distributions across landscapes, but its potential has been little explored for this purpose. Also known as ecological land classification, forest site classification, and other designations, ecosystem classification is based on the concept of ecosystems as volumetric units that include the atmosphere, topography, vegetation, and soil (Barnes et al., 1982; Dolan and Parker, 2005). The landscape is viewed as a mosaic of polygons representing different ecosystems that can be conceived at different resolutions by combining or dividing (e.g., moist versus dry ecosystems) ecosystems at different hierarchical levels (Palik et al., 2000). Ecosystem classification could be useful for understanding exotic species invasions across landscapes by integrating environmental factors and some disturbance regimes, if they are ecosystem-specific, potentially linked to exotic species distributions. If exotic species abundance and composition differ among ecosystems, ecosystem classification could also facilitate development of ecosystem-specific management strategies.

The objectives of this study were to: (1) assess relationships between native and exotic species richness and cover; (2) evaluate

relationships of environmental, disturbance, and native vegetation variables with exotic plant community distributions across the landscape; and (3) compare exotic species richness, cover, and composition among landscape ecosystems. We anticipated that: (1) native and exotic richness would be positively correlated at multiple spatial scales and native and exotic cover also would be positively correlated; (2) native vegetation, environmental, and disturbance variables would account for equal proportions of the variance in distribution of exotic species communities; and (3) distribution of exotic species communities would correspond to the distribution of ecosystems across the landscape, with moist, nutrient-rich ecosystems being the most heavily invaded.

## 2. Methods

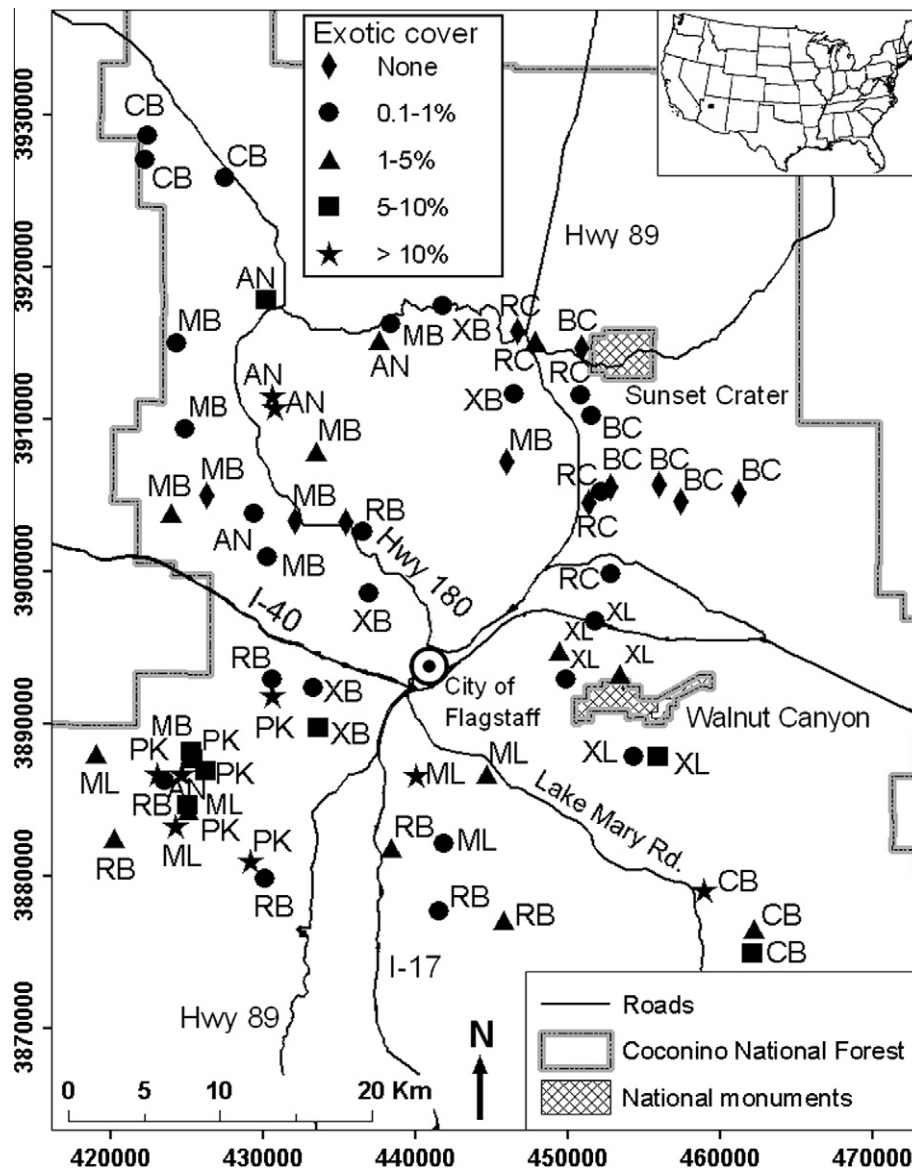
### 2.1. Study area

We conducted this study within a 110,000-ha *Pinus ponderosa* forest landscape within the Coconino National Forest and Northern Arizona University School of Forestry Centennial Forest in northern Arizona, USA (Fig. 1). Topography is primarily flat to undulating, dissected by canyons, limestone ridges, and volcanic landforms such as cinder cones. Six fire-history studies within the study area have reported fire frequencies of 2–5 years in the centuries preceding 1880 (Van Horne and Fulé, 2006). Following approximately 1880, Euro-American settlement introduced new land-use practices including livestock grazing (cattle and sheep), timber harvest, and fire exclusion. Based on a study reconstructing historical tree density at 53 sites, the 1880 density of ponderosa pine trees varied across the landscape, ranging from treeless basins several hectares in size (locally termed 'parks') and low-density (<10 trees ha<sup>-1</sup>) sites (e.g., due to high clay content likely limiting regeneration), to a site containing 183 trees ha<sup>-1</sup> (Abella and Denton, 2009). With few exceptions, such as in some parks, density of ponderosa pine trees has increased by orders of magnitude since 1880 (Bakker and Moore, 2007). The landscape was generally historically dominated by graminoids and remains so today, although herbaceous vegetation has declined overall in many areas concomitant with the increase in tree density (Covington et al., 1994). Cattle and sheep are still grazed, but at lower stocking levels than near the turn of the 20th century and grazing intensity is spatially variable (Bakker and Moore, 2007).

