ORIGINAL ARTICLE

Understorey plant community structure in lower montane and subalpine forests, Grand Canyon National Park, USA

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ABSTRACT

Aim Our objectives were to compare understorey plant community structure among forest types, and to test hypotheses relating understorey community structure within lower montane and subalpine forests to fire history, forest structure, fuel loads and topography.

Location Forests on the North Rim of Grand Canyon National Park, Arizona, USA.

Methods We measured understorey (< 1.4 m) plant community structure in 0.1-ha plots. We examined differences in univariate response variables among forest types, used permutational MANOVA to assess compositional differences between forest types, and used indicator species analysis to identify species driving the differences between forest types. We then compiled sets of proposed models for predicting plant community structure, and used Akaike's information criterion (AIC_C) to determine the support for each model. Model averaging was used to make multi-model inferences if no single model was supported.

Results Within the lower montane zone, pine–oak forests had greater understorey plant cover, richness and diversity than pure stands of ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Engelm.). Plant cover was negatively related to time since fire and to ponderosa pine basal area, and was highest on northern slopes and where Gambel oak (*Quercus gambelii* Nutt.) was present. Species richness was negatively related to time since fire and to ponderosa pine basal area, and was highest on southern slopes and where Gambel oak was present. Annual forb species richness was negatively related to time since fire. Community composition was related to time since fire, pine and oak basal area, and topography. Within subalpine forests, plant cover was negatively related to subalpine fir basal area and amounts of coarse woody debris (CWD), and positively related to Engelmann spruce basal area. Species richness was negatively related to subalpine fir basal area and amounts of CWD, was positively related to Engelmann spruce basal area, and was highest on southern slopes. Community composition was related to spruce, fir and aspen basal areas, amounts of CWD, and topography.

Main conclusions In montane forests, low-intensity surface fire is an important ecological process that maintains understorey communities within the range of natural variability and appears to promote landscape heterogeneity. The presence of Gambel oak was positively associated with high floristic diversity. Therefore management that encourages lightning-initiated wildfires and Gambel oak production may promote floristic diversity. In subalpine forests, warm southern slopes and areas with low amounts of subalpine fir and CWD were positively associated with high floristic diversity. Therefore the reduction of CWD and forest densities through managed wildfire may promote floristic diversity, although fire use in subalpine forests is inherently more difficult due to intense fire behaviour in dense spruce–fir forests.

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INTRODUCTION

Management of montane and subalpine forests requires an understanding of the range of natural variability of understorey plant community structure. 'Natural variability' is the range of ecological conditions found in intact systems, and in North America is often regarded as the range of conditions within the ecosystem prior to Euro-American settlement (Landres *et al.*, 1999). Various approaches have been used to quantify the natural variability of tree species in south-western forests, in particular, dendrochronological methods have been used to determine overstorey reference conditions (Fulé *et al.*, 1997; Mast *et al.*, 1999). However, less information is available concerning the range of natural variability of understorey plant communities.

One useful approach used to examine the variability of understorey communities has been to measure relict sites that have been relatively undisturbed since Euro-American settlement (Gildar *et al.*, 2004). Unfortunately, the vast majority of upland forests in the western USA have been affected by commercial logging, overgrazing by domestic livestock (Belsky & Blumenthal, 1997), and the exclusion of surface fires (Agee, 1993). However, Grand Canyon National Park (GCNP) contains the largest unharvested (Warren *et al.*, 1982), minimally grazed, and occasionally burned (Fulé *et al.*, 2003a) forest ecosystem in Arizona, and therefore provides valuable sites for measuring natural variability. We focused our study on lower montane and subalpine forests (*sensu* Marr, 1961; Brown & Lowe, 1980). The lower montane zone (2200–2350 m, hereafter 'montane') is dominated by ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Engelm.) and Gambel oak (*Quercus gambelii* Nutt.) forest. The upper montane zone (2350–2600 m) consists of dense ponderosa pine and mixed conifer forests that have been heavily invaded by shade-tolerant and fire-intolerant trees such as white fir [*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.] (Fulé *et al.*, 2004; Mast and Wolf, 2004); the plant community structure within this zone was examined by Huisinga *et al.* (2005) and was not included in this analysis. The subalpine zone (2600–2900 m) is a diverse mixture of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.], aspen (*Populus tremuloides* Michx.) and mixed conifer forests with ponderosa pine on southern slopes.

Natural variability of understorey plant community structure is determined by complex interactions of biotic and abiotic factors. Our use of the phrase 'plant community structure' is inclusive, including plant species composition, richness and abundance (Tilman, 1982; Krebs, 1994). In upland forest ecosystems of western North America, it has been proposed that understorey plant community assemblages are strongly influenced by fire (Crawford *et al.*, 2001; Schoennagel *et al.*, 2004), forest structure and tree species composition (Naumburg & DeWald, 1999; Chipman & Johnson, 2002), fuel load (Laughlin *et al.*, 2004) and topography (Zobel *et al.*, 1976).

Montane forest communities in the south west have evolved in an environment that historically burned every 2–20 years by low-intensity surface fires (Swetnam & Baisan, 1996; Moore *et al.*, 1999). Dendrochronological analyses of our study sites have not detected any stand-replacing fires in the montane zone before Euro-American settlement (Fulé *et al.*, 2003a), although stand-replacing fires appear to have occurred in northern Rocky Mountain ponderosa pine forests (Ehle & Baker, 2003; Pierce *et al.*, 2004). Subalpine plant communities in North America are adapted to an evolutionary environment characterized by short growing seasons and a disturbance regime of infrequent, high-intensity crown fires (Agee, 1993; Kipfmueller & Baker, 2000; Johnson *et al.*, 2001; Fulé *et al.*, 2003b). In both systems, fire has strong direct effects on understorey plant community structure by altering site conditions and microclimate. Fire also affects forest structure and fuel loads which, in turn, may directly influence the understorey plant community.

Plant community structure may be indirectly related to fire history through the effect of fire on forest structure: established overstorey trees outcompete many herbaceous species for resources (Riegel *et al.*, 1995). In montane and subalpine systems, plant production and species richness are generally positively related to light availability mediated through abundances of conifer and hardwood tree species (Daubenmire, 1943; Oosting & Reed, 1952; Ellison, 1954; Langenheim, 1962; Fonda & Bliss, 1969; Reynolds, 1969; Despain, 1973; Ffolliott, 1983; Tapia *et al.*, 1990; Stromberg & Patten, 1991; Moore & Deiter, 1992; Reich *et al.*, 2001). It has been shown that species richness is higher in conifer stands with greater light availability (Chipman & Johnson, 2002); plant production in aspen forests decreases as conifer abundance increases; and clearcutting spruce–fir stands in Colorado increases forage production (Kranz & Linder, 1973; Regelin and Wallmo, 1978; Mueggler, 1985). Hardwood species, such as aspen and Gambel oak, might have a positive effect on herbaceous plant communities relative to conifers by increasing litter quality through greater litterfall nitrogen (Daubenmire, 1953; Klemmedson, 1987, 1991; Reich *et al.*, 2001), and by changing the quality of light in the understorey.

Plant community structure may also be indirectly related to fire history through fire's reducing effects on fuel loads. Accumulated litter can intercept light, alter soil microclimates, form physical barriers to plant emergence (Facelli & Pickett,

1991), and affect germination (Sydes & Grime, 1981). Previous studies on the North Rim of GCNP have demonstrated that recently burned montane forests have shallower duff layers (semi-decomposed leaf litter) and greater understorey species richness than fire-excluded forests (Gildar *et al.*, 2004; Laughlin *et al.*, 2004; Huisinga *et al.*, 2005). Subalpine forests are known for an abundance of large coarse woody debris (CWD) (Langenheim, 1962; Despain, 1973; Crouch, 1985), which can also influence patterns of understorey vegetation.

Topography can affect community structure in the region because of increased insolation on southern slopes and prolonged snow packs on northern slopes (Fonda & Bliss, 1969; Kuramoto & Bliss, 1970; Douglas, 1972; Canaday & Fonda, 1974; Anderson *et al.*, 1979). Increased insolation on southern exposures raises soil temperatures and evaporation rates, and reduces the duration of the winter snow pack (Patten, 1963). The shorter growing season in areas of deep snow may be the most critical environmental factor affected by snow cover (Knight *et al.*, 1977). Subalpine plants commonly wilt at midday or while affected by sunflecks in response to increased insolation and water stress (Young & Smith, 1979; Smith, 1981). Plant community composition was related to

moisture gradients in the Sangre de Cristo Range, Colorado, USA (Allen & Peet, 1989), and also in short-grass prairie, Canada (Lieffers & Larkin-Lieffers, 1986). These studies suggest that moisture availability mediated by topographic position can influence understorey plant community structure across many ecosystems.

