ORIGINAL ARTICLE

Forest ecosystems of an Arizona *Pinus ponderosa* landscape: multifactor classification and implications for ecological restoration

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ABSTRACT

Aim We developed an ecosystem classification within a 110,000-ha Arizona *Pinus ponderosa* P. & C. Lawson (ponderosa pine) landscape to support ecological restoration of these forests. Specific objectives included identifying key environmental variables constraining ecosystem distribution and comparing plant species composition, richness and tree growth among ecosystems.

Location The Coconino National Forest and the Northern Arizona University Centennial Forest, in northern Arizona, USA.

Methods We sampled geomorphology, soils and vegetation on 66 0.05-ha plots in open stands containing trees of pre-settlement (*c.* 1875) origin, and on 26 plots in dense post-settlement stands. Using cluster analysis and ordination of vegetation and environment matrices, we classified plots into ecosystem types internally similar in environmental and vegetational characteristics.

Results We identified 10 ecosystem types, ranging from dry, black cinders/ *Phacelia* ecosystems to moist aspen/*Lathyrus* ecosystems. Texture, organic carbon and other soil properties reflecting the effects of parent materials structured ecosystem distribution across the landscape, and geomorphology was locally important. Plant species composition was ecosystem-specific, with C_3 *Festuca arizonica* Vasey (Arizona fescue), for instance, abundant in mesic basalt/*Festuca* ecosystems. Mean *P. ponderosa* diameter increments ranged from 2.3– 4.3 mm year^{-1} across ecosystems in stands of pre-settlement origin, and the ecosystem classification was robust in dense post-settlement stands.

Main conclusions Several lines of evidence suggest that although species composition may have been altered since settlement, the same basic ecosystems occurred on this landscape in pre-settlement forests, providing reference information for ecological restoration. Red cinders/*Bahia* ecosystems were rare historically and > 30% of their area has been burned by crown fires since 1950, indicating that priority could be given to restoring this ecosystem's remaining mapping units. Ecosystem classifications may be useful as data layers in gap analyses to identify restoration and conservation priorities. Ecosystem turnover occurs at broad extents on this landscape, and restoration must accordingly operate across large areas to encompass ecosystem diversity. By incorporating factors driving ecosystem composition, this ecosystem classification represents a framework for estimating spatial variation in ecological properties, such as species diversity, relevant to ecological restoration.

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INTRODUCTION

Geomorphology and soils vary across forest landscapes, forming mosaics of environmental complexes differing in productivity and capability to support plant communities (Hix, 1988; Archambault *et al.*, 1990; Host & Pregitzer, 1992). Ecosystem classification is a tool for identifying interrelationships among environmental variables forming environmental complexes, discerning gradients constraining vegetation distribution and productivity, and classifying volumetric environment–vegetation units into landscape ecosystems to facilitate ecosystem-specific management (Barnes *et al.*, 1982; McNab *et al.*, 1999). Goebel *et al.* (2001), for example, distinguished 21 ecosystem types along soil texture, drainage and topographic gradients on an 11,000-ha south-eastern US *Pinus palustris* P. Mill. (longleaf pine) landscape. Palik *et al.* (2000) then used the ecosystem classification to develop models for prioritizing ecosystem-specific restoration based on the historical and current rarity of different ecosystems. Ecosystem classification has been performed and utilized on numerous landscapes, including north-eastern Chinese pine-hardwood forests (Barnes *et al.*, 1992), South African ecosystems (Louw & Scholes, 2002), early successional British Columbian forests (Klinka *et al.*, 1985) and Michigan oak and wetland ecosystems (Archambault *et al.*, 1990).

A voluminous literature on ecosystem classification has apparently accrued largely in isolation from mainstream biogeography, and ecosystem classification is rarely mentioned in biogeography textbooks. However, the underpinnings of ecosystem classification correspond to several important subdivisions of biogeography (MacDonald, 2003). For example, interactions among abiotic environments and plant communities form a basis for classifying ecosystem types, and these interactions are the focus of ecological biogeography. Phytogeography is concerned with the distributions of plants, which are used in ecosystem classification to distinguish ecosystems and explain vegetation–environment relationships (Kashian *et al.*, 2003a). Numerous studies also have utilized ecosystem classifications as frameworks to study plant distributions, diversity and tree growth (e.g. Hix, 1988; Host & Pregitzer, 1992; Lapin & Barnes, 1995). While animal distributions studied in zoogeography have not been directly utilized as part of ecosystem classification to date, recent studies that have examined bird distributions have found close correspondence with existing ecosystem classifications (Kashian *et al.*, 2003b; Camp, 2004). In the eastern US southern Appalachians, for example, Camp (2004) found that *Limnothlypis swainsonii* (Swainson's warbler) was most frequent in mesic hemlock/rhododendron ecosystems, while *Helmitheros vermivorus* (worm-eating warbler) characterized xeric ecosystems previously classified by Abella *et al.* (2003). Camp (2004) concluded that the ecosystem classification was useful for modelling avian distributions across the landscape, and for identifying habitat for rare species of particular conservation concern. Palik *et al.*'s (2000) use of an ecosystem classification to prioritize ecosystem restoration provides another example of the relationship of ecosystem classification to conservation biogeography, which is concerned with protecting and restoring native species and communities. By more fully exploiting the relationships between ecosystem classification and biogeography we may enhance our understanding of species distributions, and improve our ability to conserve and restore ecosystems at landscape scales.

Ecosystem classification is increasingly being developed and utilized in the forests of the eastern USA (e.g. Lapin & Barnes, 1995; McNab *et al.*, 1999; Abella *et al.*, 2003), but little ecosystem classification or soil-site research has been published for the vast *Pinus ponderosa* P. & C. Lawson (ponderosa pine) forests of the south-western USA. Vegetation-based habitat classifications (Hanks *et al.*, 1983; Muldavin *et al.*, 1990) or soil or landform type classifications (Leven *et al.*, 1972) have been more common in these forests. Recently, however, the US Forest Service has published Terrestrial Ecosystem Surveys (TES) for several south-western national forests (Ganey & Benoit, 2002). These TES land classifications provide georeferenced maps and soil classification data similar to those of eastern US soil surveys (Miller *et al.*, 1995). Although TES have been extensively developed for south-western *P. ponderosa* forests, there are no published comparisons between TES and ecosystem classification. Such comparisons and advances in site classification would be timely to assist the development of ecosystem response functions to restoration and management prescriptions, which are urgently needed to conserve *P. ponderosa* landscapes.

Ecosystem integrity in south-western *P. ponderosa* forests has declined since Euro-American settlement (*c.* 1875) for several reasons (Fulé *et al.*, 1997; Moore *et al.*, 1999; Allen *et al.*, 2002). Historically frequent surface fires were excluded, contributing to fuel buildups and shifts to stand-replacing fire regimes. Irruptions in small-diameter tree densities and decreases in old trees have altered plant communities and wildlife habitat. Escalating small-diameter tree densities, far outside a range of historical variability, reduced native understorey plant communities in combination with livestock grazing. While the need for fuel reduction to reduce the probability of catastrophic fire is clear, many authors have further suggested that ecological restoration is needed to alleviate many other problems plaguing these forests (Covington *et al.*, 1994; Moore *et al.*, 1999; Allen *et al.*, 2002). The accelerated mortality of old trees, insect outbreaks, exotic species invasions and simplification of native communities are only a few examples of declining ecosystem integrity observed in *P. ponderosa* forests (Allen *et al.*, 2002). A scientific consensus has emerged that primary restorative treatments needed in these forests include thinning small-diameter trees and re-introducing surface fire (Covington *et al.*, 1994; Allen *et al.*, 2002), with exotic species management, seeding native species and other treatments also required on some sites (Moore *et al.*, 1999).