The study area is covered by a terrestrial ecosystem survey, the U.S. Forest Service's ecosystem classification and mapping program for national forests in Arizona and New Mexico (U.S. Forest Service, 1986). The Forest Service mapped ecosystems with a 16-ha minimum mapping unit (U.S. Forest Service, 1986; Miller et al., 1995). In our study, we included 11 terrestrial ecosystem types predominant in the study area and encompassing a range of climatic regimes and soil parent materials. Ecosystems spanned four soil orders, with major soil great groups including Ustochrepts and Ustorthents on drier sites and Eutroboralfs and Argiborolls on moister sites (Miller et al., 1995). Based on similarity in environmental and vegetation factors determined in a previous study (Abella and Covington, 2006a), we grouped plots on basalt soils from four to three ecosystems for analysis to result in 10 total ecosystems. Ecosystems ranged from xeric, nutrient-poor, black cinder ecosystems containing little understory vegetation, to moist basalt ecosystems with silt loam soils and productive understories (Table 1).

### 2.2. Data collection

Using a geographic information system (GIS), we randomly selected 6–7 mapping units of each of the terrestrial ecosystem types for sampling and generated a random point to establish a



**Fig. 1.** Locations of 66 sample plots for evaluating exotic plant communities in *Pinus ponderosa* forests of a northern Arizona landscape, USA. Plots are symbolized according to exotic plant cover. The two-letter codes represent ecosystem types: AN = aspen, BC = black cinder, CB = clay basalt, MB = mesic basalt, ML = mesic limestone, PK = park, RB = rocky basalt, RC = red cinder, XB = xeric basalt, and XL = xeric limestone. Coordinates are Universal Transverse Mercator (m), North American Datum 1927.

plot in each mapping unit. The slight variation in the number of mapping units among ecosystems resulted from rejecting units for sampling if they had been burned by wildfire and did not contain forest cover. Excepting park and aspen ecosystems that had either continuous open (park) or forest (aspen) cover, we established the plot in the nearest opening to the random point in each unit. Openings were usually located near groups of old trees (establishing prior to 1880), were ca. 0.1–1 ha in size, and were readily identifiable in the field (Larson and Churchill, 2012). We sampled openings because they contain understory vegetation, as opposed to dense post-settlement tree patches where understory vegetation is minimal or absent (Covington et al., 1994). Moreover, in a previous study we found that the probability of detecting exotic species was lowest when sampling in densely treed patches, which usually contain no exotic plants (Abella and Covington, 2006a). In May–August 2003, we measured a total of 66 plots that were sampled in a temporal sequence of alternating plots by ecosystem so there was no temporal bias to sampling. Plots were 20 × 25 m (0.05 ha) and contained 15, 1-m<sup>2</sup> subplots centered at

0.5, 5, 12.5, 20, and 24.5 m along the bottom, middle, and top 25-m sides. The areal percent cover of each vascular plant species rooted in each subplot was visually categorized as 0.1%, 0.25%, or 0.5%, 1% intervals from 1–10% cover, and 5% intervals from 10–100%. Measurement error, based on remeasuring two randomly selected subplots every six plots and calculating the difference between original and repeated measures, averaged <0.25% for total cover and <0.25 species m<sup>-2</sup>. We also surveyed the whole 0.05-ha plot for species not already detected in subplots and assigned these species a cover of 0.0067% (0.1%/15 subplots). We named species, categorized their lifeform (graminoid, forb, or shrub), and assigned native/exotic status (in North America) following NRCS (2011).

In addition to plant community composition, we recorded and derived a suite of environmental and disturbance variables on each plot. From the center of plots, we recorded slope gradient (in %, using a clinometer), aspect (transformed following Beers et al. (1966)), elevation, and geographic location (in Universal Transverse Mercator [UTM] coordinates, using a global positioning

**Table 1**  
Features of 10 ecosystem types sampled by this study in *Pinus ponderosa* forests of northern Arizona, USA.

Ecosystem <sup>a</sup>	PP (cm yr <sup>-1</sup> ) <sup>b</sup>	Texture <sup>c</sup>	SI <sup>d</sup>	SPP <sup>e</sup>	Description
Black cinder	45 ± 1	Sand	15	PS, ND	Dry, gravelly, N-poor volcanic cinders; low plant cover
Red cinder	46 ± 1	Sandy loam	15	BD, MM	Dry, gravelly, volcanic cinders; moderate plant cover
Clay basalt	55 ± 2	Clay loam	17	GS, BG	Clayey soils; drier climate than other basalt types
Xeric limestone	50 ± 1	Sandy loam	17	BG, HF	More neutral pH and climatically dry than mesic limestone
Mesic limestone	64 ± 4	Sandy loam	21	FA, MM	Climatically moister and lower pH (6.1) than xeric limestone
Xeric basalt	57 ± 4	Loam	21	MM, MC	Least N of basalt ecosystems; drier sites
Rocky basalt	67 ± 6	Loam	18	SI, PC	Rocky sites with low plant cover; clay loam subsoils
Mesic basalt	59 ± 4	Silt loam	23	FA, CG	High water-holding capacity soils; bunchgrasses dominate
Aspen	66 ± 8	Loam	21	LL, LA	Deep soils high in N; <i>Populus tremuloides</i> overstory
Park	65 ± 2	Clay loam	–	SA, AG	Treeless basins; deep soils; concentrated grazing

<sup>a</sup> Forest service terrestrial ecosystem survey identification numbers (Miller et al., 1995) for the ecosystems are as follows: black cinder = 558, red cinder = 513, clay basalt = 523, xeric limestone = 500, mesic limestone = 536, xeric basalt = 570 and 551, rocky basalt = 585, 570, and 582, mesic basalt = 582, 551, 570, and 585, aspen = 611, and park = 55.

<sup>b</sup> Precipitation is derived from PRISM (Daly et al., 2008) and is mean ± SD based on site averages.

<sup>c</sup> Soil properties are for the 0–15 cm layer from Abella and Covington (2006a).

<sup>d</sup> Site index (m, base age 100 yr) from Miller et al. (1995).