Our objective was to identify the combination of these biotic and abiotic variables that provides the best model to explain variation in understorey plant community structure within montane and subalpine forests. Determining the best set of explanatory variables to make robust predictions about the structure of plant communities has been a central theme in ecology for decades. The traditional approach has been to test null hypotheses with normal theory-based statistics such as the F test; but F tests have been shown to select simpler models even when more complex ones were more appropriate (Ludden *et al.*, 1994). Model-selection techniques grounded in likelihood theory, such as Akaike's information criterion (AIC_C), are increasingly being used in ecology to draw inferences from a set of competing hypotheses (Johnson & Omland, 2004). Model selection simultaneously confronts several competing hypotheses with data, and is used to identify a single best model or, if
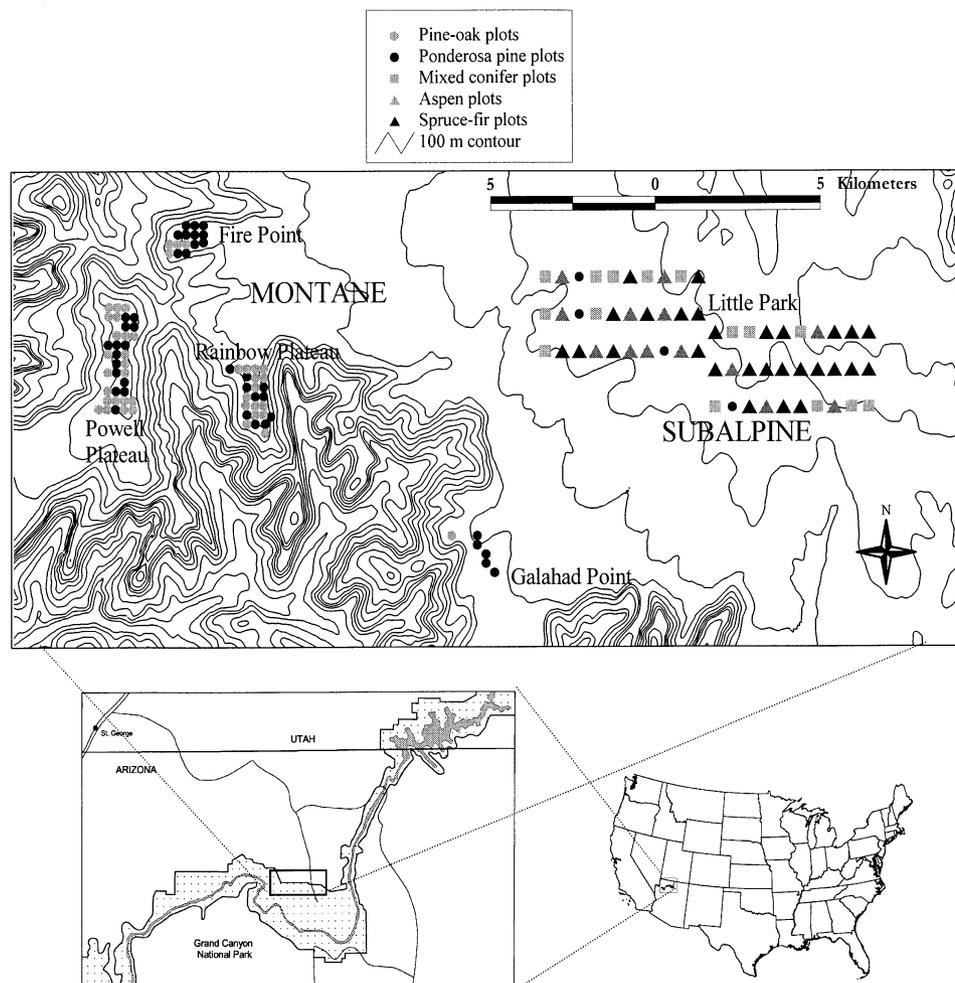
Figure 1 Distribution of study sites and plot locations on the North Rim of Grand Canyon National Park in northern Arizona, USA.

there is no single best model, to make inferences based on weighted support from several competing models (Burnham & Anderson, 2002). We used the literature and theory to develop sets of models explaining understorey plant community structure, and used AIC to determine which model or combination of models was best supported by our data.

STUDY AREA

The study sites are located on the North Rim of GCNP (Fig. 1), at the southern extent of the Kaibab Plateau, a dome-shaped land form with gradual relief and complex drainage (Merkle, 1962). Plot locations spanned an elevational gradient from 2200 to 2800 m, and contained a range of slopes, aspects and forest types. The montane forests are dominated by *P. ponderosa* and *Q. gambelii*. Montane forest understoreys on the North Rim are composed primarily of C_3 grasses such as *Poa fendleriana* (Steud.) Vasey and *Elymus elymoides* (Raf.) Swezey, unlike other ponderosa pine forests of northern Arizona, which are more often dominated by C_4 grasses such as *Bouteloua* spp. and *Muhlenbergia* spp. (Arnold, 1950). Therefore montane forests on the North Rim may be floristically more similar to Rocky Mountain lower montane forests, which are slightly cooler and wetter than other south-western pine forests.

The subalpine forests are dominated by Engelmann spruce, subalpine fir, quaking aspen, white fir and Douglas fir [*Pseudotsuga menziesii* (Mirbel) Franco]. Subalpine forest understoreys in Arizona differ floristically from those in the Rocky Mountains and the Pacific Northwest, particularly due to the absence of *Vaccinium* spp. and bryophytes (Dauben-mire, 1943; Patten, 1963; Fonda & Bliss, 1969; Despain, 1973), and the occurrence of ponderosa pine on southern slopes (Rasmussen, 1941). We refer to this zone as 'subalpine' because it is dominated by spruce–fir forests, although we acknowledge that high-elevation forests on the Kaibab Plateau differ somewhat from those in other subalpine areas in the western USA (Rasmussen, 1941; Merkle, 1954, 1962).

Soils on the North Rim have been tentatively classified as Typic Paleustalfs (A. Dewall, National Resource Conservation Service, pers. comm.) derived from Kaibab limestone. The 56-year average annual precipitation at the North Rim ranger station (elevation 2564 m) is 647 mm; much of this total precipitation falls as snow in the winter months, with an average annual snowfall of 3560 mm. Precipitation is generally lower in the montane zone and higher in the subalpine zone; Pearson (1931) estimated that Arizona ponderosa pine forests receive 540 mm and spruce–fir forests 870 mm precipitation annually. Temperatures range from an average July maximum of 25.1 °C to an average January minimum of −8.2 °C (Western Regional Climate Center, http://www.wrcc.dri.edu).

The North Rim of GCNP provides valuable sites for studying plant community reference conditions. Limited livestock grazing occurred on the Kaibab Plateau as early as 1871 (Woodbury, 1944) and significant cattle grazing occurred by 1885 (Rasmussen, 1941), but cattle and sheep grazing essentially ceased in GCNP in the mid-1930s, when a fence was built along the boundary to exclude domestic animals. This fence still excludes most domestic livestock, although occasionally animals trespass into GCNP where downed logs have damaged the fence. In addition, remote lower montane forests on the North Rim of GCNP have had relatively uninterrupted fire regimes (Fulé et al., 2002, 2003a,b) because it was difficult for firefighters to access remote areas in the early 1900s. Moreover, GCNP advocates the restoration of ecological processes, and therefore has allowed lightning-initiated fires to burn since the 1980s. As a result, these relict sites are rare examples of western forest landscapes close to the range of natural variability (Fulé et al., 2002). As such, they offer a place to test hypotheses about how plant community structure is related to biotic and abiotic factors under conditions of minimal anthropogenic disturbance.

Fire-scar analyses indicate that montane forests burned frequently before 1880 (6–9-year mean fire return interval; Fulé et al., 2003a). Around 1880, when Euro-American settlement began, the frequent surface-fire regime in south-western pine forests was disrupted by overgrazing and a successful fire-suppression policy. Post-1880, landscape-scale surface fires are therefore relatively rare events in south-western forests. Several landscape-scale surface fires occurred after 1880 in lower montane forests on the North Rim (Table 1; Fulé et al., 2003a). Many fires occurred on Powell and Rainbow Plateaus, a few

Table 1 Fire history and number of 0.1-ha plots within each forest type at each study site

| Study site | Fire history* | | Forest type | | | | |
	Number of fires since 1879	Last large fire year	Pine-oak	Ponderosa pine	Mixed conifer	Aspen	Spruce–fir
Montane (*n* = 82)							
Powell Plateau	12	1987	22	14	–	–	–
Rainbow Plateau	8	1993	15	10	–	–	–
Fire Point	5	1923	4	11	–	–	–
Galahad Point	0	1879	1	5	–	–	–
Subalpine (*n* = 60)							
Little Park	0	1879	–	4	15	13	28

*Data from Fulé et al. (2003a,b).

occurred on Fire Point, and no fires occurred on Galahad Point (Fig. 1; Table 1). The Galahad Point and Fire Point sites are more accessible to fire crews, which is probably why they have burned less frequently and longer ago than the more remote Powell and Rainbow Plateaus (Fig. 1). Inclusion of all sites in the analysis was important to assess the effects of a variable fire regime on the understorey community.

The subalpine forests at Little Park (Fig. 1) historically had a mixed-severity fire regime, which consisted of a mixture of low-intensity surface fires on warm, southern slopes (31-year mean fire return interval) and infrequent, patchy, stand-replacing fires (currently 120–230 years since the last fire) (Fulé et al., 2003b). No significant fires have occurred at Little Park since 1879 (Table 1). However, the absence of fire since 1879 at high elevation is not entirely out of the historical range of variability, since these forests typically experience long intervals between fires (Agee, 1993). Approximately 60% of the forest at Little Park originated from stand-replacing fire (Fulé et al., 2003b).

METHODS

Data collection

Permanent plots based on the National Park Service's fire-monitoring protocol (NPS, 1992; Reeberg, 1995) were established in the study area to examine forest structure, composition and fire histories across the elevation gradient. Each plot was classified according to forest type (see below) and elevation zone (montane or subalpine). Plots were located on a 300-m grid in the montane zone and a 600 × 1200-m grid in the subalpine zone. The wider grid spacing in the subalpine zone was used to capture the landscape-level heterogeneity of a mixed-severity fire regime (Fulé et al., 2003a,b). Analyses with Moran's I (unpublished) found no evidence for spatial autocorrelation among understorey variables, so plots were considered independent of each other. Each plot was 0.1 ha (20 × 50 m) in size and oriented with the 50-m sides uphill–downhill to maximize sampling variability along the elevation gradient. Forest structure-sampling methods and results were reported by Fulé et al. (2002, 2003b).