A key point is that the goals of ecological restoration are not necessarily to re-create replicas of pre-settlement ecosystems. Rather, the objective is to align the current degraded ecosystems on a trajectory toward recovery within an approximate range of historical variability characterizing the evolutionary environ-

ments of native species (Morgan *et al.*, 1994; Moore *et al.*, 1999). Evolutionary environments are key concepts in both restoration ecology and biogeography (Morgan *et al.*, 1994; MacDonald, 2003). A recent study by Palik *et al.* (2000) showed how ecosystem classification can provide insight into the evolutionary environments of native plant communities, based on the observation that environments vary geographically within landscapes. Topography and soil parent material are relatively stable landscape features, making present-day ecosystems classified using those stable features a source of reference information on evolutionary environments (White & Walker, 1997).

We undertook this study to develop a multifactor ecosystem classification within a 110,000-ha *P. ponderosa* landscape in northern Arizona, USA. Specific objectives included: (1) identifying primary environmental and vegetational gradients and their interrelationships associated with ecosystem distribution, (2) comparing community composition, species richness and tree growth among classified ecosystems, and (3) providing examples of applications for ecological restoration and hypothesis generation for future research. Our study focuses on advancing the biogeographical disciplines of ecological biogeography, phytogeography and conservation biogeography in this region through the use of ecosystem classification.

METHODS

Study area

We performed this study at elevations between 1920 and 2660 m in the Northern Arizona University Centennial Forest and in the north half of the Coconino National Forest near the city of Flagstaff, AZ (Fig. 1). *Pinus ponderosa* is the dominant tree

species and forms extensive pure stands, but sometimes occurs with *Quercus gambelii* Nutt. (Gambel oak) or *Populus tremuloides* Michx. (trembling aspen). Precipitation increases and temperatures decrease from east to west across the study area, with precipitation ranging from 42–56 cm year^{-1}, snowfall from 152 to 233 cm year^{-1} and maximum mean daily temperatures from 15.7 to 17.5 °C (Western Regional Climate Center, Reno, NV, USA). Topography is primarily flat or undulating (slope gradients < 10%), occasionally punctuated by cinder cones, ravines and low hills. Volcanic activity has been widespread, with the most recent eruptions occurring *c.* 900 years ago in the Sunset Crater Volcanic Field in the north-eastern part of the study area (Moore *et al.*, 1976). Soil parent materials include basalt, volcanic cinders, benmoreite, mixed igneous rocks, and limestone (Welch & Klemmedson, 1975). Major soil subgroups are Typic and Udic Argiborolls, Typic and Mollic Eutroboralfs, Typic Ustorthents and Vitrandic Ustochrepts (Miller *et al.*, 1995). Lightning-ignited surface fires in pre-settlement forests occurred on average at least once every 10 years, maintaining open stand structures (Fulé *et al.*, 1997). Most of the study area, however, has had sustained fire exclusion, timber harvest and heavy livestock grazing since settlement, which may have influenced present-day ground-flora composition in some areas (Moore *et al.*, 1999).

Site selection

We used a digital TES map (Miller *et al.*, 1995) in a geographical information system to randomly select six mapping units for sampling in each of 11 TES types (55, 500, 513, 523, 536, 551, 558, 570, 582, 585 and 611) encompassing a range of soils. These TES types served as an *a priori* stratification for sampling, a procedure
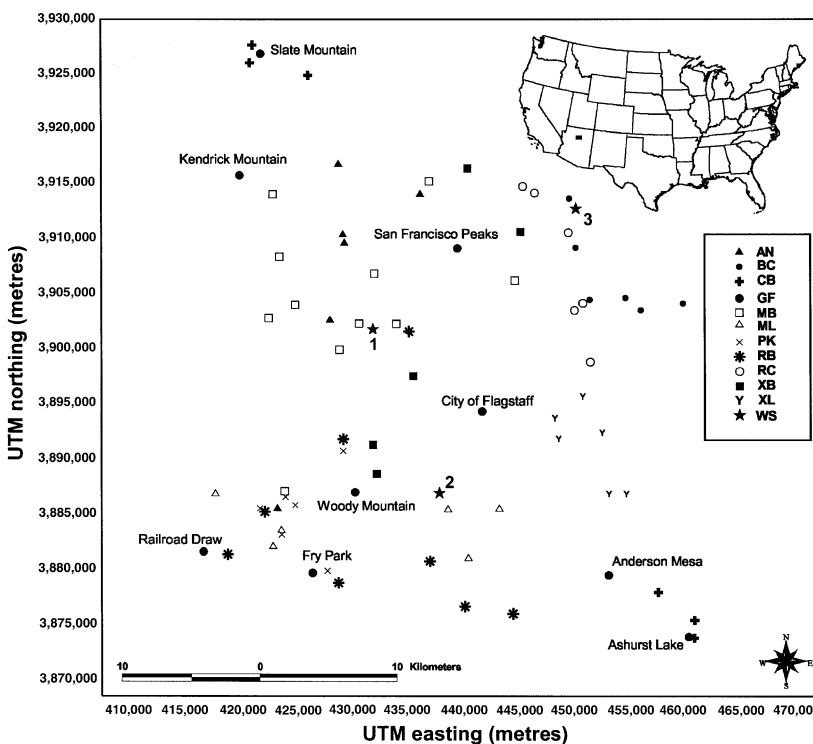
Figure 1 Distribution of 66 sample plots and their classification into ecosystem types for a *Pinus ponderosa* landscape in northern Arizona, USA (UTM zone 12). Geographical features are abbreviated as GF and weather stations as WS. Although at similar elevations (2128–2244 m), precipitation based on > 35 years of records averages 42 cm year^{-1} at the eastern weather station 1 (Sunset Crater), 54 cm year^{-1} at central station 2 (Flagstaff Airport) and 56 cm year^{-1} at station 1 (Fort Valley). Ecosystem type abbreviations are as follows: AN = aspen/*Lathyrus*, BC = black cinders/*Phacelia*, CB = clay basalt/*Gutierrezia*, MB = mesic basalt/*Festuca*, ML = mesic limestone/mixed flora, PK = park/*Symphyotrichum*, RB = rocky basalt/*Sporobolus*, RC = red cinders/*Bahia*, XB = xeric basalt/*Muhlenbergia* and XL = xeric limestone/*Bouteloua*.

commonly employed in the iterative process of ecosystem classification (Host *et al.*, 1992). We sampled a 0.05-ha (20 m × 25 m) plot in each mapping unit in areas exhibiting open canopies, relatively intact understoreys and no apparent major recent disturbance. Areas dominated by trees of pre-settlement origin most frequently met these criteria (Kerns *et al.*, 2003). These 66 open-canopy plots were used to develop the ecosystem classification, and we sampled an additional 26 plots in dense post-settlement stands in 536, 570 and 585 TES mapping units to ascertain classification viability in dense stands. These stands typically exceeded 1000 *Pinus ponderosa* trees ha^{-1}, in contrast to typical densities of < 150 trees ha^{-1} in stands of pre-settlement origin.

Environmental measurements

We sampled plots from May to August 2003. On each plot, we recorded elevation, transformed aspect (Beers *et al.*, 1966), slope gradient and terrain shape index (McNab, 1989). Terrain shape index measures local topographical geometry, and we based measurements on eight clinometer sightings every 45° to a change in topographical shape (Abella, 2003). We measured surface rock cover by recording substrate every 0.3 m along a 25-m transect, and obtained rock samples later identified by a geologist (Sam Bourque, Ecological Restoration Institute, Flagstaff, AZ, USA). We collected composite soil samples from depths of 0–15 and 15–50 cm from two pits per plot, and examined deeper layers to 150 cm or to an impervious layer using a bucket auger. Soil samples were air dried, sieved through a 2-mm sieve, and analysed for $CaCO_3$ equivalent [Goh *et al.*'s (1993) approximate gravimetric method], texture (hydrometer method), pH (1 : 2 soil:0.01 M $CaCl_2$), and organic C and total N (C/N analyser after removal of inorganic C with HCl) following Bartels & Bigham (1996) and Dane & Topp (2002). Analytical errors averaged < 5% based on a repeated measurement every 10 samples. We also estimated soil available water capacity using Saxton *et al.*'s (1986) equations incorporating texture, gravel content and organic matter (estimated as organic C × 1.724).