<sup>e</sup> Characteristic understory native species from Abella and Covington (2006b): PS = *Phacelia sericea*, ND = *Nama dichotomum*, BD = *Bahia dissecta*, MM = *Muhlenbergia montana*, GS = *Gutierrezia sarothrae*, BG = *Bouteloua gracilis*, HF = *Hymenopappus filifolius*, FA = *Festuca arizonica*, MC = *Machaeranthera canescens*, SI = *Sporobolus interruptus*, PC = *Pedicularis centranthera*, CG = *Carex geophila*, LL = *Lathyrus lanszwertii*, LA = *Lupinus argenteus*, SA = *Symphyotrichum ascendens*, and AG = *Allium geyeri*. Native species richness and cover by ecosystem are provided in Fig. 3.

system). At the southwestern and northeastern corners of plots, we collected a 0–15 cm sample of the mineral soil from soil pits. We analyzed the <2-mm fraction of samples for texture (hydrometer method), pH (1:2 soil:CaCl<sub>2</sub>), organic C and total N (C/N analyzer), and CaCO<sub>3</sub> equivalent (gravimetric method) following Sparks (1996) and Dane and Topp (2002). We converted nutrient concentrations to contents based on bulk density averaged from two, 280-cm<sup>3</sup> soil cores with coarse fragment (>2 mm) volume included. We obtained average annual precipitation and temperature (using average minimum or maximum temperature returned results similar to average annual) for each plot using PRISM climate data (Daly et al., 2008). We obtained several indicators of disturbance on plots including a grazing intensity variable (three categories of low, medium, and high) from Laughlin and Abella (2007), distance in km to the nearest source of water (usually to livestock tanks which can concentrate animal use and disturbance), and distance in km to the nearest road (based on mapped roads) from georeferenced layers supplied by the U.S. Forest Service (Coconino National Forest, Flagstaff, Arizona).

### 2.3. Data analysis

We calculated frequency (% of the 66 plots occupied) for each species and its average percent cover (based on the mean of 15 subplots plot<sup>-1</sup>) and relative percent cover. Relative percent cover was calculated using the midpoints of cover classes for each species on each plot as: (cover of species/∑ cover of all species) × 100. For each plot, we calculated the mean number of species (richness) m<sup>-2</sup> and the total number of species.

We assessed exotic species richness and cover relationships with habitat variables using several techniques. We examined relationships between native and exotic richness at the two scales (m<sup>2</sup> and 500 m<sup>2</sup>) and between native and exotic cover using best-fit regressions that maximized coefficients of determination. To assess multivariate relationships for exotic species richness and cover, we used multiple regression with all potential environmental, disturbance, and native vegetation variables input as candidate variables and with native vegetation variables excluded to isolate influences of abiotic variables (SAS Institute, 2009). We used one-way analysis of variance to compare exotic species richness (m<sup>2</sup> and 500-m<sup>2</sup> scales) and cover and relative cover among ecosystems followed by Tukey's test for mean separation (SAS Institute, 2009). All variables met assumptions of equal variance

(Levene's test) and normality (Shapiro–Wilk test) after relative cover was log transformed.

We evaluated patterns of exotic species composition using indicator species analysis and multi-response permutation procedures. At different hierarchical levels starting with a broad, two-group classification of dry (the first four ecosystems of Table 1) and moist (the last six) ecosystems, and ending at the finest resolution with 10 groups corresponding to each of the ecosystems, we used indicator species analysis (Dufrene and Legendre, 1997) to identify species that significantly corresponded to different ecosystem groupings. Indicator species analysis combines the relative frequency (based on the number of sampling units, in our case, plots that a species occupied within a group) and relative abundance (relative cover in our study) to produce an indicator value ranging from 0% (no fidelity to a group) to 100% (high fidelity to a group) for each species. We calculated *P*-values through 1000 permutations and implemented the analysis in PC-ORD (McCune and Mefford, 1999). To compare exotic species composition (relative cover) among ecosystems, we used multi-response permutation procedures, with a Bonferroni correction for multiple tests applied for pairwise comparisons among ecosystems (corrected *P* = 0.001; McCune and Mefford, 1999).

### 3. Results

We recorded a total of 271 species (251 native and 20 exotic) on the 66 plots. Of the exotic species, 10 were annuals or biennials, two were annuals–perennials, and eight were perennials (Table 2). All of the exotic species were forbs or grasses; none were shrubs. *Taraxacum officinale*, *Tragopogon dubius*, *Bromus tectorum*, *Verbascum thapsus*, and *Poa pratensis* were the most prevalent exotic species. The total relative cover of exotic species ranged from 0% to 47% among plots and averaged 4 ± 8% (±1 SD) across all plots.

Native and exotic species richness was positively correlated at both the m<sup>2</sup> and 500-m<sup>2</sup> scales (Fig. 2). Native and exotic species cover was also positively correlated, but the correlation was weaker.

Multiple regressions including native vegetation and environmental variables (no disturbance variables were statistically significant in these models) accounted for similar amounts of the variance in exotic species richness (50% of variance) and cover (51%; Table 3). Models excluding native vegetation variables and including only environmental and disturbance variables portrayed



**Table 2**  
Exotic species and their frequency among ecosystem types in *Pinus ponderosa* forests of northern Arizona, USA.

	Ecosystem <sup>b</sup>										Overall <sup>c</sup>
	BC	RC	CB	XL	ML	XB	RB	MB	AN	PK	
	Frequency (%)										
<b>Forb</b>											
<i>Taraxacum officinale</i> (P) * <sup>a</sup>	0	0	0	0	67	60	75	64	83	50	42
<i>Tragopogon dubius</i> (AB) *	0	50	83	33	67	60	50	27	17	50	42
<i>Verbascum thapsus</i> (B) *	17	50	17	33	33	60	75	36	0	17	35
<i>Lactuca serriola</i> (A)	0	67	67	33	0	0	25	27	17	33	27
<i>Linaria dalmatica</i> (P)	0	33	17	50	33	40	0	27	0	0	20
<i>Convolvulus arvensis</i> (P) *	0	0	33	0	0	0	0	9	0	50	9
<i>Polygonum aviculare</i> (AP) *	0	0	0	0	0	0	0	0	0	83	8
<i>Sisymbrium altissimum</i> (AB)	0	33	33	17	0	0	0	0	0	0	8
<i>Erodium cicutarium</i> (AB) *	0	17	0	17	0	20	0	9	0	0	6
<i>Cirsium vulgare</i> (B) *	0	0	0	0	0	0	0	9	0	0	2
<i>Descurainia sophia</i> (A)	0	0	0	0	0	0	0	9	0	0	2
<i>Melilotus officinalis</i> (AP) *	0	0	17	0	0	0	0	0	0	0	2
<i>Taraxacum laevigatum</i> (P)	0	0	0	0	0	0	0	0	17	0	2
<b>Grass</b>											
<i>Bromus tectorum</i> (A) *	0	50	83	83	50	60	13	36	0	0	36
<i>Poa pratensis</i> (P) *	0	0	0	0	67	0	63	27	67	100	33
<i>Poa compressa</i> (P)	0	0	0	0	0	20	13	0	17	100	14
<i>Bromus japonicus</i> (A)	0	0	33	0	17	0	0	0	0	0	5
<i>Dactylis glomerata</i> (P) *	0	0	0	0	0	0	13	0	17	0	3
<i>Bromus rubens</i> (A)	0	0	0	0	0	0	13	0	0	0	2
<i>Thinopyrum intermedium</i> (P) *	0	0	0	0	0	0	13	0	0	0	2