We sampled understorey plant cover, species richness and species composition in the summers of 1998–2001. Understorey plant communities were sampled using belt- and point-intercept transects. Complete species lists were made of all vascular plants (forbs, grasses, sedges, shrubs, and young trees below breast height, < 1.4 m) and ferns within two 10 × 50-m belt transects per plot. Each species found in the study area occurred on zero, one, or two belt transects per plot; these data were used for the analysis of community composition and the assessment of relative abundance. We lumped species to the generic level when vegetative characteristics were insufficient to warrant identification to species. For example, 'Chenopodium spp.' includes Chenopodium fremontii, Chenopodium berlanderii, and possibly others. Nomenclature follows USDA NRCS (2004). Species were classified into five functional groups: annual forbs

(including biennial forbs); perennial forbs (including one fern species); graminoids; shrubs; and trees. We did not sample bryophytes since they are poorly represented in south-western subalpine forests. Understorey species richness did not vary in correspondence with year of sampling, indicating that differences detected between zones or forest types were not due to inter-annual climatic differences or sampling effects.

A 50-m point-intercept transect was established in the centre of each belt transect, and the presence of vascular plants and trees below breast height was recorded at a point every 30 cm along each transect. A plant was recorded if any part of its living biomass occurred on a point along the line. We summed the data from the two transects per plot, yielding a total of 332 points per plot. Percentage foliar cover was calculated by dividing the number of points containing a plant by the 332 points per plot.

Forest floor characteristics, including duff (Oe + a horizons; semi-decomposed leaf litter) and CWD were measured on four permanent 15.24-m planar transects per plot, using the method outlined by Brown (1974) and Sackett (1980). The duff layer comprised the combined fermentation and humus layers located between the litter layer and mineral soil (Brown, 1974). Rotten and sound CWD were combined in this analysis, and included downed logs > 7.62 cm in diameter. We recorded the diameter and length of downed logs to estimate the mass of CWD in $Mg\ ha^{-1}$.

Topography was measured using an index of moisture availability (IMA) calculated for each plot as:

$$IMA = \cos(aspect - 45) \times slope\ category$$

where the following slope categories were used: 0 (< 1%), 1 (1–7%), 2 (8–15%), 3 (16–25%), 4 (> 25%). These categories were adapted from those of Batek et al. (1999) to fit the steeper western terrain. Therefore the index ranges from −4 (xeric, steep, south-facing slopes) to + 4 (mesic, north-facing slopes). This classification provides an index of moisture availability as influenced by drainage and exposure.

Time since fire

A wealth of fire history information was available for our montane study sites; fire history was not examined for subalpine forests because probably none has burned since 1879 (Fulé et al., 2003b). We estimated the number of years since the last surface fire (hereafter, 'time since fire') for each plot in the montane forests using two complementary sources: fire perimeter maps and interpolation of fire scar data. Fire perimeter maps were obtained from the National Park Service and included fires since the 1980s. Long-term fire histories of the study sites by Fulé et al. (2003a,b) included fire events since the 1700s. Plots at Powell and Rainbow Plateaus last burned 5–11 years before sampling; plots at Fire Point, 75–119 years before sampling; and plots at Galahad Point, 122 years before sampling (Table 1).

To interpolate fire scar data, we mapped the locations of all sampled trees in a GIS (ARCVIEW 3.3; ESRI, 2002). The areal

extents of fires recorded by at least 10% of the trees sampled were estimated using Thiessen polygons (Farris *et al.*, 2004). This method requires virtually no parameterization or assumptions, and closely resembles approaches used in the fire history literature (Farris *et al.*, 2004). Time since fire was determined by overlaying the plots on the fire polygons. Plots located within the perimeters of multiple fires were assigned the date of the most recent fire. This approach to mapping fires has limitations and cannot directly estimate time since fire, so the uncertainty about our estimates added error to the models. However, Farris *et al.* (2004) found a strong spatial correlation (81%) between ground-surveyed fire perimeters and Thiessen polygons generated from fire-scarred trees in a southern Arizona forest. Most of the error in their study was due to underestimation of actual fire size, so our estimates for time since fire could be high.

Previous studies of fire effects on understorey vegetation have noted potential confounding effects of time since fire and fire frequency, and have therefore held one variable constant to study the effects of the other (Fox & Fox, 1986), or have taken a multivariate approach (Watson & Wardell-Johnson, 2004). In our study, fire frequency and time since fire were highly correlated: sites that have burned recently have also burned frequently, and *vice versa* (Table 1). We chose to use time since fire, instead of fire frequency, for this analysis as the data resolution per plot was higher for time since fire.

Forest type

In companion studies of forest structure (Fulé *et al.*, 2002, 2003b), plots were classified into four forest types (ponderosa pine, mixed conifer, aspen and spruce–fir) on the basis of their overstorey importance values, which had been calculated as the sum of relative frequency (stem density) and relative abundance (basal area) (Taylor, 2000). For example, a plot was considered an aspen plot if aspen had the highest importance value of all tree species on that plot, even if there was a large conifer component. Therefore ponderosa pine forest was dominated by ponderosa pine; mixed conifer forest by Douglas-fir and white fir; aspen forest by aspen; and spruce–fir forest by Engelmann spruce and subalpine fir. *Picea pungens* Engelm. (blue spruce) was grouped with *P. engelmanii* due to identification difficulties (Fulé *et al.*, 2003b). We further subdivided plots in the ponderosa pine forest type into 'pine–oak' forest if a plot contained Gambel oak, and into 'ponderosa pine' forest if it did not contain oak (Table 1). In total, therefore, we recognized five forest types for this analysis: pine–oak, ponderosa pine, mixed conifer, aspen and spruce–fir.

Univariate analyses comparing forest types were carried out on nine plant community structural characteristics: total species richness (number of species per 0.1 ha); species richness in each of five functional groups (annual forbs, perennial forbs, graminoids, shrubs, trees); total exotic species richness; plant cover (%); plant diversity (Shannon's H'). Comparisons of univariate community characteristics between forest types were made with Kruskal–Wallis H tests ($\alpha = 0.05$) as data did not meet assumptions of normality or equal variances. Significant

results were followed by *post hoc* multiple comparisons made with Bonferroni-adjusted Mann–Whitney U tests.

Multivariate analyses

We used non-metric multidimensional scaling (NMDS) ordinations to illustrate compositional differences in understorey vegetation among plots across the study area. Ordination of species composition was conducted using PC-ORD software (ver. 4.25; McCune & Mefford, 1999). NMDS arranges the plots in a configuration that minimizes the inter-plot distances (stress). We used the Bray–Curtis distance measure (Faith *et al.*, 1987) with random starting configurations, 100 runs with real data, a maximum of 400 iterations per run, and a stability criterion of 0.00001. A Monte Carlo test with 9999 randomizations was used to determine how likely the observed stress value of the final solution would be by chance alone. Species that occurred on < 5% of the plots were omitted from the ordination and from analyses of species composition, but were included in univariate analyses of species richness (following McCune & Grace, 2002).

Comparisons of species composition among forest types within elevation zones were made with permutational MANOVA using DISTLM5 software (Anderson, 2005). This software permits the analysis of multivariate data with any distance measure and linear model, and can handle unbalanced designs. The calculated statistic is termed a 'pseudo-F' and is calculated, like a traditional F statistic, as the sum of the squared distances among groups divided by the sum of the squared distances within groups (for details see Anderson, 2001; McArdle & Anderson, 2001). Data were untransformed and unstandardized. Dissimilarities were calculated using the Bray–Curtis distance measure. If differences were detected between groups, pairwise comparisons were made with a pseudo-t statistic (Anderson, 2001). P values were calculated by permuting the observations 9999 times, so no assumptions regarding the distributional form of the data were required.

The indicator species analysis (ISA) routine in PC-ORD was used to explain the results of the permutational MANOVA by determining which species were most abundant and most frequent within the defined groups. Groups were defined based on results of the permutational MANOVA. In particular, forest types that did not differ in community composition were grouped together for the ISA. This method allowed us to detect which species differed between elevation zones, and which drove the statistical differences between forest types. An indicator value (INDVAL) is the product of the relative abundance (calculated by species presence on number of belts per plot) and relative frequency (calculated by species presence on number of plots) of a species (Dufrêne & Legendre, 1997). INDVAL was calculated for each species in each grouping (between elevation zones and among forest types within each zone). Species were considered to be indicators of the group in which they had the largest INDVAL. Indicator species had to have $P < 0.05$ (assessed using Monte Carlo randomizations with 999 permutations) and INDVAL > 25 (Dufrêne & Legendre, 1997). An INDVAL of 25 would occur, for example,

Table 2 Mean (±SD) and range of independent variables* used in multivariate and univariate multiple regressions

Variable set	Montane		Subalpine	
Independent variable	Mean ± SD	Range	Mean ± SD	Range
Fire history				
Time since fire (years)	58 ± 47	5–119	122	122
Topography				
IMA	−0.6 ± 1.6	−3.9–2.9	−0.5 ± 1.6	−3.6–3.9
Forest structure (basal area; m² ha⁻¹)*				
Ponderosa pine	22.4 ± 11.7	0.8–56.6	4.2 ± 5.5	0–31.1
Gambel oak	0.8 ± 1.4	0–6.8	–	–
Aspen	0.001 ± 0.005	0–0.04	5.0 ± 4.4	0–19.0
Engelmann spruce	–	–	8.7 ± 6.7	0–28.6
Subalpine fir	–	–	6.9 ± 8.2	0–30.6
Fuel load				
Duff-Oa + e horizon (cm)	2.2 ± 1.2	0.6–7.1	2.5 ± 1.2	0.03–5.61
Coarse woody debris (Mg ha⁻¹)	12.6 ± 24.4	0–142.4	49.9 ± 47.1	0–214.5

*Only variables that were used in the final models are included; see Fulé *et al.* (2002, 2003b) for full details of forest structure at these sites.

if a species occurred on 50% of the plots in a group and had a relative abundance of at least 50% in that group.