On three plots randomly selected in each of six ecosystem types, we measured gravimetric 0–15 cm soil moisture (24 h, 105 °C oven drying) averaged from two soil cores each of 208 cm^3 per plot. We selected these six ecosystem types for moisture measurements to span a range of expected moisture levels based on texture and organic C analyses. We made moisture measurements during the driest period of the year, on 19 June 2004 after no measurable precipitation had fallen since April (Western Regional Climate Center, Reno, NV, USA). Measurement errors averaged < 5% based on analysing a duplicate sample every six samples.

Vegetation measurements

In 15, 1-m^2 subplots per plot centred at 0.5, 5, 12.5, 20 and 24.5 m along plot axes, we visually categorized areal per cent cover of each ground-flora species rooted in subplots. 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. Measurement error, based on remeasuring two randomly selected subplots every six plots, averaged < 0.25% for total cover and < 0.25 species m^{-2}. We also made a complete census of species in whole plots on a presence/absence basis, and assigned these species a frequency of one and the lowest cover for computing importance values (average of relative frequency and relative cover summing to 100% on a plot basis). Nomenclature follows USDA-NRCS (2004).

To measure tree growth, we cored two dominant, open-grown *P. ponderosa* of pre-settlement origin on each open-canopy plot at 0.4 m above ground level. Cores were sanded, mounted and cross-dated using local tree-ring chronologies (Fulé *et al.*, 1997). We measured diameter increment between ages of 50 and 150 years at 0.4 m height to avoid potential measurement inaccuracies due to missed piths, while providing a growth measure in the early–middle life stage of *P. ponderosa* (Schubert, 1974). We used diameter increment as a growth measure rather than site index, because site index equations have not been developed for old, uneven-aged south-western *P. ponderosa* stands as sampled for this study.

Statistical analysis

We developed the ecosystem classification by classifying and ordinating the environmental matrix using cluster analysis (variables relativized by maximums, Euclidean distance, Ward's linkage method) and principal components analysis (correlation matrix) in PC-ORD (McCune & Mefford, 1999). We classified and ordinated the importance value vegetation matrix using cluster analysis (Sørensen distance, −0.25 flexible beta linkage) and non-metric multidimensional scaling (auto-pilot, thorough mode). After identifying seven plot groupings in these analyses, with 24 remaining plots chiefly of basalt parent materials not clearly distinguished, we performed a second iteration of classification and ordination separately on these 24 plots. This analysis identified three plot groupings distinguished by soil properties and plant composition. We also used abundances of ecological species groups, classified in previous research on the plots (Abella, 2005), to help discriminate ecosystems. Species groups consist of plant species that share similar environmental affinities, and have frequently been developed in conjunction with ecosystem classification to categorize plant distributions and differentiate ecosystems (Kashian *et al.*, 2003a). The final ecosystem classification was based on plot groups internally similar in environmental properties and species composition. We employed cluster analysis and ordination iteratively as complementary analyses, but we present only the results of ordinations to portray plot groupings and continuous variation (Host *et al.*, 1992).

We compared means of environmental variables, species richness and *P. ponderosa* diameter increment among classified ecosystems using one-way analysis of variance and Fisher's least significant difference in SAS JMP (SAS

Institute, 2002). Raw data approximated assumptions of equal variance (Levene test) and normality (Shapiro–Wilk W test).

RESULTS AND DISCUSSION

Classification

We classified and named 10 landscape ecosystem types on the basis of diagnostic environmental features and characteristic species along a continuum ranging from the black cinders/*Phacelia* ecosystem, with the driest surface soils and lowest plant cover, to moist aspen/*Lathyrus* and treeless park/*Symphyotrichum* ecosystems (Table 1 & Fig. 2). Other ecosystems differed more subtly, such as the xeric basalt/*Muhlenbergia* ecosystem differentiated from the mesic basalt/*Festuca* ecosystem by exhibiting sandier soils, less organic C and more *Muhlenbergia montana* (Nutt.) A.S. Hitchc. (mountain muhly) than *Festuca arizonica* Vasey (Arizona fescue). Seven ecosystems corresponded with a respective TES type, whereas three ecosystems each occurred on combinations of the 551, 570, 582, and 585 TES types, mostly containing basalt parent material (Miller *et al.*, 1995). Of six plots sampled in the 582 TES type, for example, we classified four into the mesic basalt/*Festuca* and two into the rocky basalt/*Sporobolus* ecosystems. This increased internal mean Sørensen similarities of understorey vegetation from 44% within the 582 TES type to 55% within this study's mesic basalt/*Festuca* ecosystem. Results suggest that TES broadly differentiated distinctively different

ecosystems, but did not detect multivariate interactions among environmental variables distinguishing closely related ecosystems (Fig. 3). Similar to eastern US soil surveys, however, TES is a starting point for understanding ecosystem distribution on this landscape (Pregitzer *et al.*, 2001). By identifying interrelationships, ecosystem classification is useful for refining or complementing TES in south-western USA national forests.

Environmental complexes

Ecosystems were primarily differentiated along soil gradients (Fig. 3), reflecting differences among soil parent materials based on the presence or absence of volcanic activity (Welch & Klemmedson, 1975). In contrast with ecosystem classification in the eastern USA, where geomorphology often forms an initial layer distinguishing ecosystems (Hix, 1988; Host & Pregitzer, 1992; Abella *et al.*, 2003), ecosystem distribution was not closely associated with the geomorphological variables of aspect, slope gradient or terrain shape index. Slope gradients averaged < 8% in all ecosystems except for the red cinders/*Bahia* ecosystem, so most plots did not exhibit strong aspects. Terrain shape index was mostly near zero, reflecting fairly linear topography (McNab, 1989). This index averaged only a slightly convex value (−2.1) in the red cinders/*Bahia* ecosystem because of the convex cinder cones this ecosystem often occupied. The park/*Symphyotrichum* ecosystem had weakly concave (1.9) terrain shapes, consistent with this ecosystem's occurrence in depressions a few metres lower than the surrounding forested topography

Table 1 Summary of diagnostic environmental properties and examples of characteristic plant species of *Pinus ponderosa* landscape ecosystems, northern Arizona

Ecosystem type
Black cinders/*Phacelia* (558), $n = 6*$
Gravelly, surficial volcanic cinders 10–15 cm thick; low ground-flora cover; *Phacelia sericea*, *Nama dichotomum*
Red cinders/*Bahia* (513), $n = 6$
Xeric, sandy loam soils; slow tree growth, moderate ground-flora cover; *Bahia dissecta*, *Muhlenbergia montana*
Clay basalt/*Gutierrezia* (523), $n = 6$
Rocky, clay loam soils of climatically dry sites; slow tree growth; heavily grazed; *Gutierrezia sarothrae*, *Bouteloua gracilis*
Xeric limestone/*Bouteloua* (500), $n = 6$
Sandy loam soils of neutral pH low in total N and organic C; climatically dry sites; *Bouteloua gracilis*, *Hymenopappus filifolius*
Mesic limestone/mixed flora (536), $n = 6$
Climatically moist sandy loam soils; variable geomorphology; high plant diversity; *Festuca arizonica*, *Muhlenbergia montana*
Xeric basalt/*Muhlenbergia*† (551, 570), $n = 5$
Lowest N and organic C of basalt ecosystems; *Muhlenbergia montana*
Rocky basalt/*Sporobolus* (570, 582, 585), $n = 8$
High surface rock cover; slowest tree growth of basalt ecosystems; *Sporobolus interruptus*, *Pedicularis centranthera*
Mesic basalt/*Festuca* (551, 570, 582, 585), $n = 11$
Silt loam soils high in N and organic C; rapid tree growth and productive understoreys; *Festuca arizonica*, *Carex geophila*
Aspen/*Lathyrus* (611), $n = 6$
Mixed *Populus tremuloides–Pinus ponderosa*; deep sola > 1 m thick; high N and organic C; *Lathyrus lanszwertii*, *Lupinus argenteus*
Park/*Symphyotrichum* (55), $n = 6$
Treeless basins 1 to > 1000 ha in size; clay loam soils with deep sola; heavily grazed; *Symphyotrichum ascendens*, *Allium geyeri*