<sup>a</sup> A = annual, AB = annual-biennial, AP = annual-perennial, B = biennial, and P = perennial. \*\* denote species on Fowler et al.'s (2008) compilation of species that were intentionally seeded or seed contaminants in North America. Some other species not part of Fowler et al.'s (2008) compilation, such as *Poa compressa*, also are likely part of intentional seedings or seed contamination.

<sup>b</sup> BC = black cinder, RC = red cinder, CB = clay basalt, XL = xeric limestone, ML = mesic limestone, XB = xeric basalt, RB = rocky basalt, MB = mesic basalt, AN = aspen, and PK = park.

<sup>c</sup> Frequency among all 66, 0.05-ha plots.

26–32% of the variance among exotic species measures. Combinations of variables best estimating exotic species measures varied by the measure of exotics and whether models included native species. For example, exotic richness  $m^{-2}$  was most strongly explained by geographic location and native plant cover. When native species variables were removed, however, distance to water and slope gradient were included in the model, replacing location variables. Native richness or individual native species were related to exotic species richness at the 500- $m^2$  scale and to exotic species relative cover, but not to exotic richness  $m^{-2}$ . While exotic species cover was positively related to total native cover, it was negatively related to cover of two dominant native species, *Muhlenbergia montana* and *Bouteloua gracilis*.

Exotic species richness  $m^{-2}$ , cover, and relative cover were strongly related to ecosystem types (Fig. 3). Mean exotic richness  $m^{-2}$  varied from 0 in the black cinder to 1.6 species in the park ecosystem ( $F_{9,56} = 10.86$ ,  $P < 0.001$ ). In general, moist ecosystems were more heavily invaded than dry ecosystems. Variation among ecosystems did not statistically differ ( $F_{9,56} = 1.83$ ,  $P = 0.080$ ) at the 500- $m^2$  scale, but the overall pattern of variation at the extremes was the same: black cinder contained the fewest and park ecosystems the most exotic species. Exotic species raw ( $F_{9,56} = 6.48$ ,  $P < 0.001$ ) and relative cover ( $F_{9,56} = 4.00$ ,  $P < 0.001$ ) differed among ecosystems, being greater in park and aspen ecosystems than in drier ecosystems.

Exotic species community composition varied across ecosystems based on multi-response permutation procedures ( $A = 0.18$ ,  $P < 0.001$ ). Composition of park ecosystems differed from all ecosystems except mesic limestone, mesic basalt, and aspen. This difference was driven by *Poa compressa*, as park ecosystems averaged  $1.4 \pm 0.9\%$  ( $\pm 1$  SD) while differing communities averaged  $0.001 \pm 0.007\%$ , and by *P. pratensis* where parks exhibited  $4.0 \pm 3.6\%$  compared to an absence of this species in ecosystems that differed from parks. Exotic communities in xeric limestone ecosystems differed from all but clay basalt and xeric basalt ecosys-

tems. *B. tectorum* relative cover was greater in xeric limestone than in differing ecosystems, with  $0.8 \pm 1.6\%$  compared to  $0.03 \pm 0.15\%$ . Black cinder ecosystems differed from xeric limestone, mesic limestone, rocky basalt, and park ecosystems. Five of six plots of the sparsely invaded black cinder ecosystem were free of exotic plants.

Distributional patterns of individual species were harder to discern than those of community measures because more than half the species were infrequent, occupying <10% of plots (Table 2). However, indicator species analysis at different hierarchical ecosystem groupings and ecosystem-level analyses of frequency revealed that some species showed fidelity to some ecosystems. At the broadest grouping (moist versus dry ecosystems), *B. tectorum* indicated drier sites (indicator value [IV] = 44,  $P = 0.013$ ). *P. pratensis* (IV = 50,  $P < 0.001$ ) and *T. officinale* (IV = 69,  $P < 0.001$ ) indicated moist sites. At the finest resolution (ecosystem level), *P. compressa* (IV = 83,  $P < 0.001$ ) and *Polygonum aviculare* (IV = 83,  $P < 0.001$ ) indicated park ecosystems. *T. officinale* (IV = 69,  $P = 0.003$ ) and *P. pratensis* (IV = 46,  $P = 0.024$ ) both indicated aspen ecosystems. Considering plot frequencies among ecosystems, *T. officinale* only occurred in the six moist ecosystems, *P. aviculare* only in parks, *P. pratensis* and *P. compressa* only in moist ecosystems, and *Sisymbrium altissimum* only in drier ecosystems (Table 2). *T. dubius*, *V. thapsus*, and *Lactuca serriola* displayed no clear site affinities.