Model selection

The first step in model selection is the articulation of several biologically plausible models (Johnson & Omland, 2004). Each model is composed of a response variable (e.g. plant cover), a list of predictor variables (e.g. time since fire), and the postulated sign of the relationship between each predictor and the response (Tables 3 & 4). We used 10 plant community structural characteristics as response variables: total species richness; species richness in each of five functional groups (annual forbs, perennial forbs, graminoids, shrubs, trees); total exotic species richness; plant cover; plant diversity; understorey community composition. We followed USDA NRCS (2004) to classify plant species as exotic or non-native in North America.

Explicit mathematical models of plant community structure in these ecosystems were uncommon in the literature, but general hypotheses or statements about how plant communities are structured were abundant. We included a hypothesis for testing if: (1) a significant relationship between predictor variables and a response variable of interest in this study was presented in the literature, or (2) a general statement was proposed in the literature about how communities were structured. An example of the first type is 'the number of herbaceous species was inversely related to the percent cover of evergreen trees and shrubs in the community ($R^2 = 0.38$)' (Zobel *et al.*, 1976, p. 151). Examples of the second type, which were much more common, include 'there is usually a luxuriant herbaceous growth under the aspen' (Patten, 1963, p. 380), or the 'herbaceous understorey in spruce–fir stands is very sparse' (Ellison, 1954, p. 174). In some cases we created combinations from simpler models, and some models were used to test response variables beyond those originally specified. We restricted our attention to models with no more than four independent variables so that models could be applied practically by other researchers. The

predictor variables used are listed in Table 2, and the sets of models and their sources are listed in Tables 3 and 4 for the montane and subalpine zones, respectively.

For univariate response variables we used JMP-IN 5.1.2 software (SAS Institute, 2004) to obtain residual sums of squares for each model tested. For understorey community composition, we used distance-based multivariate multiple regression (McArdle & Anderson, 2001; see Anderson *et al.*, 2004 for another example of this procedure) via DISTLM5 to obtain residual sums of squares for each model tested.

For each response variable, we calculated AIC_C for each model in the set (Tables 3 and 4). The AIC_C value for each model in the set was rescaled to Δ_i by subtracting the AIC_C of the model with the smallest AIC_C. The resulting Δ_i values were then converted to Akaike weights (w_i) as:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R} \exp\left(\frac{1}{2}\Delta_i\right)}$$

where R is the number of models in the set (for details see Burnham & Anderson, 2002). The w_i of the models in a set sum to 1; each w_i can be interpreted as the probability that it is the best model in the set.

If no single model was overwhelmingly supported by the data ($w_i > 0.95$), we used model averaging to make multi-model inferences (Burnham & Anderson, 2002). Model averaging entails calculating a weighted average of parameter estimates ($\hat{\theta}$),

$$\hat{\theta} = \sum w_i \hat{\theta}_i$$

where $\hat{\theta}_i$ is the parameter estimate from the ith model. In these cases we ordered the models from highest to lowest w_i and made inferences on the subset of models where $\Sigma w_i > 0.95$. Results were very similar if we used this subset of models or the full set of models (data not shown).

If the sign of an explanatory variable in the final model differed from its sign in a bivariate relationship with the

Table 3 Sets of proposed models used in model selection for understorey plant community structure in lower montane forests. Community composition (a multivariate metric) was scaled using multivariate multiple regression by Anderson (2005)

Response variable	Model	Hypothesized explanatory variables and signs of relationships (if applicable)	Source(s)
Cover	1	(−) Time since fire	Harris & Covington (1983), Oswald & Covington (1983), Vose & White (1991)
	2	(−) Pine	Merkle (1962), Ffolliott (1983), Moore & Deiter (1992), Naumburg & DeWald (1999)
	3	(+) Oak	Reynolds et al. (1970), Klemmedson (1987, 1991), Rosenstock (1998)
	4	(+) IMA	Zobel et al. (1976)
	5	(−) Pine ($\exp^{-x}$)	McPherson (1993)
	6	(−) Time since fire, (−) Pine	Griffis et al. (2001)
	7	(−) Pine, (−) Duff	Daubenmire (1943)
	8	(−) Time since fire, (−) Pine, (−) Duff	Covington & Moore (1994)
	9	(−) Time since fire, (−) Pine, (+) Oak	Combination of models 1, 2 and 3
	10	(−) Time since fire, (−) Pine, (+) Oak, (+) IMA	Combination of models 4 and 9
Richness*	1	(−) Pine	Allen et al. (1991)
	2	(+) Oak	Reynolds et al. (1970), Klemmedson (1987, 1991), Rosenstock (1998)
	3	(+) IMA	Lieffers & Larkin-Lieffers (1986), Chipman & Johnson (2002)
	4	(−) Duff	Laughlin et al. (2004)
	5	(−) Pine, (−) IMA	Zobel et al. (1976)
	6	(−) Time since fire, (−) Pine	Crawford et al. (2001), Griffis et al. (2001)
	7	(−) Time since fire, (−) Pine, (−) Duff	Covington & Moore (1994)
	8	(−) Time since fire, (−) Pine, (+) Oak	Combination of models 2 and 6
	9	(−) Time since fire, (−) Pine, (+) Oak, (+) IMA	Combination of models 3 and 8; Chipman & Johnson (2002)
Diversity (H')	1	(+) IMA	Lieffers & Larkin-Lieffers (1986), Chipman & Johnson (2002)
	2	(+) Oak	Reynolds et al. (1970), Klemmedson (1987, 1991), Rosenstock (1998)
	3	(−) Time since fire, (−) Pine, (−) Duff	Covington & Moore (1994)
	4	(−) Time since fire, (−) Pine, (−) Duff, (+) IMA	Combination of models 1 and 3
	5	(−) Time since fire, (−) Pine, (−) Duff, (+) Oak	Combination of models 2 and 3
	6	(−) Time since fire, (−) Pine, (+) Oak, (+) IMA	Combination of models 1 and 5 (excluding duff to reduce complexity)
Community composition	1	Time since fire	Vose & White (1991), Watson & Wardell-Johnson (2004)
	2	Pine	Naumburg & DeWald (1999), Naumburg et al. (2001)
	3	IMA	Lieffers & Larkin-Lieffers (1986), Allen & Peet (1989)
	4	Pine, IMA	Merkle (1962)
	5	Time since fire, Pine, IMA	Combination of models 1 and 4
	6	Time since fire, Pine, Oak, IMA	Model 5 + Oak: Reynolds et al. (1970), Klemmedson (1987, 1991), Rosenstock (1998)

*This set of models was applied to total species richness, species richness of each of five functional groups (annual forbs, perennial forbs, graminoids, shrubs, trees), and total exotic species richness.

response variable, we considered it to be an inconsistent predictor and dropped it from the model. Adjusted coefficients of determinism (adj-R^2) for the final models were determined by calculating the residual sums of squares using the parameter estimates calculated via model averaging. All adj-R^2 calculated for the final models were within 6% of the adj-R^2 as calculated with least squares for the model containing those explanatory variables.

RESULTS

Forest types across both zones

Pine–oak forests had the highest understorey plant cover of any forest type on the North Rim (Fig. 2). Understorey plant cover was 66% greater and species richness 16% greater in pine–oak than in ponderosa pine forests. The higher cover in pine–oak

Table 4 Sets of proposed models used in model selection for understorey plant community structure in subalpine forests. Community composition (a multivariate metric) was scaled using multivariate multiple regression by Anderson (2005)

Response variable	Model	Hypothesized explanatory variables and signs of relationships (if applicable)	Source(s)
Cover	1	(+) Aspen	Daubenmire (1943), Langenheim (1962), Patten (1963)
	2	(−) IMA	Daubenmire (1943), Billings & Bliss (1959), Holway & Ward (1963), Kuramoto & Bliss (1970), Canaday & Fonda (1974), Knight et al. (1977), Anderson et al. (1979)
	3	(−) Conifer sapling density	Stromberg & Patten (1991)
	4	(−) Spruce, (−) Fir	Oosting & Reed (1952), Anderson et al. (1969), Crouch (1985)
	5	(−) All conifers	An extension of model 4 due to presence of other conifers
	6	(−) Fir, (−) IMA	Fonda & Bliss (1969)
	7	(−) Spruce, (−) Fir, (−) Duff	Ellison (1954), Patten (1963)
	8	(−) Spruce, (−) Fir, (−) CWD	Crouch (1985)
	9	(−) Spruce, (−) Fir, (−) Duff, (−) CWD	Despain (1973)
Richness*	1	(+) Aspen	Lynch (1955)
	2	(−) IMA	Holway & Ward (1963), Chipman & Johnson (2002)
	3	(−) Conifer sapling density	Stromberg & Patten (1991)
	4	(−) Spruce, (+) Aspen	Reich et al. (2001)
	5	(−) Spruce, (−) Fir	Crouch (1985)
	6	(−) All Conifers	An extension of model 5 due to presence of other conifers
	7	(−) Spruce, (−) Fir, (+) Aspen	Daubenmire (1943)
	8	(−) Spruce, (−) Fir, (−) IMA	Holway & Ward (1963), Zobel et al. (1976), Chipman & Johnson (2002)
	9	(−) Spruce, (−) Fir, (−) CWD	Plant cover model 7
Diversity (H′)	1	(−) Conifer sapling density	Stromberg & Patten (1991)
	2	(−) Spruce, (+) Aspen	Reich et al. (2001)
	3	(−) Spruce, (−) Fir	Plant cover model 4
	4	(−) All conifers	An extension of model 3 due to presence of other conifers
	5	(−) Spruce, (−) Fir, (−) Duff	Plant cover model 7
	6	(−) Spruce, (−) Fir, (−) CWD, (−) IMA	Plant cover model 8; Chipman & Johnson (2002)
	7	(−) Spruce, (−) Fir, (+) Aspen	Richness model 7
	8	(−) Spruce, (−) Fir, (−) IMA	Chipman & Johnson (2002)
Community composition	1	IMA	Billings & Bliss (1959), Holway & Ward (1963), Patten (1963), Young & Smith (1979), Smith (1981), Allen et al. (1991)
	2	All conifers	Plant cover model 5
	3	Spruce, Aspen	Reich et al. (2001)
	4	Spruce, Fir, CWD	Despain (1973)
	5	Spruce, Fir, CWD, IMA	Combinations of models 1 and 4