*Terrestrial ecosystem survey (Miller *et al.*, 1995) types on which ecosystems occurred are given in parenthesis followed by the number of plots classified into ecosystems.
†Basalt ecosystems also contained plots with benmoreite and mixed igneous parent materials.

Figure 2 Examples of ecosystems of a *Pinus ponderosa* landscape, northern Arizona, USA. The black cinders/*Phacelia* ecosystem (a) contains dry surface soils of loose volcanic cinders, low ground-flora cover and high importance of *Phacelia sericea* and other annuals (452,800 mE, 3,905,545 mN, zone 12). The mesic basalt/*Festuca* ecosystem (b) has silt loam soils, high understorey cover of *Festuca arizonica* and *Lupinus argenteus* and rapid *P. ponderosa* diameter growth (438,407 mE, 3,916,244 mN). The treeless park/*Symphyotrichum* ecosystem (c) occupies depressions, is heavily grazed and has a high abundance of *Symphyotrichum ascendens* and *Erigeron divergens* (425,369 mE, 3,887,662 mN). Photographs by S. R. Abella, summer 2003.

(Strahler, 1944). While geomorphology may influence the composition of ecosystems in rare, localized areas, such as in particularly deep ravines that we did not sample (Crawford Zimmerman *et al.*, 1999), the flat to undulating topography on most of the landscape minimally affects ecosystem distribution.
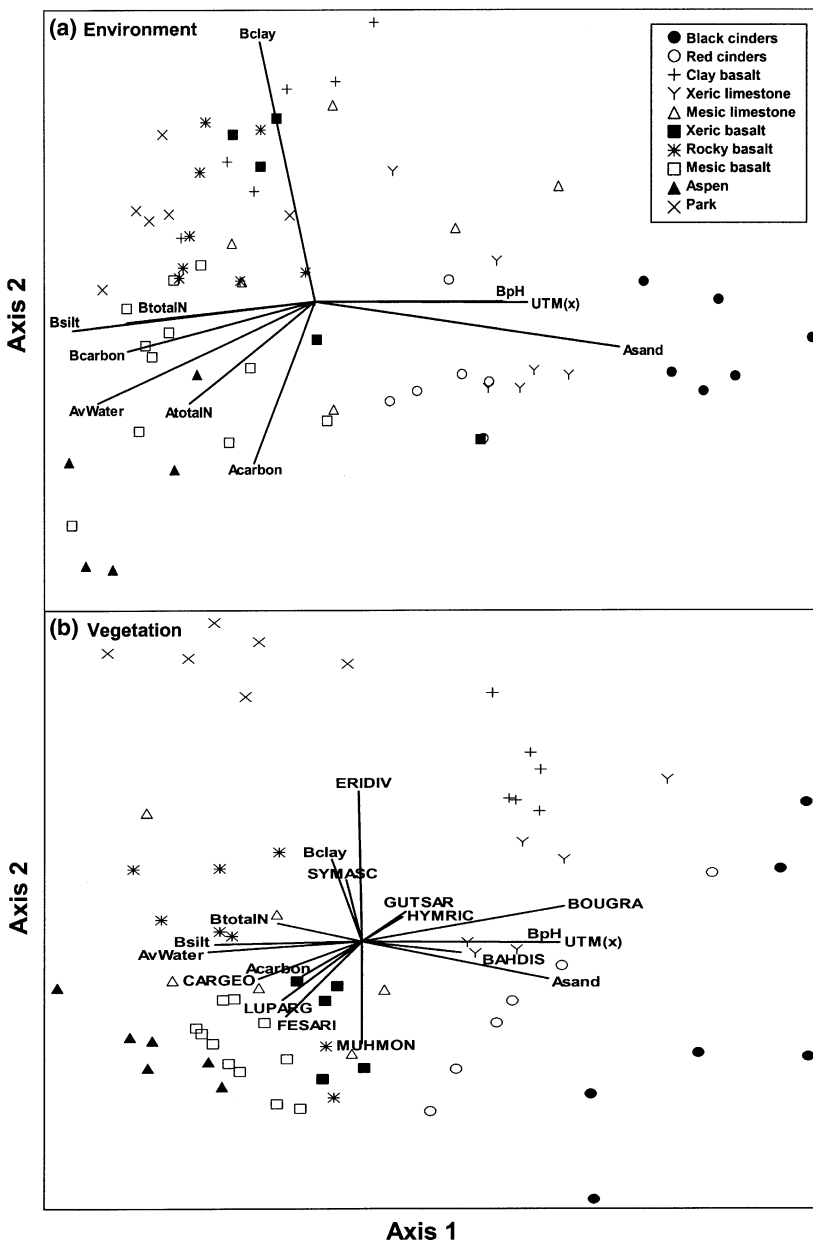
Figure 3 Principal components analysis ordination of environmental variables (a) and non-metric multidimensional scaling ordination of vegetation (b) of a *Pinus ponderosa* landscape, northern Arizona, USA. For soil variables, $A = 0–15$ cm and $B = 15–50$ cm. UTM(x) partly portrays a geographical gradient of increasing precipitation from east to west across the study area. Vector abbreviations for species in (b) are as follows: BAHDIS = *Bahia dissecta*, BOUGRA = *B. gracilis*, CARGEO = *Carex geophila*, ERIDIV = *Erigeron divergens*, FESARI = *Festuca arizonica*, GUTSAR = *Gutierrezia sarothrae*, HYMRIC = *Hymenoxys richardsonii*, LUPARG = *Lupinus argenteus*, MUHMON = *Muhlenbergia montana*, and SYMASC = *Symphyotrichum ascendens*.

Soil properties such as texture and organic C, in contrast to geomorphological variables, sharply differed among ecosystems (Table 2). The sand concentration from 0 to 15 cm in the black cinders/*Phacelia* ecosystem, for example, exceeded 90%. The red cinders/*Bahia* and limestone ecosystems also were sandy, with 0–15 cm sand concentrations averaging between 53% and 63%. Clay basalt/*Gutierrezia*, rocky basalt/*Sporobolus* and park/*Symphyotrichum* ecosystems contained the most clay from 0 to 50 cm. High clay concentrations in park/*Symphyotrichum* ecosystems, combined with the flat depressions occupied by parks, may explain early accounts that some parks were seasonally shallow lakes (Kircher, 1910). Parks have probably become drier because of hydrological alterations from livestock tanks (Rusby, 1889). Siltier textures, higher organic C and 0.03–0.05 m^3 m^{-3} greater water-holding capa-

cities (Saxton *et al.*, 1986) partly distinguish the mesic basalt/*Festuca* ecosystem from other basalt ecosystems. Organic C and total N concentrations were also large in the aspen/*Lathyrus* ecosystem, probably reflecting this ecosystem's high productivity where mean ground-flora cover was highest (35%). The low-density cinders in black and red cinder ecosystems (Moore *et al.*, 1976) result in higher gravel and lower N and organic C contents volumetrically than on a weight basis (Welch & Klemmedson, 1975), decreasing soil fertility in these ecosystems.