## 4. Discussion

### 4.1. General patterns

Some of the general ecological principles advanced in the literature and our *a priori* expectations for distributions of exotic species communities were supported by the data, while others were not. We found support for the principle that native and exotic species richness and cover are positively correlated in landscape-scale sampling studies (Stohlgren et al., 1999; Gilbert and Lechowicz, 2005;

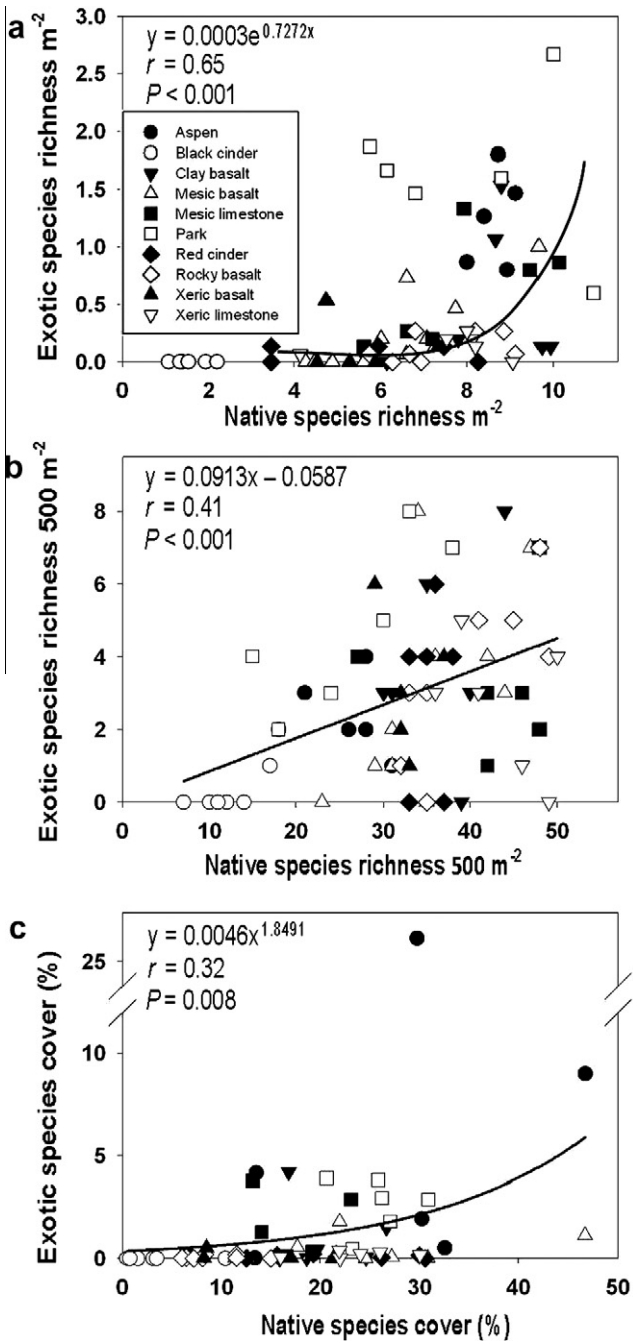


Fig. 2. Relationships between native and exotic species richness at the (a)  $m^2$  and (b)  $500\text{-}m^2$  scale, and (c) the relationship between native and exotic plant cover in *Pinus ponderosa* forests of northern Arizona, USA.

Fornwalt et al., 2010). However, we found that environmental variables were more strongly related than disturbance to exotic species richness and cover. Moreover, we introduced a tool – ecosystem classification – new to invasive species science that shows promise for integrating factors (both environment and disturbance along with management history) apparently related to exotic species distribution. As anticipated, moist ecosystems were generally most invaded. Findings further have important implications for managing exotic species related to information needs identified by mandates such as the National Invasive Species Council (Clinton, 1999) and U.S. Forest Service (2004) guidelines for managing species invasions. Results can help managers understand characteristics of forest sites that are most invaded (useful for mapping and mon-

itoring of invasions), identify exotics that are most prevalent to partly help prioritize species for monitoring and management, and prioritize particular ecosystems for management and develop ecosystem-specific management strategies. Evidence for our *a priori* hypotheses about native–exotic species relationships, the relative importance of habitat variables, and relationships of ecosystem classification with distributions of exotic species communities is important both for advancing theory on species invasions and formulating management strategies.

#### 4.2. Native–exotic species relationships

The hypothesis that native and exotic species richness would be positively correlated was supported, indicating that sites with high native richness were the most invaded. Determining the underlying mechanisms behind the observed positive correlations requires experimental research. Mechanisms could be related to environmental conditions, influences of species richness *per se*, or other factors. Positive correlations can result from site conditions favorable for natives also being favorable for exotics, coupled with the ability of some or all of these species to thus far coexist (Levine et al., 2004). The data provide some support for the hypothesis that the most invaded sites were favorable for both native and exotic species. The top two invaded ecosystems both share the characteristic of lack of *P. ponderosa* dominance: aspen ecosystems have only small proportions of *P. ponderosa* and park ecosystems have no tree overstories. These conditions alleviated a well-known limitation to understory growth in *P. ponderosa* forests, as many studies have reported negative correlations between *P. ponderosa* tree density and understory productivity likely due to heavy shading, litter production, and resource use by the trees (Sabo et al., 2009). Moreover, both native ( $r = 0.55$ ) and exotic ( $r = 0.51$ ) species richness  $m^{-2}$  were positively correlated with soil total N and negatively with sand ( $r = -0.58$  native,  $-0.43$  exotic). This suggested that sites high in N and water-holding capacity (primarily of the aspen and park ecosystems) were favorable to both species groups. On the other hand, the least-invaded ecosystem (black cinder) had the driest, most nutrient-poor surface soils of all ecosystems (Table 1). This ecosystem, also with the fewest native species, was apparently unfavorable for the establishment of native and exotic species.