*This set of models was applied to total species richness; species richness of each of five functional groups (annual forbs, perennial forbs, graminoids, shrubs, trees); and total exotic species richness.

forests was not due to oak, as plant cover remained higher if oak cover was excluded from the comparison. Shannon's index (H′) of diversity was highest in pine–oak, aspen and mixed conifer forests, and total species richness of the understorey was highest in pine–oak, aspen and spruce–fir forests. Annual forb species richness was highest in pine–oak and ponderosa pine forests; annuals were nearly absent from aspen, mixed conifer and spruce–fir forests. Perennial forb species richness was highest in pine–oak forests and lowest in aspen and spruce–fir forests. Graminoid species richness did not vary among forest types. Shrub richness was greatest in pine–oak forests, while understorey tree species richness was greatest in aspen, mixed conifer and spruce–fir forests. Exotic species richness was highest in pine–oak and ponderosa pine forests (Fig. 2).

Montane zone

Univariate plant community structure response variables

The best-fitting subset of models explained 58% of the variation in plant cover and 43% of the variation in total species richness (Table 5). Species richness of several functional groups was very poorly explained by these models (adj-R^2 < 0.10). As predicted (Table 3), time since fire and ponderosa pine basal area were negatively correlated with response variables (Table 5; Fig. 3). We predicted that Gambel oak basal area would be positively correlated with the response variables (Table 3), and this was true for all variables except perennial forb species richness. We
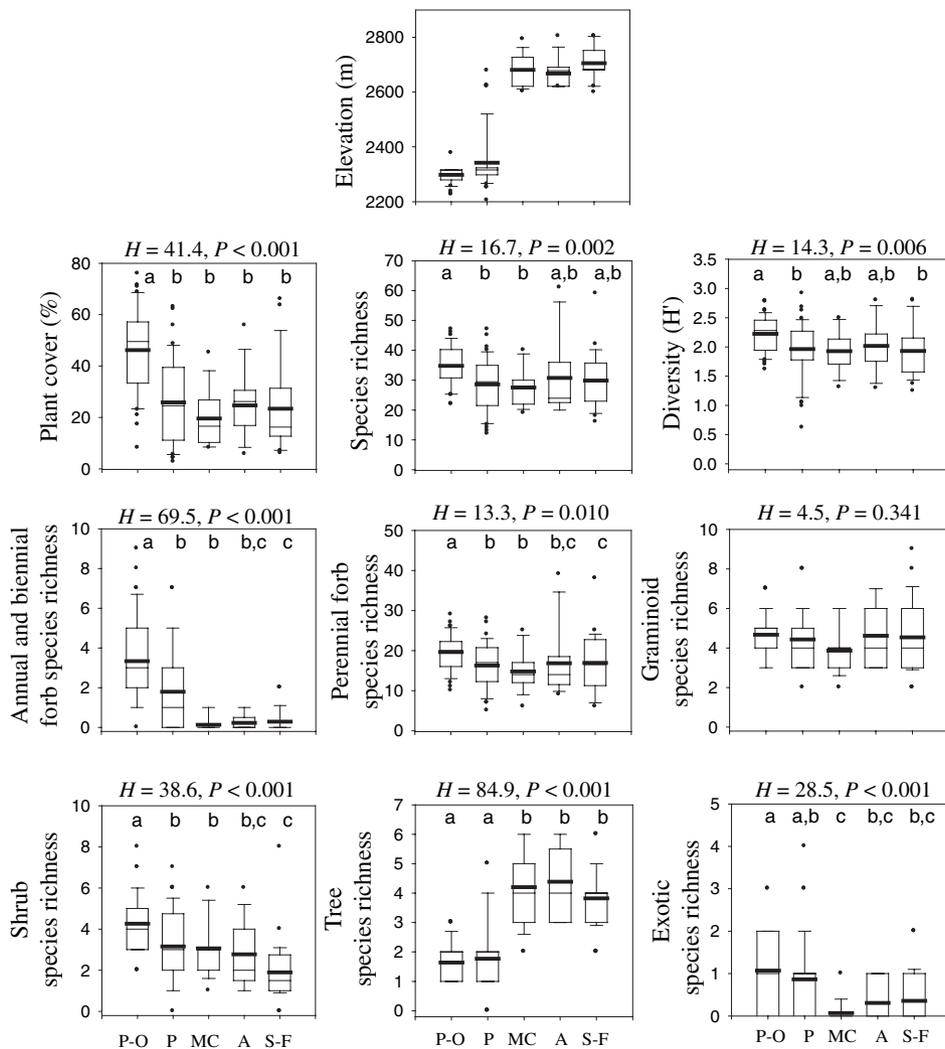
Figure 2 Comparisons of plant community structure between forest types. Species richness is reported at the 0.1-ha scale. Different lower-case letters indicate significant differences between forest types (Bonferroni-adjusted α = 0.005). P–O = pine–oak ($n = 42$); P = ponderosa pine ($n = 44$); MC = mixed conifer ($n = 15$); A = aspen ($n = 13$); S–F = spruce–fir ($n = 28$). Box-plot: lower and upper boundaries of box = 25th and 75th percentiles, respectively; thick horizontal line = mean; thin horizontal line = median; vertical lines (whiskers) below and above box = 10th and 90th percentiles; dots = outliers.

predicted that positive IMA values would be positively correlated with response variables, and this was true for plant cover and diversity, but not for species richness (Table 5).

Community composition among forest types

We identified 134 species across the montane zone. The NMDS analysis of understorey community composition focused on the 86 species found on at least 5% of the plots. Thirty-five species were significant indicators (INDVAL > 25) of montane forests (Table 6).

Understorey community composition differed significantly between pine–oak and ponderosa pine forest types (pseudo-$F = 4.9$, $P = 0.0001$), and this variation is illustrated in the NMDS ordination (Fig. 4). *Mahonia repens*, *Solidago velutina* and *Collinsia parviflora* were indicators of pine–oak

forest, and *P. ponderosa* seedlings were an indicator of ponderosa pine forest (Table 6).

Models predicting that community composition was significantly correlated with fire history, forest structure and topography (Table 3) were supported. Time since fire, basal areas of pine and oak, and IMA explained 22% (adj-R^2) of the total variation in species composition (Table 5). Individually, time since fire and oak basal area explained the most variation (16% and 4%, respectively).

Subalpine zone

Univariate plant community structure response variables

The best fitting subset of models explained 33% of the variation in understorey diversity (H') and 27% of the

Table 5 Linear models* developed with multi-model inference to describe relationships between plant community structure and fire history, forest structure, fuel load, and topography in montane forests ($n = 82$)

Understorey community structure response variables†	Models	Σw_i	γ Intercept (b_0)	Fire history Time since fire	Forest structure (basal area) Ponderosa pine	Gambel oak	Fuel load Duff	Topography IMA	Adj-R^2
Plant cover (%)	8, 9, 10	0.9868	56.6	−0.222	−0.644	+2.756		+1.082	0.58
Species richness	6, 7, 8, 9	1.0000	39.2	−0.118	−0.142	+0.106		−0.037	0.43
Diversity (H')	3, 4, 5, 6	1.0000	2.5	−0.005	−0.011	+0.010		+0.002	0.38
Annual forb richness	8, 9	0.9565	3.4	−0.026	−0.007	+0.411		−0.002	0.39
Perennial forb richness	6, 7, 8, 9	1.0000	22.3	−0.075	−0.057	−0.078	−0.059	−0.030	0.41
Community composition	4, 5, 6	0.9981		‡	‡	‡		‡	0.22

*Linear models can be derived from the table, which lists the coefficients for each explanatory variable that contributed to the full model. For example, the equation for plant cover is as follows:

Plant cover (%) = 56.6 − 0.222(time since fire) − 0.644(pine basal area) + 2.756(oak basal area) + 1.082(IMA).

†Models for tree, shrub, exotic, and graminoid species richness are not shown since they explained < 10% of the variation.