Mean pH ranged from 5.9 to 7.0 across ecosystems, exceeding 6.5 in xeric limestone/*Bouteloua*, clay basalt/*Gutierrezia*, and cinder ecosystems (Table 2). The mesic limestone/mixed flora ecosystem had among the lowest 0–15 cm pH; we also did not detect appreciable $CaCO_3$

Table 2 Soil properties of forest ecosystems of a northern Arizona *Pinus ponderosa* landscape. All variables are % by weight except for pH

Variable	Depth (cm)	Ecosystem type									
		Black cinders	Red cinders	Clay basalt	Xeric limestone	Mesic limestone	Xeric basalt	Rocky basalt	Mesic basalt	Aspen	Park
Gravel	0–15	48a (17)*	39abc (23)	45ab (24)	11e (18)	22d (40)	36bc (19)	35bc (31)	31cd (24)	41abc (32)	37bc (23)
	15–50	38bc (25)	39abc (27)	54a (13)	26c (60)	49ab (33)	53a (30)	48ab (31)	36bc (39)	31c (48)	49ab (9)
Sand	0–15	93a (5)	63b (6)	30ef (17)	63b (19)	53bc (26)	45cd (44)	35def (14)	35def (23)	39de (15)	27f (22)
	15–50	87a (20)	57b (8)	24e (6)	51bc (20)	40cd (37)	35de (51)	31de (22)	35de (28)	37de (23)	31de (32)
Silt	0–15	6f (62)	28e (12)	38cd (20)	24e (15)	32de (31)	41bc (32)	44bc (9)	53a (15)	49ab (12)	42bc (21)
	15–50	10d (120)	32bc (14)	31bc (24)	25c (11)	31bc (58)	36b (14)	35b (20)	48a (18)	49a (10)	36b (31)
Clay	0–15	1d (123)	8c (15)	31a (35)	13c (69)	14c (36)	14c (55)	21b (18)	12c (17)	12c (27)	31a (25)
	15–50	4f (154)	10ef (42)	44a (17)	24cd (44)	29bc (45)	28bc (53)	34b (29)	17de (29)	14e (33)	34bc (20)
pH	0–15	6.5bcd (3)	6.6b (1)	6.6bc (4)	6.9a (3)	6.1ef (5)	6.3de (5)	6.0fg (2)	6.1fg (4)	6.4cde (3)	5.9g (3)
	15–50	6.7b (2)	6.8ab (1)	6.8b (4)	7.0a (2)	6.4c (8)	6.3cd (5)	6.0e (4)	6.2cde (3)	6.2cde (3)	6.1de (1)
$CaCO_3$†	0–15	0.8 (23)	0.0 (0)	0.0 (0)	3.3 (191)	0.1 (108)	0.7 (172)	0.4 (156)	0.3 (117)	0.3 (100)	0.3 (158)
	15–50	0.8 (138)	0.7 (244)	0.0 (0)	28.0 (195)	1.7 (132)	0.1 (214)	0.6 (218)	0.4 (70)	1.8 (217)	0.6 (220)
Organic C	0–15	1.5cde (63)	2.1bc (24)	1.3e (17)	1.1e (24)	1.3de (35)	1.3de (23)	1.9bcd (28)	2.2b (31)	3.1a (28)	1.6bcde (16)
	15–50	0.3d (51)	0.9bc (31)	1.0bc (37)	0.9bc (31)	0.8c (28)	1.0bc (24)	1.1bc (34)	1.2b (42)	1.7a (23)	1.0bc (16)
Total N	0–15	0.07f (36)	0.12bcd (23)	0.13bcd (17)	0.07f (39)	0.08ef (27)	0.09def (33)	0.11cde (18)	0.14bc (33)	0.26a (30)	0.15b (12)
	15–50	0.02e (111)	0.07d (20)	0.11b (13)	0.08cd (43)	0.07d (24)	0.08cd (35)	0.08cd (29)	0.10bc (34)	0.15a (18)	0.13ab (16)
Moisture‡	0–15	0.5d (60)	1.7cd (59)	–	4.1bc	–	–	–	5.6b (27)	10.7a (17)	8.4a (32)

*Values are mean (coefficient of variation). Means without shared letters within rows differ at $P < 0.05$.

†$CaCO_3$ equivalent.

‡Gravimetric soil moisture (% oven dry weight) measured on 19 June 2004 during the driest period of the year in the study area; –, not measured.

equivalents in this ecosystem. CaCO₃ equivalent was the only soil property not significantly different among ecosystems, with the highest, but variable, amount in the xeric limestone/*Bouteloua* ecosystem. While pH does not seem to be driven by carbonate equilibria on this landscape, high-pH ecosystems are apparently associated with parent materials rich in exchangeable bases that also occupy dry sites where leaching rates may be slower.

Principal components analysis portrayed correlations among environmental variables and their relative importance in structuring the environmental matrix, with 40% of variance explained by principal component 1, 20% by component 2 and 10% by component 3 (Fig. 3a). Component loadings were well balanced among 17 important environmental variables included in the analysis, consistent with ecosystem classification theory that ecosystem distribution is structured by multivariate combinations of environmental variables rather than only single-factor gradients (Barnes *et al.*, 1982; Host & Pregitzer, 1992; Goebel *et al.*, 2001). Variables exhibiting the highest loadings on component 1 included 0–15 cm sand (loading = −0.34), 15–50 cm silt (0.30), Universal Transverse Mercator (UTM) easting (−0.29), 0–50 cm available water (0.29), 15–50 cm C and N (both 0.27) and 15–50 cm pH (−0.26). Based on three weather stations (Fig. 1) and a regional climate study (Jameson, 1969), UTM easting is probably partly correlated with a precipitation gradient increasing by *c.* 14 cm year⁻¹ from east to west across the study area. Ecosystems containing soils with low water-holding capacities also tended to occur in eastern parts of the study area, where low precipitation may amplify these dry-soil properties (Fig. 1). Dry-season gravimetric soil moisture differed by more than a factor of 20 across ecosystems, expressing these contrasting environmental complexes (Table 2). Parent material and its influence on soil properties, modified regionally by precipitation gradients and locally by rockiness or geomorphological gradients, constrained the distribution, productivity and composition of ecosystems on this landscape.

Species composition and richness

A total of 271 plant species occurred on the 66 open-canopy plots, with some species like *Phacelia sericea* (Graham) Gray (purplefringe) of the black cinders/*Phacelia* ecosystem and *Symphyotrichum ascendens* (Lindl.) Nesom (western aster) of the park/*Symphyotrichum* ecosystem, restricted to one ecosystem type (Table 3). *Muhlenbergia minutissima* (Steud.) Swallen (annual muhly), *Nama dichotomum* (Ruiz & Pavón) Choisy (wishbone fiddleleaf) and other annuals dominated the black cinders/*Phacelia* ecosystem. These data concur with theories that annuals are successful in ecosystems of unpredictable moisture (Philippi, 1993), but may also be related to continuous disturbances caused by movements of the loose cinders (Fig. 2a). Grazing-resistant *Gutierrezia sarothrae* (Pursh) Britt. & Rusby (broom snakeweed) or *Erigeron divergens* Torr. & Gray (spreading fleabane) dominated clay basalt/*Gutierrezia* or park/*Symphyotrichum* ecosystems, prob-

ably the most heavily grazed ecosystems (Clary, 1975). Mesic limestone/mixed flora ecosystems, exhibiting intermediate soil resources (Table 2), shared species of many ecosystems and had no clear dominant species. This finding seemingly concurs with hypotheses that intermediate resource levels promote species coexistence (Tilman & Pacala, 1993).