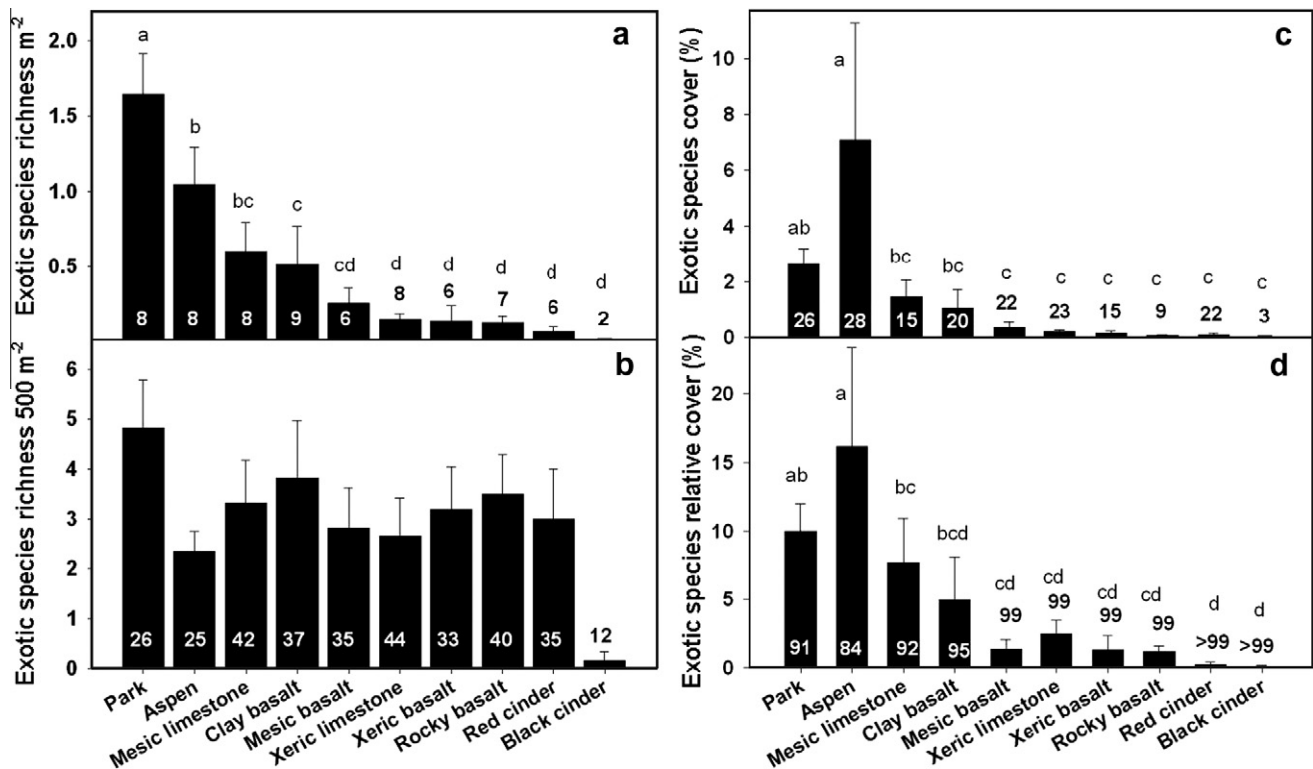
Palmer and Maurer (1997) offered three explanations for how species richness *per se* might promote invasion. First, high species richness can enhance environmental heterogeneity (e.g., multi-layered vegetation), creating a diversity of microsites available for colonization by invaders. Understory vertical and horizontal structure was more complicated in the most-invaded ecosystems compared to the least invaded (black cinder), but more detailed methods quantifying structure would be needed to evaluate patterns in intermediately invaded ecosystems. Second, sites with high richness can have a greater chance of containing a species promoting invasion (i.e. ‘sampling effect’), such as a species that enhances soil N availability. This is difficult to evaluate in our data, as it is not known which species in the *P. ponderosa* forest flora might facilitate invasion. Moreover, legumes (e.g., *Lupinus argenteus*) that may fix N occurred in some heavily invaded ecosystems (e.g., aspen) but not others (park), and characteristics of potential invasion-facilitators may vary among ecosystems. Additionally, high species richness could have the opposite effect: a greater chance of a site containing an invasion-inhibiting species (Fargione and Tilman, 2005). Third, ecological equivalency can facilitate high invasibility of species-rich sites. This theory suggests that species can coexist because the environment is segregated into patches, and while competitive exclusion can occur within a patch, the ‘winner’ will vary from patch to patch, if the species are equivalent, thus increasing overall site species richness. None of our sample sites contained  $>57\%$  total plant cover, with vegetated patches

**Table 3**

Relationships of habitat variables with exotic species richness and cover for *Pinus ponderosa* forests of northern Arizona, USA. Partial  $r^2$  values (with the parameter estimate  $\times 100$  in parentheses) are presented for each variable significant at  $P < 0.05$  included in multiple regressions estimating the exotic species response variables.

	Exotic species richness $m^{-2}$	Exotic species richness $500 m^{-2}$	Exotic species cover ( $\log_{10} \%$ )
<i>Environmental and native plant descriptors</i>			
Intercept	23.16	163.24	39.43
UTM y (m)	0.14 (–0.0005)	0.05 (–0.004)	0.04 (–0.001)
UTM x (m)	0.16 (–0.0006)	–	–
Native cover (%)	0.10 (0.4)	–	0.19 (4.9)
Gravel (% wt.)	0.05 (0.3)	0.08 (5.9)	–
pH	0.05 (8.4)	–	–
Native species $500 m^{-2}$	–	0.17 (10.7)	–
<i>Erigeron divergens</i> (%) <sup>a</sup>	–	0.15 (21.4)	–
<i>Elymus elymoides</i> (%)	–	0.05 (55.3)	–
<i>Muhlenbergia montana</i> (%)	–	–	0.12 (–6.4)
<i>Bouteloua gracilis</i> (%)	–	–	0.16 (–5.9)
Model $R^2$	0.50	0.50	0.51
<i>Environmental data only</i>			
Intercept	0.12	221.86	55.86
Distance to water (m)	0.18 (–0.03)	–	–
Slope gradient (%)	0.09 (–4.2)	–	–
Gravel (% wt.)	0.05 (1.8)	–	–
UTM y (m)	–	0.17 (–0.006)	0.09 (–0.001)
Sand (%)	–	0.09 (–3.4)	–
Soil total N ( $g m^{-2}$ )	–	–	0.17 (–0.4)
Model $R^2$	0.32	0.26	0.26

<sup>a</sup> Cover for individual native species is raw cover.



**Fig. 3.** Mean exotic species richness at the (a)  $m^2$  and (b)  $500\text{-}m^2$  scale, and exotic species (c) raw and (d) relative cover among 10 ecosystem types of *Pinus ponderosa* forests of northern Arizona, USA. Error bars are standard errors of means. Means without shared letters differ ( $P < 0.05$ ). Numbers at the base of or above bars are native species richness or cover.

alternating with bare ground or litter. At an experimental *P. ponderosa* forest site, McGlone et al. (2011) found that established vegetated patches (whether comprised of native perennial plants or the exotic annual *B. tectorum*) were resistant to invasion, implying that new species would need to invade openings rather than vegetated patches. The many mechanisms that might result in observed invasibility patterns lend themselves to multifactor

experiments that manipulate these factors and also include the potential for interactions among the factors and ecosystem types across the landscape.