‡These variables explained variation in species composition, but we do not report their coefficients because there is no clear interpretation with a multivariate response. Community composition (a multivariate metric) was scaled using multivariate multiple regression in Anderson (2005).
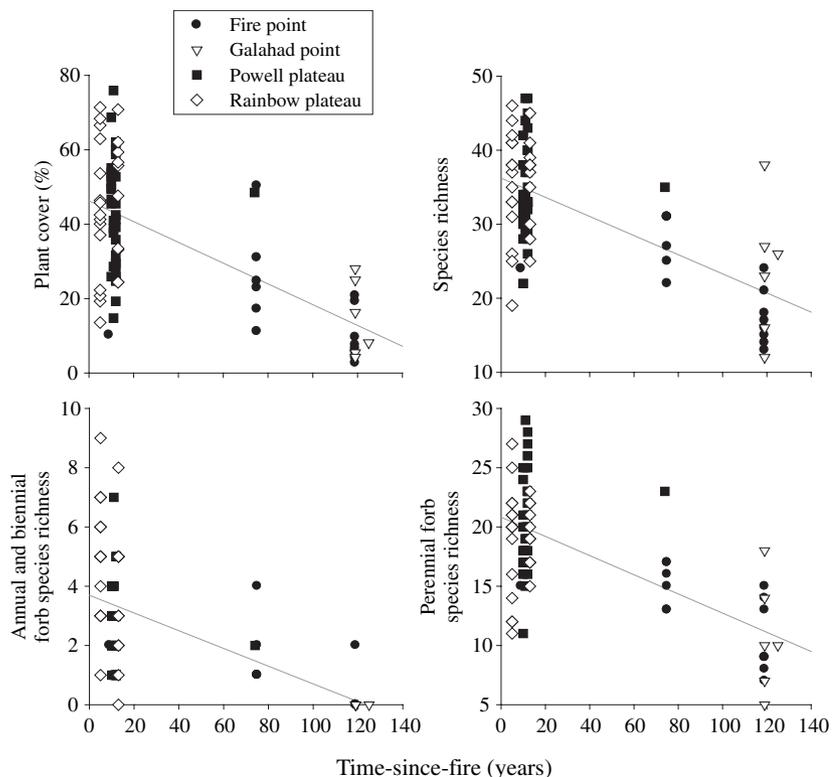
Figure 3 Relationships between time since fire (years) and plant community structure; species richness is reported at the 0.1-ha scale. Note the large variability associated with low values of time since fire.

variation in total understorey species richness for the subalpine zone (Table 7). Species richness of several functional groups was very poorly explained by these models (adj-R^2 < 0.10). As predicted, subalpine fir basal area was negatively correlated with understorey plant cover, richness and diversity. Engelmann spruce basal area was correlated with the response variables, but unexpectedly the sign of the relationship was positive. Duff depth was negatively correlated with plant cover, and the amount of CWD was negatively correlated with plant cover and richness, but not diversity (H'). Southern exposures, as indicated by their IMA values, were associated with high species richness, particularly of perennial forbs (Table 7).

Table 6 Indicator species associated with montane and subalpine zones and with forest types within each zone on the North Rim of Grand Canyon National Park*

Indicator species	INDVAL†	Montane		Subalpine			
		Pine–oak‡	Pine	Pine	MC	Aspen	S–F
Montane zone (both forest types)							
Delphinium nuttallianum Pritz. ex Walp.	84.7	**82–96**	**73–80**	13–25	–	–	2–4
Robinia neomexicana Gray§	82.7	**92–96**	**69–83**	–	13–13	8–8	–
Quercus gambelii Nutt.	78.0	**98–100**	**45–55**	–	–	–	–
Agoseris glauca (Pursh) Raf.	74.9	**76–90**	**64–78**	–	–	4–8	14–18
Eriogonum racemosum Nutt.	74.7	**88–95**	**88–93**	25–25	10–7	8–15	36–39
Elymus elymoides (Raf.) Swezey	64.5	**89–98**	**86–93**	50–50	40–60	42–47	41–46
Erigeron spp. (annual and biennial)	60.1	**63–79**	**52–68**	25–25	3–7	19–23	12–18
Mertensia macdougalii Heller	56.1	**44–55**	**44–58**	–	–	–	–
Artemisia carruthii Wood ex Carruth.	55.1	**50–68**	**40–48**	–	–	4–8	–
Lomatium foeniculatum (Nutt.) Coult. & Rose	54.9	**36–53**	**50–60**	–	–	–	–
Poa fendleriana (Steud.) Vasey	53.6	**100–100**	**100–100**	75–75	73–87	69–77	88–89
Penstemon linarioides Gray	50.0	**40–55**	**36–48**	–	–	–	–
Machaeranthera canescens (Pursh) Gray	49.1	**44–57**	**34–45**	–	–	8–8	–
Astragalus castaneiformis S. Wats.	48.8	**36–48**	**33–50**	–	–	–	–
Arabis spp.	48.2	**44–60**	**35–43**	–	–	15–13	5–11
Ericameria nauseosa (Pallas ex Pursh) Nesom & Baird	47.6	**44–57**	**31–38**	–	–	–	–
Cirsium spp.	46.7	**68–76**	**46–55**	38–50	23–33	31–31	21–25
Allium spp.	46.3	**38–60**	**26–33**	–	–	–	–
Polygonum douglasii Greene	45.3	**44–57**	**29–35**	–	–	–	2–4
Heterotheca villosa (Pursh) Shinners	42.8	**39–48**	**40–53**	–	–	8–15	11–18
Lathyrus lanzwertii Kellogg var. *leucanthus* (Rydb.) Dorn	42.7	**55–57**	**27–28**	–	–	–	–
Ceanothus fendleri Gray	42.0	**46–62**	**34–55**	50–75	13–20	27–31	7–11
Lotus utahensis Ottley	40.8	**55–69**	**56–65**	63–75	47–53	38–38	25–25
Bromus tectorum L.	39.0	**29–43**	**24–35**	–	–	–	–
Lupinus hillii Greene	37.2	**40–43**	**54–65**	13–25	3–7	15–25	34–36
Amelanchier utahensis Koehne	35.4	**33–40**	**18–30**	–	–	–	–
Symphoricarpus oreophilus Gray	34.8	**36–48**	**19–30**	13–25	3–7	–	4–4
Calochortus spp.	32.9	**27–36**	**19–30**	–	–	–	–
Phlox gracilis (Hook.) Greene	32.9	**26–38**	**16–28**	–	–	–	–
Hymenopappus filifolius Hook.	31.8	**25–33**	**23–33**	–	3–7	–	–
Lithophragma tenellum Nutt.	31.7	**14–19**	**34–45**	–	–	–	–
Gayophytum diffusum Torr. & Gray	29.9	**29–38**	**22–28**	–	–	–	–
Townsendia exscapa (Richards.) Porter	26.8	**17–24**	**19–30**	–	–	–	–
Comandra umbellata (L.) Nutt.	28.2	**29–38**	**14–20**	–	–	–	2–4
Phacelia egena (Greene ex Brand) Greene ex J.T. Howell	27.6	**37–40**	**19–28**	25–25	3–7	12–23	4–7
Pine–oak forest							
Mahonia repens (Lindl.) G. Don	48.1	**65–74**	35–45	88–100	77–93	73–77	34–39
Solidago velutina DC.	45.1	**61–74**	39–50	38–50	30–47	35–46	21–32
Collinsia parviflora Lindl.	34.3	**39–45**	13–15	–	–	–	–
Ponderosa pine forest							
Pinus ponderosa P. &C. Lawson	49.6	32–52	**53–80**	25–50	20–40	23–38	16–29
Subalpine zone (all forest types)							
Populus tremuloides Michx.	94.3	1–2	11–13	**100–100**	**100–100**	**100–100**	**100–100**
Juniperus communis L.	93.3	–	–	**75–100**	**83–93**	**92–100**	**73–89**
Abies lasiocarpa (Hook.) Nutt.	88.3	–	–	**63–75**	**70–73**	**73–85**	**95–100**
Fragaria virginiana Duchesne	84.7	–	–	**50–50**	**80–87**	**85–92**	**79–89**
Picea engelmanii Parry ex. Engelm.	81.7	–	–	**13–25**	**60–87**	**77–85**	**71–86**
Goodyera oblongifolia Raf.	81.7	–	–	**25–50**	**77–93**	**85–92**	**66–75**
Abies concolor (Gord. & Glend.) Lindl. ex Hildebr.	68.6	2–5	6–10	**75–75**	**77–87**	**77–85**	**46–61**
Chamerion angustifolium (L.) Holub	68.3	–	–	**13–25**	**37–53**	**50–77**	**57–79**
Bromus ciliatus L.	67.2	33–43	21–30	**100–100**	**80–93**	**88–92**	**75–86**
Hieracium fendleri Schultz-Bip.	56.1	10–15	16–26	**75–100**	**63–80**	**38–54**	**52–64**