Grass distribution differentiated closely related basalt ecosystems, with C₄ *M. montana* important in the xeric basalt/*Muhlenbergia* ecosystem and C₃ *F. arizonica* prominent in the mesic basalt/*Festuca* ecosystem (Table 3). These distributions, combined with the great importance of C₄ *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (blue grama) in climatically dry ecosystems, support predictions that C₄ species have greater water-use efficiencies and competitive abilities in dry habitats than C₃ species (Wentworth, 1983). The rocky basalt/*Sporobolus* ecosystem was distinguished by the high importance of *Sporobolus interruptus* Vasey (black dropseed), *Lathyrus laetivirens* Greene ex Rydb. (aspen peavine), and *Pedicularis centranthera* Gray (dwarf lousewort). Legumes including *Lupinus argenteus* Pursh (silver lupine), *Vicia americana* Muhl. Ex Willd. (American purple vetch) and *Lathyrus lanszwertii* var. *leucanthus* (Rydb.) Dorn (Nevada vetchling) predominated in the aspen/*Lathyrus* ecosystem. It is possible these legumes contributed to the high levels of soil N in this ecosystem (Crews, 1999). The park/*Symphyotrichum* ecosystem also contained several mesophytic species, including *Iris missouriensis* Nutt. (Rocky Mountain iris) and *Allium geyeri* S. Wats. (Geyer's onion), uncommon elsewhere.

Limestone ecosystems possessed the most species per 500-m² plot, and richness per plot also averaged > 38 species in rocky basalt/*Sporobolus*, clay basalt/*Gutierrezia* and red cinders/*Bahia* ecosystems (Fig. 4a). Black cinders/*Phacelia* and aspen/*Lathyrus* ecosystems, occupying extremes of low and high productivity and soil-resource gradients, had the fewest species per plot. The aspen/*Lathyrus* ecosystem, however, exhibited high richness per 1-m² subplot, reflecting high species densities at fine grains in this ecosystem but rapid levelling off of species richness (Fig. 4b). Ecosystem distribution predicted spatial variation in species composition and richness on this landscape reasonably well, presumably because the ecosystem framework integrated factors that were constraining composition and richness (Lapin & Barnes, 1995).

Pinus ponderosa growth

The oldest tree was dated to 1646, and all trees in the data set were of pre-settlement origin, recording growth rates in presettlement forests. Mean *P. ponderosa* diameter growth differed by nearly a factor of two across ecosystems (Fig. 5). The slowest growth occurred in the red cinders/*Bahia* ecosystem, whereas the fastest growth occurred in aspen/*Lathyrus* ecosystems containing mixed *P. ponderosa*–*Populus tremuloides* forests. Growth rates also tended to be 0.7–0.8 mm year⁻¹ higher in mesic basalt than in rocky or xeric basalt ecosystems, probably reflecting the mesic basalt's greater rooting volume because of fewer rocks and more available water. While the

Table 3 Importance values and 0.05-ha plot frequencies for 24 common and diagnostic species on 66 open-canopy plots in forest ecosystems of a northern Arizona *Pinus ponderosa* landscape. Species are arranged from dry to moist affinities, and values in bold represent ecosystems in which a species was most important. These 24 species (of 271 total detected species) are representative examples of species that were previously classified on this landscape into ecological species groups useful for distinguishing ecosystem types (Abella, 2005)

Species	Ecosystem type									
	Black cinders	Red cinders	Clay basalt	Xeric limestone	Mesic limestone	Xeric basalt	Rocky basalt	Mesic basalt	Aspen	Park
Phacelia sericea	**5 (50)***	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Nama dichotomum	**5 (33)**	0 (0)	< 1 (33)	0 (0)	< 1 (17)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Chenopodium graveolens	**22 (83)**	2 (100)	0 (0)	0 (0)	< 1 (17)	< 1 (20)	< 1 (38)	0 (0)	0 (0)	< 1 (17)
Muhlenbergia minutissima	**8 (33)**	0 (0)	0 (0)	0 (0)	< 1 (17)	< 1 (20)	< 1 (38)	< 1 (9)	0 (0)	< 1 (17)
Bahia dissecta	5 (100)	**9 (100)**	0 (0)	< 1 (67)	0 (0)	< 1 (20)	0 (0)	< 1 (27)	0 (0)	0 (0)
Bouteloua gracilis	18 (83)	14 (100)	**26 (100)**	24 (100)	2 (33)	< 1 (20)	< 1 (25)	0 (0)	0 (0)	1 (17)
Gutierrezia sarothrae	0 (0)	1 (67)	**6 (100)**	2 (83)	0 (0)	0 (0)	0 (0)	< 1 (9)	0 (0)	0 (0)
Heliomeris longifolia	0 (0)	0 (0)	**6 (83)**	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Hymenoxys richardsonii	0 (0)	< 1 (17)	**2 (100)**	3 (100)	< 1 (33)	1 (80)	< 1 (13)	< 1 (18)	0 (0)	< 1 (33)
Muhlenbergia montana	7 (17)	19 (83)	< 1 (17)	10 (50)	11 (83)	**29 (100)**	7 (75)	13 (100)	5 (83)	0 (0)
Cirsium wheeleri	0 (0)	< 1 (50)	< 1 (100)	< 1 (83)	3 (83)	**5 (100)**	3 (100)	2 (91)	< 1 (50)	0 (0)
Elymus elymoides	**9 (83)**	8 (100)	4 (100)	6 (83)	11 (100)	8 (100)	11 (100)	9 (100)	10 (100)	2 (83)
Poa fendleriana	0 (0)	4 (67)	1 (67)	2 (100)	**4 (83)**	5 (100)	10 (100)	4 (100)	4 (100)	< 1 (17)
Blepharoneuron tricholepis	0 (0)	0 (0)	< 1 (17)	0 (0)	2 (67)	2 (80)	**5 (75)**	< 1 (18)	0 (0)	< 1 (17)
Sporobolus interruptus	0 (0)	0 (0)	0 (0)	0 (0)	< 1 (33)	0 (0)	**6 (63)**	0 (0)	0 (0)	0 (0)
Carex geophila	0 (0)	< 1 (17)	< 1 (17)	< 1 (17)	2 (83)	3 (100)	9 (100)	**11 (100)**	6 (100)	1 (50)
Festuca arizonica	0 (0)	0 (0)	0 (0)	3 (67)	9 (67)	9 (80)	1 (50)	**18 (100)**	17 (100)	0 (0)
Lupinus argenteus	0 (0)	0 (0)	0 (0)	< 1 (17)	2 (50)	2 (60)	< 1 (25)	**9 (100)**	13 (100)	< 1 (33)
Vicia americana	0 (0)	0 (0)	0 (0)	< 1 (17)	2 (100)	< 1 (40)	1 (50)	2 (82)	**6 (100)**	0 (0)
Lathyrus lanszwertii	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	< 1 (36)	**6 (67)**	0 (0)
Erigeron divergens	0 (0)	0 (0)	11 (100)	2 (100)	2 (83)	2 (80)	3 (75)	1 (73)	0 (0)	**19 (100)**
Muhlenbergia wrightii	0 (0)	0 (0)	3 (83)	0 (0)	0 (0)	0 (0)	< 1 (13)	< 1 (9)	0 (0)	**13 (100)**
Coreopsis tinctoria	0 (0)	0 (0)	< 1 (17)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	**6 (83)**
Symphyotrichum ascendens	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	**6 (100)**

*Values are mean importance value (% frequency). Importance values are in % and are the average of relative cover and relative frequency.

black cinders/*Phacelia* ecosystem contained inhospitable surface soils, variable, but on average rapid, diameter growth occurred once a tree became established. This paradox may result because of minimal ground-flora competition, deep subsoils (> 1.5 m) consisting of alternating cinder–soil layers retaining subsoil moisture, or loose soils facilitating development of extensive, branched root systems (Haasis, 1921). Colton (1932) also noted that rapid diameter growth occurred on black cinder soils near Sunset Crater in the study area, and Lindsey (1951) found that the greatest mean increment of 3.4 mm year^{-1} among central New Mexico soils he studied occurred on volcanic cinder soils.