Based on Palmer and Maurer's (1997) proposed mechanisms, it could be hypothesized that in mensurative studies, the native:exotic species richness correlation is strongest at broader (such as  $500 m^2$ ) than at finer scales ( $m^2$ ). Larger areas would include more

species, greater chances for equivalency, and more patch structure and heterogeneity. However, we actually observed a stronger positive relationship between native and exotic richness at the  $m^2$  compared to  $500\text{-}m^2$  scale. This finding also differs from Keeley et al. (2003), where native and exotic richness were more positively correlated ( $r = 0.67$ ) at  $1000\text{-}m^2$  than  $m^2$  ( $r = 0.26$ ) scales in California Sierra Nevada conifer forests. Apparently in our study, the averaging of the 15,  $m^2$  subplots spatially distributed within a plot captured mechanisms responsible for the positive relationship, or the number of exotic species  $500\text{-}m^2$  had begun to saturate. With the exception of the black cinder ecosystem, there was evidence for saturation in that exotic species richness  $500\text{-}m^2$  was more consistent among ecosystems than was exotic richness  $m^2$ . In other words, the  $500\text{-}m^2$  plots may have detected the majority of exotic species in the vicinity of plots which was reasonably consistent across ecosystems (with most averaging 3–4 exotic species  $\text{plot}^{-1}$ ), tempering variation in exotic richness between native species-poor and species-rich sites (Fig. 3).

The relationship between native and exotic species cover also was positive, but weaker than for species richness. What appeared consistent, however, based on examining the scatterplot, was a threshold where sites with less than about 10% native cover did not support the higher levels of exotic cover that could occur on sites containing >10% native cover (Fig. 2). This may arise from dry, infertile environments not being favorable for either exotic or native species. Many sites with >10% native cover, however, also supported minimal amounts of exotic cover. In these cases, the identity of the native species might be more tightly linked to community invasibility than total native cover, serving to temper native:exotic cover relationships (Abella et al., in press). For example, the native perennial bunchgrasses (e.g., *Festuca arizonica*) and sedges (e.g., *Carex geophila*) are strong competitors (Pearson, 1942) and may have reduced exotic cover on some of the sites with high native cover.

#### 4.3. Relative importance of habitat variables

Contrary to our hypothesis that native vegetation, environmental factors, and disturbance would account for equal proportions of the variance in exotic species communities, native vegetation and environmental factors were more closely related to exotic species communities than the disturbance variables. Only distance to water (linked primarily to artificial tanks where livestock and disturbance are concentrated) entered exotic species models as a disturbance variable and only when native vegetation variables were not included (Table 3). However, our findings related to disturbance should be placed within the sampling context of the study. For instance, we did not sample intensively disturbed areas such as severe burns, expected to promote exotic plants (Floyd et al., 2006; Hunter et al., 2006; Fornwalt et al., 2010). Examining a range of disturbances across ecosystems warrants further research to understand if disturbance and ecosystem type interact statistically to influence exotic species communities. The landscape also was the scale of our sampling. We did not specifically sample, for instance, fine-scale gradients (e.g., a scale of tens of meters) in distance from roads that can be related to exotic plant distribution (e.g., Fowler et al., 2008; Mortensen et al., 2009), though not always (e.g., Craig et al., 2010). We also acknowledge that our measures of disturbance are crude (e.g., categorical variable of grazing intensity). Yet, some other studies have used similar measures of disturbance and have found stronger relationships with exotic plant distributions (e.g., Gelbard and Harrison, 2003). The possible importance of historical disturbances, such as late 1800s grazing and railroad line development, in creating opportunities for exotic plant introduction and spread should not be dismissed but are difficult to retrospectively evaluate.

While a central tenet in invasive species science is that disturbance promotes invasions, we also should not assume that disturbance is always the principal driving factor for the establishment and spread of exotic plant invasions (Alpert et al., 2000; Eschtruth and Battles, 2009). Our finding of weaker relationships of exotic plants with disturbance than with native vegetation and environmental factors concurs with findings of some other studies including in *P. ponderosa* forests. In Colorado, for instance, Fornwalt et al. (2003) found that no exotic species measures differed between a study area where logging, grazing, and most human recreation had been excluded for the past 100 years compared to an area where these uses had occurred. Specifically considering grazing, studies in *P. ponderosa* forests have not reported that grazed areas contain more abundant exotic plants than ungrazed areas. Studying a 93-year-old livestock grazing enclosure within our study area, Bakker et al. (2010) concluded that differences in plant composition were negligible inside and outside the enclosure. Similarly, Sorensen and McGlone (2010) found that cover of the exotic annual *B. tectorum* averaged 1% both inside and outside of 2-year-old enclosures, while Rambo and Faeth (1999) reported that exotic cover was actually greater outside (21%) compared to inside (13%) enclosures. Again, however, a historical context is needed, because all of these studies occurred in a contemporary period of less intensive grazing than occurred in the past (Bakker and Moore, 2007). Furthermore, several of the exotic plants we recorded were specifically introduced for range 'improvements' to provide livestock forage or were seed contaminants (Fowler et al., 2008).

#### 4.4. Utility of ecosystem classification

The hypothesis that exotic plant communities differed among ecosystems was supported, with a general gradient of decreasing invasion from moist to dry ecosystems. The specific patterns, however, suggested that factors other than general moisture availability were related to invasion patterns and were captured by the ecosystem classification. For example, the rocky basalt ecosystem is moist (Table 1) but had among the lowest exotic richness  $m^2$  and exotic cover. Rocky soils and clay bands near the surface may have limited plant establishment (Abella and Covington, 2006a). Aspen ecosystems, among the most heavily invaded, contained different overstories, leaf litter, soil properties, and likely animal use (Martinsen et al., 1990) than other ecosystems, all of which may have influenced the growing environment for plants. The mesic basalt ecosystem contained silty soils high in N and available water, which could be predicted to promote invasion, yet this ecosystem was not among the most heavily invaded. Native species identity in this ecosystem may have been important because the ecosystem was dominated by perennial bunchgrasses and sedges that might competitively constrain invasion (McGlone et al., 2011). An additional factor warranting consideration and future research is that geographic locations of sites of some ecosystems were clustered. Spatial correlation of sites within ecosystems would be expected if particular geographic regions have a climate that supports only certain ecosystems or if soil parent material is spatially clustered (Urban et al., 2000). For example, sites of the black cinder ecosystem were clustered in the northeastern part of the study area because this was an area of recent volcanic activity that also was climatically dry (Fig. 1). This type of spatial structure can be viewed as a positive for helping to understand species distributions if other factors (e.g., broad-scale species dispersal) are also related to this spatial structure (Hawkins, 2012). However, sites of other ecosystems were not spatially clustered, such as the widely dispersed aspen ecosystem or the clay basalt ecosystem which contained sites separated by over 65 km (Fig. 1). These ecosystems appeared to re-occur wherever their characteristic environments were located.