Table 6 *continued*

Indicator species	INDVAL†	Montane Pine–oak‡	Pine	Subalpine Pine	MC	Aspen	S–F
Carex spp.	52.2	88–100	93–100	**100–100**	**97–100**	**100–100**	**100–100**
Pedicularis centranthera Gray	51.9	1–2	12–13	**75–100**	**67–67**	**54–75**	**45–46**
Pyrola spp.	51.7	–	–	**13–25**	**53–60**	**35–46**	**43–54**
Erigeron spp. (perennial)	51.0	14–19	18–28	**50–5**	**63–67**	**54–69**	**57–64**
Packera multilobata (Torr. & Gray ex Gray) W.A. Weber & A. Löve	48.5	40–52	15–22	**100–100**	**63–73**	**65–75**	**57–64**
Thlaspi montanum L.	45.1	–	–	**38–75**	**27–40**	**12–23**	**48–57**
Antennaria marginata Greene	44.4	–	–	**38–50**	**37–40**	**35–54**	**36–46**
Castilleja spp.	41.6	1–2	1–3	**63–75**	**17–33**	**27–38**	**34–46**
Arenaria lanuginosa (Michx.) Rohrb. ssp. *saxosa* (Gray) Maguire	38.8	–	–	**13–25**	**37–62**	**27–46**	**20–36**
Chimaphila umbellatum (L.) W. Bart.	33.3	–	–	-	**47–53**	**12–15**	**23–36**
Pseudocymopterus montana (Gray) Coult. & Rose	30.6	15–21	18–30	**38–50**	**27–53**	**23–31**	**45–46**
Senecio wootonii Greene	25.0	–	–	**38–50**	**17–27**	**19–23**	**18–21**
Non-spruce–fir forest¶							
Penstemon barbatus (Cav.) Roth	31.7	20–29	15–20	**38–50**	**30–40**	**35–46**	13–18
Corallorrhiza maculata (Raf.) Raf.	31.6	7–14	–	**38–50**	**13–20**	**23–46**	2–4
Spruce–fir forest							
Arenaria fendleri Gray	43.2	–	–	–	10–13	27–38	**48–57**
Penstemon virgatus Gray	37.2	7–12	15–20	–	–	4–8	**29–39**
Hymenoxys subintegra Cockerell	35.5	–	–	–	7–7	12–15	**38–43**
Pseudotsuga menziesii (Mirbel) Franco	34.7	–	–	38–50	27–33	35–46	**5–7**
Muhlenbergia montana (Nutt.) A.S. Hitchc.	31.4	–	–	–	7–13	31–38	**43–43**
Potentilla hippiana Lehm.	29.0	–	–	13–25	7–7	8–8	**34–36**
Androsace septentrionalis L.	27.7	–	–	–	–	8–15	**20–32**

*Data presented for each species under each forest type are percentage of belt transects and percentage of plots in which the species was detected (sample sizes for each forest type and zone are listed in Table 1). For example, *Delphinium nuttallianum* occurred on 82% of belt transects and 96% of plots within montane pine–oak forests. Bold text indicates elevation zone or forest type with which a species was most strongly associated. Analyses within zones did not include data from other elevation zones.

†INDVAL (indicator value) = relative abundance × relative frequency (for details of calculation see Dufrêne & Legendre, 1997). All plants listed had INDVAL > 25 and $P < 0.05$.

‡Forest type codes: pine–oak = ponderosa pine–Gambel oak; pine = ponderosa pine; MC = mixed conifer; S–F = spruce–fir.

§Those listed as indicator species refer to seedlings of these species found on plots, not mature overstorey trees.

¶Aspen, mixed conifer and ponderosa pine forests were grouped together for analyses within the subalpine zone because their compositions did not differ based on permutational MANOVA (see Methods and Results).

Community composition among forest types

We identified 120 species in the understorey across the subalpine zone. The analysis of community composition focused on the 70 species found on at least 5% of the plots. Twenty-two species were significant indicators (INDVAL > 25) of subalpine forests (Table 5).

Understorey community composition differed between forest types within the subalpine zone (pseudo-$F = 2.2$, $P = 0.004$), and is illustrated in the NMDS ordination (Fig. 4). Spruce–fir forests differed in composition from all other forest types (ponderosa pine, pseudo-$t = 1.6$, $P = 0.026$; mixed conifer, pseudo-$t = 1.9$, $P = 0.005$; aspen, pseudo-$t = 1.5$, $P = 0.039$), but other forest types did not differ in composition (all pseudo-$t < 1.1$, $P > 0.350$). *Arenaria fendleri*, *Penstemon virgatus*, *Hymenoxys subintegra*, *P. menziesii*, *Muhlenbergia montana*, *Potentilla hippiana* and *Androscae septentrionalis* were indicators of spruce–fir forest, and *Penstemon*

barbatus and *Corallorhiza maculata* were indicators of non-spruce–fir forest (aspen, mixed conifer and ponderosa pine forests combined; Table 5).

Models predicting that community composition should be related to forest structure, fuel load and topography (Table 4) were supported. Basal areas of Engelmann spruce, subalpine fir and aspen, CWD and IMA explained 18% (adj-R^2) of the total variation in species composition (Table 7). Individually, Engelmann spruce basal area and amount of CWD explained the most variation (9% and 7%, respectively).

DISCUSSION

Montane zone

The negative relationship between time since fire and understorey plant cover and richness supports the hypothesis that
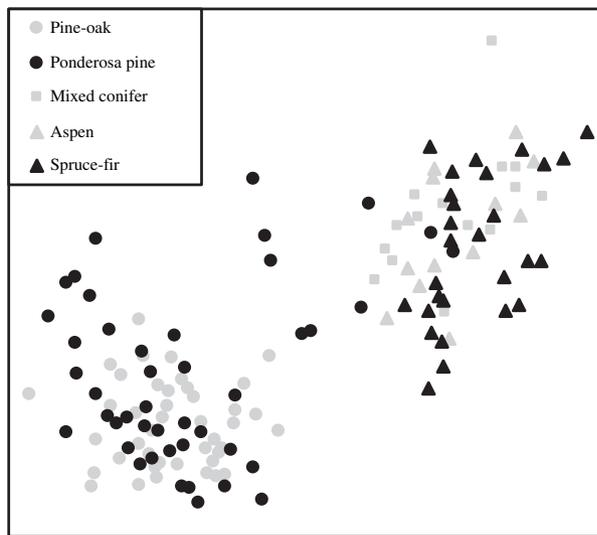
Figure 4 Non-metric multidimensional scaling (NMDS) ordination of understorey plant communities in montane and subalpine forests on the North Rim of Grand Canyon National Park. Each plot is coded by forest type; plot symbols match those in Fig. 1. Montane and subalpine forests are clearly distinguished by the clouds of points at lower left and upper right, respectively. NMDS plot determined using presence and abundance of 102 species on 142 plots (these species occurred on at least 5% of plots); the final solution had two dimensions; stress = 16.8, $P = 0.0099$.

herbaceous diversity in south-western ponderosa pine forests is maintained by frequent, low-intensity fires which reduce pine densities and fuel loads. This was also supported by other studies on the North Rim (Gildar et al., 2004; Laughlin et al., 2004). Elsewhere in North America, an interaction between time since fire and canopy cover (an interaction term in a multiple regression model), interpreted as an

indicator of light availability, was negatively correlated with species richness in mixed wood boreal forests (Chipman & Johnson, 2002). Similarly, in an ecosystem where stand-replacing crown fires are typical in Yellowstone National Park, Wyoming, high total plant cover and species richness were correlated with shorter fire intervals (Schoennagel et al., 2004). Our results also agree with studies in the woodland flora of Australia (Morrison et al., 1996; Watson & Wardell-Johnson, 2004) that found time since fire to be correlated with community composition.

Time since fire may also be important for preserving landscape-scale heterogeneity with respect to plant community structure. The variability in plant cover and annual forb richness is much greater on sites that have burned recently and frequently (Fig. 3) than on sites that have not burned for over 60 years. However, variability in total species richness and in perennial forb richness was not noticeably greater in recently burned forests than in fire-excluded forests. Apparently, plant cover and annual species are more sensitive than total species richness and perennial forb richness to variations in conditions created by fire.

Our results agree with previous studies that have shown high ponderosa pine abundance to depress understorey plant production (Ffolliott, 1983; Tapia et al., 1990; Moore & Deiter, 1992) since pine trees create deep shade, intercept precipitation and compete for soil resources (McLaughlin, 1978; Riegel et al., 1995; Naumburg & DeWald, 1999). Pine abundance was also related to variation in species composition, suggesting that differences in forest structure could cause changes in floristic assemblages.

The positive correlations between oak basal area and understorey plant cover and richness are not well understood. Gambel oak has been shown to be valuable to breeding birds and small mammals in ponderosa pine forests (Reynolds et al., 1970; Rosenstock, 1998). Interestingly, our study suggests that

Table 7 Linear models* developed with multi-model inference to describe relationships between plant community structure and forest structure, fuel loads, and topography in subalpine forests ($n = 60$)

Understorey community structure response variables†	Models	Σw_i	y-intercept (b_0)	Forest structure (basal area) Engelmann spruce	Subalpine fir	Aspen	Fuel load Duff	CWD	Topography IMA	Adj-R^2
Plant cover (%)	4, 8, 9	0.9554	23.7	+0.704	−0.504		−0.089	−0.077		0.20
Species richness	8, 9	0.9804	29.7	+0.537	−0.173			−0.074	−0.171	0.27
Diversity (H')	6	0.9985	2.1	+0.012	−0.012			−0.004	−0.048	0.33
Perennial forb richness	8, 9	0.9720	16.3	+0.391	−0.114			−0.054	−0.050	0.23
Graminoid richness	9	0.9819	4.8	+0.085	−0.040			−0.015		0.25
Community composition	1, 3, 4, 5	0.9840		‡	‡	‡	‡	‡		0.18

*Linear models can be derived from the table, which lists the coefficients for each explanatory variable that contributed to the full model. For example, the equation for plant cover is as follows:

Plant cover (%) = 23.7 + 0.704(spruce basal area) − 0.504(subalpine fir basal area) − 0.089(duff) − 0.077(CWD).

†Models for tree, shrub, annual and exotic richness are not shown as they explained < 10% of the variation.

‡These variables explained variation in species composition, but we do not report their coefficients because there is no clear interpretation with a multivariate response. Community composition (a multivariate metric) was scaled using multivariate multiple regression by Anderson (2005).

there is a positive relationship between plant abundance and the presence of oak in montane forests. This effect may be mediated by oak litter, as oak positively influences soil fertility (Klemmedson, 1987, 1991). This relationship might also be a function of the quality and quantity of light beneath the broadleaved oaks; further research is warranted.