Previous research in south-western *P. ponderosa* forests has produced conflicting results on whether *P. ponderosa* growth differs among land classification units (Meurisse *et al.*, 1975; Stansfield *et al.*, 1991). Mathiasen *et al.* (1987), for example, found that site index did not differ among seven vegetation-based habitat types in Colorado, New Mexico and northern Arizona. Verbyla & Fisher (1989) also concluded that habitat types did not reliably predict *P. ponderosa* site index in southern Utah because of wide environmental variation within habitat types. Meurisse *et al.* (1975), however, reported site indices ranging from 17 to 26 m (base age 100 years) that

differed significantly among 12 northern Arizona soil series. Our findings combined with those of Lindsey (1951) and Meurisse *et al.* (1975) suggest that land classifications such as soil or ecosystem classification are useful for predicting *P. ponderosa* growth, because these classifications incorporate environmental variables affecting growth (Cox *et al.*, 1960).

Classification in dense stands

A possible criticism of this ecosystem classification is that it was developed in open stands of pre-settlement origin, whereas most of the landscape contains dense post-settlement stands typically exceeding 1000 trees ha^{-1}, exhibiting low ground-flora cover, and often requiring the most intensive restoration (Abella & Covington, 2004). Species composition differentiated by ecosystem type even more strongly in dense than in open stands, and ecosystems in dense stands also differentiated along rock cover, texture and other gradients as in open stands (Fig. 6). Mesic limestone/mixed flora ecosystems in dense stands had sandy soil textures and no clear dominant species similar to their open counterparts, while grass distribution and environmental gradients distinguished basalt ecosystems. The ecosystem specificity of plant composition may have intensi-
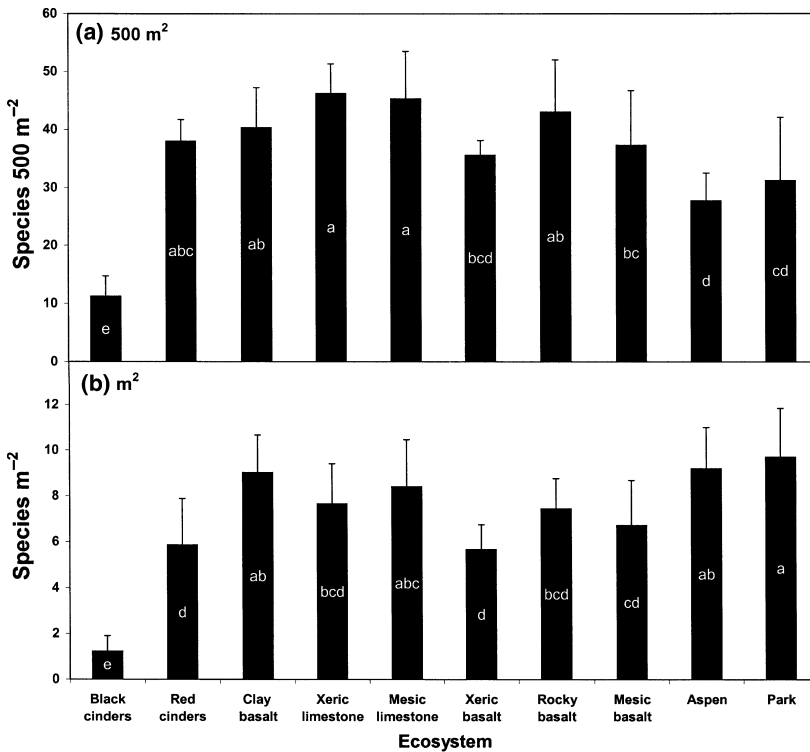
Figure 4 Mean species richness (a) per 500-m^2 plot and (b) per 1-m^2 subplot for forest ecosystems of a *Pinus ponderosa* landscape, northern Arizona, USA. Means without shared letters differ at $P < 0.05$. Error bars are 1 SD.
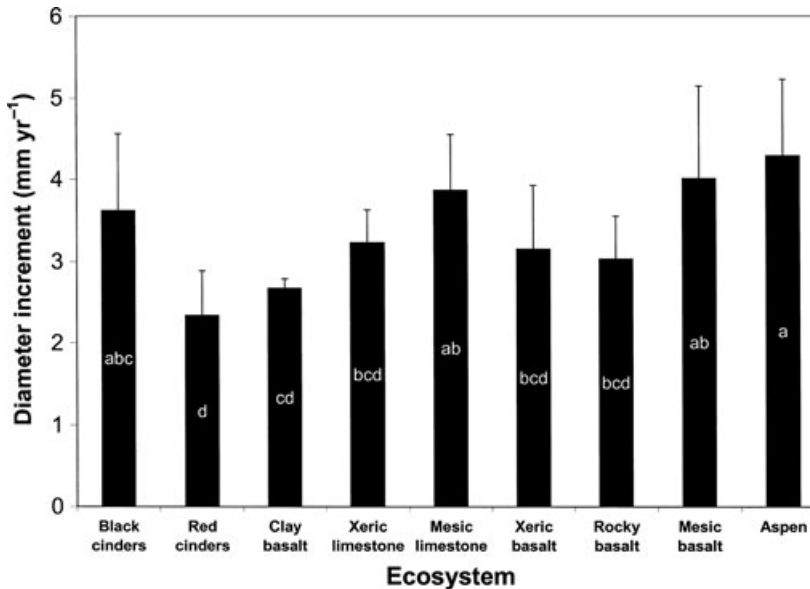
Figure 5 Mean *Pinus ponderosa* diameter increment among forest ecosystems of a *P. ponderosa* landscape, northern Arizona, USA. Means without shared letters differ at $P < 0.05$. Error bars are 1 SD.

fied in dense stands because only high-fidelity species persisted below dense canopies, precluding more widespread and opportunistic species able to occupy open stands.