We hypothesize that the ecosystem classification was related to exotic species communities because it reflected interconnected environmental, disturbance, and management regimes. In other words, ecosystem-specific environments may have led to ecosystem-specific disturbance and management regimes. For instance, parks have unique environments because they are treeless, occupy low positions in the landscape that accumulate water, and often have clayey soils (Abella and Covington, 2006a). These are also locations where native ungulates and livestock congregate; thus grazing (or grazing-related activities such as livestock herding) may have been important in this particular ecosystem even if not reflected in overall landscape patterns. In another example, black cinder ecosystems have unique environments characterized by coarse, gravelly soils. These droughty, N-poor soils in turn limit plant productivity and suitability for construction of livestock watering tanks. As a result, livestock management and range improvements through intentional seeding of exotic plants would not be anticipated to be as important in this ecosystem in comparison to others (Abella and Covington, 2006a). While the regression models using continuous independent variables accounted for ca. 50% of the variation in exotic species measures, these variables (e.g., soil laboratory data) are expensive to obtain. The ecosystem classification is already available to forest managers as a map, and it accounted for orders of magnitude variation among forest sites in exotic plant abundance (Fig. 3). The data suggest that ecosystem classification integrated co-varying factors related to exotic community distribution and is a useful tool for landscape-scale exotic species management.

#### 4.5. Species distributions, introduction history, and impacts

The exotic species we detected appear widespread in southwestern *P. ponderosa* forests and many were introduced intentionally. For example, 14 of the 20 species detected in our study were also detected by Fowler et al. (2008) at sites in three northern Arizona national forests including our study forest. Excepting *Taraxacum laevigatum*, 19 of our study's species were on Sieg's (2003) list of exotic plants of *P. ponderosa* forests.

Over half of the exotic species in our study were on Fowler et al.'s (2008) compilation of exotic species surmised to have been intentionally introduced to North America or introduced as seed contaminants (Table 2). It is difficult to evaluate which species, in what quantities, and in which locations exotic plants were seeded specifically within our study area. Rangeland seeding projects have occurred for over 70 years, foresters and others sometimes carried seed bags and sowed seed during routine travels and project visits (C.W. Denton, U.S. Forest Service retired, personal communication, 2012), and little or no documentation exists for most seedings. Lavin and Springfield (1955), however, do provide specific examples of seeding the exotics *Dactylis glomerata*, *P. pratensis*, and *Thinopyrum intermedium* for livestock within our study area, and based on Fowler et al. (2008), several other species have likely been seeded specifically within the study area. Some exotic species we recorded, such as *Melilotus officinalis*, *D. glomerata*, and *T. intermedium*, also have been used for wildfire revegetation in the past 40 years in the Southwest (Peppin et al., 2011). While the importance of these intentional seedings in the establishment and spread of exotic plants is not known relative to other dispersal mechanisms (e.g., transport by animals, wind, and human forest visitors), the potential impact of intentional seeding and seed contamination should not be overlooked (Fowler et al., 2008).

The stage of invasion of the species in our study is not clear, nor is it apparent what impacts these species have had in the past or may have in the future (Crooks, 2005). Many exotics seeded for revegetation purposes have the ability to spread from introduction sites, as Williamson and Harrison (2002) documented for *D. glomerata* in California grasslands and woodlands, at least under certain

climatic and site conditions. A common invasion pattern is a lag phase after introduction, which can last many decades, followed by exponential population growth of species with high invasiveness (Crooks, 2005). Few data on long-term spread rates of exotic species are available for *P. ponderosa* forests, highlighting the potential application of plot networks such as this study, combined with other methods (e.g., surveys) for monitoring exotic plant distributions. Impacts of the invaders to indigenous ecosystems may include competing with native plants, altering forage for native herbivores and livestock, modifying soil properties, and changing fuel characteristics that can alter fire ecology (Parker et al., 1999). Not all of the invaders may impact indigenous ecosystems equally, however, potentially influencing which species are the priorities for management. For example, *B. tectorum* is known to alter soil properties and fuel characteristics (Upadhyaya et al., 1986). In contrast, species such as *T. officinale* may have less substantial impact, or in the case of species such as *V. thapsus*, disappear from vigorous stands of native species (Stoddard et al., 2011). Moreover, managers might be less concerned about the study area's exotic perennial grasses, which provide forage values, but more concerned about species such as *B. tectorum* or *Linaria dalmatica* that have little documented benefit relative to their harmful effects in indigenous ecosystems (Sieg et al., 2003).

#### 4.6. Conclusion

Results can help meet information needs identified by the National Invasive Species Council (Clinton, 1999) and U.S. Forest Service (2004) guidelines for managing exotic species. For example, while not intended as an exhaustive botanical survey, the data provide a landscape-scale inventory of exotic species. This inventory identified species that are currently infrequent, which can assist with early detection, including detecting a species (*T. laevigatum*) not previously found on lists of exotic plants in southwestern *P. ponderosa* forests (Sieg et al., 2003). Relating exotic species community measures to native vegetation and environmental factors helped to identify areas of the landscape that were most invaded, which generally included sites with high fine-scale (1 m<sup>2</sup>) native species richness, high soil N and available water (excepting rocky basalt sites), and low amounts of native perennial bunchgrasses. This study also found that ecosystem classification was valuable for understanding invasion patterns across the landscape and is useful for exotic species management planning. For example, management strategies may be ecosystem-specific: in the little-invaded black cinder ecosystem, early detection of new invaders may be a primary strategy, whereas containing existing invasions may be more important in heavily invaded ecosystems.

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