Our results indicate that the cooler, wetter northern slopes of montane forests can produce more understorey vegetation per unit area (cover), but the warmer, drier southern slopes accommodate more species. Our findings agree with a study of coniferous forests in the western Cascades of Oregon, USA where herbaceous richness was highest on drier sites, but herbaceous cover was highest on cooler, wetter sites (Zobel et al., 1976). In contrast, species diversity was highest on northern slopes in short-grass prairie (Lieffers & Larkin-Lieffers, 1986).

Subalpine zone

Many studies have suggested a positive relationship between aspen abundance and understorey production and species richness (Langenheim, 1962; Fonda & Bliss, 1969; Despain, 1973; Mueggler, 1985; Stromberg & Patten, 1991; Brown, 1994; Reich et al., 2001), probably due to superior litter quality (Daubenmire, 1943) and greater litterfall nitrogen (Reich et al., 2001) in aspen stands. However, this study did not confirm that relationship. This discrepancy may be a result of our gridded sampling scheme, which did not intentionally target pure aspen stands (see Methods). Many aspen stands on the North Rim have not burned for over 100 years and therefore contain numerous conifers. Conifer densities in aspen stands might explain why aspen and mixed conifer forest understorey compositions were indistinguishable. Elsewhere in northern Arizona, aspen forests had the highest plant cover among many forest types, but had relatively low species richness (Fisher & Fulé, 2004; S. Abella, Northern Arizona University, pers. comm.). Aspen stands in northern Arizona had high plant cover values, indicating high herbaceous production, but unlike other regions they had relatively low species richness.

Many researchers have suggested that plant cover and species richness would be negatively related to conifer abundance, as the sparse herbaceous layer in spruce–fir forests is often attributed to dense canopies and thick litter layers (Ellison, 1954; Patten, 1963; Zobel et al., 1976; Stromberg & Patten, 1991). Our study confirms this relationship for subalpine fir, probably due to the deep shade and acidic litter underneath fir trees. Spruce and fir abundance explained some variation in community composition in our study, but clear-cutting spruce–fir stands did not significantly change plant community composition in Colorado (Crouch, 1985).

Given the general agreement that conifer abundance decreases understorey plant production, it was surprising that understorey plant cover, richness and diversity were positively correlated with Engelmann spruce abundance. This result disagrees with every model proposed about plant community structure in spruce–fir forests (Table 4). Subalpine forests on the Kaibab Plateau differ from most North American subalpine communities in that a greater proportion of other conifer species (e.g. Douglas-fir, ponderosa pine) are present on southern slopes. Perhaps this combination of overstorey trees and their interactions in this subalpine environment caused this unusual observation; this discrepancy deserves further study and should be considered a tentative result.

We have observed that species richness is often higher on plots that were located in close proximity to mountain meadows (data not shown). Similarly, Fonda & Bliss (1969) observed that plots within a subalpine fir forest contained more species if they were closer to the openings in the forest. Merkle (1962) reported generally high total herbaceous plant cover (34–45%) in meadows (or 'parks') on the Kaibab Plateau, and noted differences in species composition between meadows and forests. Despain (1973) also noted a distinct difference in composition between meadows and forests in the Big Horn Mountains, Wyoming.

Large volumes of CWD are commonly found in spruce–fir forests (Langenheim, 1962; Despain, 1973; Crouch, 1985), increasing with time since fire (Agee, 2002). Crown fires can drastically reduce overstorey and understorey cover in subalpine forests, but understorey cover can return to unburned levels within 3 years (Turner et al., 1999). Perhaps plant cover and diversity in these communities gradually decline as CWD accumulates, tree densities increase, and availability of resources such as light or space declines. This would suggest that understorey diversity is highest following crown fires. Plant cover and species richness were positively correlated with short fire intervals in subalpine forests in Yellowstone National Park (Schoennagel et al., 2004), although this result contrasted with studies from other ecosystems subject to crown fires (Paine et al., 1998).

Topography was correlated with understorey species richness, diversity and community composition, but was not related to plant cover. Warmer, southern exposures harboured more species than cooler, northern exposures. Snow-pack location is strongly correlated with topography (Billings, 1973), and the persistence of winter snow pack strongly influences plant community structure in subalpine forests (Fonda & Bliss, 1969; Kuramoto & Bliss, 1970; Douglas, 1972; Canaday & Fonda, 1974; Knight et al., 1977; Anderson et al., 1979). Although we did not measure snow pack on these sites, the Kaibab Plateau receives an average of 3.56 m snow each winter, and snow depths of 1–3 m have been recorded (Merkle, 1962). The influence of snow pack on vegetation in other subalpine ecosystems in North America suggests that it plays an equally important role in structuring Arizona subalpine ecosystems.

Comparison of montane and subalpine zones

Montane and subalpine plant communities are defined by elevation zone (Löve, 1970; MacMahon & Anderson, 1982;

Peet, 2000). Differing climates and fire regimes are perhaps the strongest abiotic influences on plants within these zones. In contrast to the subalpine zone, the montane zone is low enough in elevation that it is not affected by prolonged snow packs during the growing season (Fonda & Bliss, 1969; Knight et al., 1977), which could explain why diversity is higher on north slopes in the montane zone, yet lower on north slopes in the subalpine zone. Also, the frequent fire regime in montane forests could be a stronger adaptive force than the mixed-severity fire regime of subalpine forests (patchy, stand-replacing with some surface fires; see Fulé et al., 2003b), as it is a more regular and common disturbance.

Annual forb species richness was greatest in montane forests and was negatively correlated with time since fire. Annual forbs are common in montane forests following disturbances such as wildfire (Gibson, 1988; Huston, 1994; Crawford et al., 2001; Laughlin et al., 2004; Huisinga et al., 2005), which agrees with Grime's (1977) hypothesis that annual species are more abundant on frequently disturbed sites. However, annual forbs were rare in the subalpine zone (Fig. 2), perhaps because it has not burned since at least 1879. An alternative hypothesis is that annual forbs are naturally absent in high-elevation spruce–fir forests, although Went (1953) documented at least 40 annual plants at high elevations in the Sierra Nevada, California, and Schoennagel et al. (2004) detected many annual plants in subalpine forests that had short fire intervals.

Management implications

The long-term protection of these forests from logging, grazing and complete fire suppression has allowed these sites to maintain key elements of 'wildness' (Fulé et al., 2002). Our consideration of these forests as relict sites is supported by the low abundance of exotic species on the North Rim (Fig. 2), in contrast to studies at another high-elevation site in Arizona (Fisher & Fulé, 2004), and outside the park boundary in the Kaibab National Forest (Crawford et al., 2001). Similar results of low exotic abundance in remote forests of Yellowstone National Park were reported by Turner et al. (1999) and Schoennagel et al. (2004), which led them to suggest that seeding or other management activities to reduce the spread of exotics were not justified in remote, protected landscapes. However, continued monitoring of exotic species on the North Rim, especially after wildfires, remains justified and important.

In montane forests, low-intensity wildfire is an important ecological process that maintains understorey communities within the range of natural variability and may promote landscape heterogeneity. Crown fires may have occurred in central and northern USA ponderosa pine forests (Ehle & Baker, 2003), especially during warmer climate intervals (Pierce et al., 2004), but evidence of crown fires in south-western ponderosa pine forests prior to Euro-American settlement has not been reported (Swetnam & Baisan, 1996; Fulé et al., 2003a). Community composition was shifted toward higher similarity with reference sites after a managed wildfire on Fire Point (Laughlin et al., 2004), and plant diversity was highest on sites

that have burned frequently and recently in this study. The preservation of key ecosystem processes, most importantly lightning-initiated wildfire, is an important component of ecological restoration of south-western ponderosa pine forests (Allen et al., 2002). Therefore we recommend the continued use of wildfire and prescribed fire as management tools in North Rim montane forests. Moreover, based on the positive associations of oak with wildlife and plant diversity, we suggest maintaining various growth forms of Gambel oak within south-western montane forests through no-cutting policies.

The subalpine forests have not burned for over 120 years, which is not out of the historical range of variability. Subalpine forests across North America have stand-replacing crown-fire regimes, although some surface fires burned in North Rim subalpine forests due to the drier and more open south slopes (Fulé et al., 2003b). Stand-replacing fires are an important ecological process in the subalpine zone (Johnson et al., 2001) and should be incorporated into management plans. However, fire use in subalpine forests is fraught with risks due to intense fire behaviour in dense spruce–fir stands, so it is inherently more difficult to preserve these high-energy ecological processes due to dangers and to public perception of denuded post-fire landscapes. Stand-replacing or mixed-severity fires could initiate the development of pure aspen stands or open conifer stands, which could also promote understorey productivity. In short, we recommend fire use in any ecosystem where fire has played an ecologically important role historically, but acknowledge that fire use in subalpine ecosystems is inherently more difficult than in montane ecosystems.

To conclude, despite the insights gained through this study, much of the natural variability in these ecosystems was not accounted for in our models. No model explained more than 60% of the variation in plant community structure within the montane zone, or more than 35% of the variation within the subalpine zone, indicating that additional factors are structuring these communities. Potential factors that were not explored in this study include native ungulate herbivory (Huffman & Moore, 2003) and soil nutrient resources (Grace et al., 2000; Weiher et al., 2004). Nonetheless, the models that we used demonstrate that some of the variability in understorey plant community structure in these forests is explained by fire history, forest structure, fuel loads and topography. The ranges of variability reported here (Tables 2 & 6; Fig. 2 & 4) and by Fulé et al. (2002, 2003a,b) can be used as benchmarks for assessing future change (Landres et al., 1999) and to determine whether current management practices result in ecosystems that fall within the natural range of variability for the North Rim of Grand Canyon National Park.

Restoration Institute. This work was funded by grants from the National Park Service, Bureau of Land Management, and the Joint Fire Science Program.

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Editor: Mark Bush