Implications for ecological restoration

Reference conditions

Estimating reference conditions is a major goal in restoration ecology and conservation biogeography (White & Walker, 1997). Reference conditions for Arizona *P. ponderosa* forests are usually considered to be *c.* 1875 (European settlement) because this is the most recent time at which these forests are thought to have been free of degrading factors such as fire exclusion (Moore *et al.*, 1999). Three lines of evidence suggest that ecosystems similar to those classified in this study occurred on this landscape at the time of settlement: (1) abiotic variables such as soil texture forming the backbones of ecosystems are considered relatively stable landscape features (Palik *et al.*, 2000), (2) major differences in tree growth occurred among sites in pre-settlement forests (Fig. 5) and (3) historical reports and photographs provide accounts of
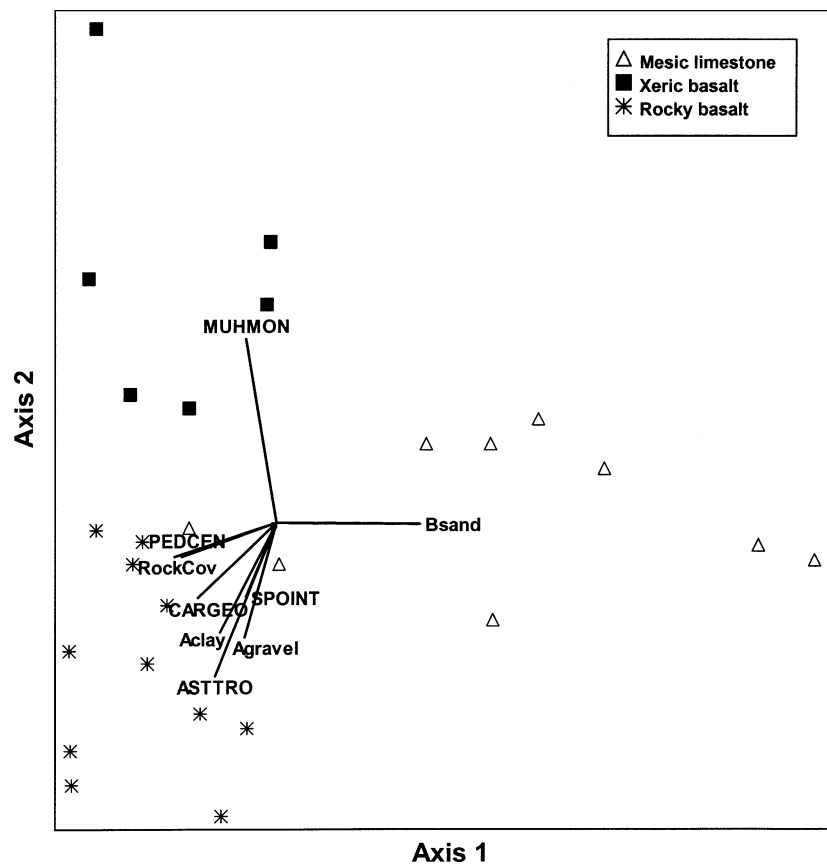
Figure 6 Non-metric multidimensional scaling ordination of ground-flora vegetation and ecosystem type classifications for 26 plots in dense *P. ponderosa* post-settlement stands (> 1000 trees ha^{-1}), northern Arizona, USA. For soil variables, $A = 0$–15 cm and $B = 15$–50 cm depth. Vector abbreviations for species are as follows: ASTTRO = *Astragalus troglodytus*, CARGEO = *Carex geophila*, MUHMON = *Muhlenbergia montana*, PEDCEN = *Pedicularis centranthera*, SPOINT = *Sporobolus interruptus*.

geographically specific occurrences of ecosystems like parks and sites exhibiting different soil texture and rock cover (Rusby, 1889; Leiberg *et al.*, 1904; Kircher, 1910). An important point is that while grazing and other factors may have altered the species composition of some ecosystems since settlement (Hanson, 1924), these are similar ecosystem types but with different species composition. A given ecosystem type may contain multiple species compositions during different time periods (Archambault *et al.*, 1990; Goebel *et al.*, 2001; Abella *et al.*, 2003). This is consistent with a guiding premise of ecosystem classification that vegetation comprises only one, and usually the least stable, of three basic landscape ecosystem components of geomorphology, soils and vegetation (Barnes *et al.*, 1982).

Reference conditions for herbaceous vegetation are not well known in *P. ponderosa* forests, similar to many ecosystems (Moore *et al.*, 1999), hampering efforts to define and restore target communities (Bakker *et al.*, 2000). Although historical accounts suggest that most native species currently on this landscape occurred in pre-settlement forests, these accounts provide little information about species distributions and, unfortunately, were also recorded after the initiation of heavy livestock grazing (Vasey, 1888; Britton, 1889). While herbarium records and other reconstructive methods (e.g. Kerns *et al.*, 2003) may provide additional clues to past composition, the present study's information on modern ecosystems is one of the few currently available references on species–soil

relationships. Although imperfect like other reference information, and best used in combination with other data sources, modern ecosystems are an important source of reference information (White & Walker, 1997; Palik *et al.*, 2000).

The current distributions of some species among ecosystems, for example, probably places approximate bounds on where these species occurred in pre-settlement forests (Table 3). In contrast to *M. montana*, for instance, *F. arizonica* is absent from dry ecosystems such as the red cinders/*Bahia* ecosystem and probably did not occur in such ecosystems in pre-settlement forests. *Festuca arizonica* is a C$_3$ species poorly adapted to xeric sites (Sage & Monson, 1999). If a land manager has limited funds to purchase seeds for revegetating a moist, loamy basalt site burned by wildfire, for example, revegetating the site with *F. arizonica* and other native species of the mesic basalt/*Festuca* ecosystem seems more accurate than using general species mixes that may not have grown on these sites. Furthermore, experiments with current ecosystems, such as re-introducing fire and comparing the responses of different ecosystems, may enhance our understanding of past composition of the diverse ecosystems on this landscape.

Prioritization and scale

Ecological restoration in the study area has largely been prioritized near the city of Flagstaff in the wildland–urban interface, which is prudent because recent wildfires in

P. ponderosa forests have threatened human settlements (Allen *et al.*, 2002). This approach may well not prioritize other ecosystems farther from settlements, however, that also require restoration (Palik *et al.*, 2000). The red cinders/*Bahia* ecosystem, for example, was historically rare, based on its soil distribution, occupying < 1840 ha or < 1.7% of the study area (Miller *et al.*, 1995). About 9/32 (28%) of this ecosystem's mapping units (> 30% of its area) have also been burned by crown fires since 1950, suggesting that the red cinders/*Bahia* ecosystem is the most endangered landscape ecosystem in the study area. Priority could be given to restoring this ecosystem's remaining mapping units to forestall further losses by crown fires. This application illustrates that ecosystem classification might be useful as a data layer in geographical information systems for gap analysis (Scott *et al.*, 1993).

Ecosystem turnover occurs at broad extents on this landscape, with mapping units sometimes exceeding 1000 ha (Miller *et al.*, 1995). This differs from ecosystem classification in many eastern US forests where ecosystem turnover is spatially rapid (Lapin & Barnes, 1995; McNab *et al.*, 1999; Goebel *et al.*, 2001). Broad-extent turnover suggests that restoring dispersed mapping units of different ecosystems or large areas will be required to encompass ecosystem diversity in restoration on this landscape. The sizes of restoration units required to encompass multiple ecosystem types, for instance, could be conceptualized as an ecosystem–area curve. Financial and other resources for conducting restoration are often limited, suggesting that an important topic of future research is estimating the optimal sizes and distributions of restoration units to maximize cumulative ecosystem diversity included in restoration.

CONCLUSION

Ecosystem distribution on this landscape followed the distribution of soil properties and parent materials, modified by regional precipitation gradients and locally by variables such as rock cover and geomorphology. An important area of future research is examining rare ecosystems such as springs or deep ravines (Crawford Zimmerman *et al.*, 1999) which we did not sample and which may be keystone ecosystems requiring special restoration (Stohlgren *et al.*, 1997). It is important to recognize that vegetation is one of the more transient and easily changed ecosystem components, whereas properties such as soil parent material are fixed for long time periods. This persistence suggests that the same basic ecosystems currently on this landscape occurred at the time of settlement. Multiple classifications, such as vegetation or stand condition classes, in combination with ecosystem classification, will probably provide the most comprehensive site information data base to guide restoration. A given ecosystem type may contain constituent sites widely differing in current conditions, with the mesic basalt/*Festuca* ecosystem, for example, currently containing sites burned by crown fire or showing indications of overgrazing. Relatively intact sites within ecosystems, however, exhibited high degrees of similarity, suggesting that

reference conditions within ecosystem types may be similar. This study provides an initial ecosystem framework for ecological restoration on this landscape that can be improved by future research that: (1) measures past species composition, fire regime and stand structure reference conditions among ecosystems, (2) estimates ecosystem-specific differences between reference and current conditions, (3) identifies target communities for restoration and ecosystem-specific vegetation successional sequences and (4) replicates restoration experiments across ecosystem types to measure ecosystem-specific responses.

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BIOSKETCHES

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