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The role of environmental gradients in non-native plant invasion into burnt areas of Yosemite National Park, California

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ABSTRACT

Fire is known to facilitate the invasion of many non-native plant species, but how invasion into burnt areas varies along environmental gradients is not well-understood. We used two pre-existing data sets to analyse patterns of invasion by non-native plant species into burnt areas along gradients of topography, soil and vegetation structure in Yosemite National Park, California, USA. A total of 46 non-native species (all herbaceous) were recorded in the two data sets. They occurred in all seven of the major plant formations in the park, but were least common in subalpine and upper montane conifer forests. There was no significant difference in species richness or cover of non-natives between burnt and unburnt areas for either data set, and environmental gradients had a stronger effect on patterns of non-native species distribution, abundance and species composition than burning. Cover and species richness of non-natives had significant positive correlations with slope (steepness) and herbaceous cover, while species richness had significant negative correlations with elevation, the number of years post-burn, and cover of woody vegetation. Non-native species comprised a relatively minor component of the vegetation in both burnt and unburnt areas in Yosemite (percentage species = 4%, mean cover < 6.0%), and those species that did occur in burnt areas tended not to persist over time. The results indicate that in many western montane ecosystems, fire alone will not necessarily result in increased rates of invasion into burnt areas. However, it would be premature to conclude that non-native species could not affect post-fire succession patterns in these systems. Short fire-return intervals and high fire severity coupled with increased propagule pressure from areas used heavily by humans could still lead to high rates of invasion, establishment and spread even in highly protected areas such as Yosemite.

Keywords

Biological invasions, community invasibility, environmental gradients, fire, invasive plants, mediterranean-type ecosystems.

INTRODUCTION

Fire suppression policies initiated in the latter part of the 19th and early part of the 20th centuries have had two broad, interrelated effects on western montane ecosystems in the USA (Kilgore, 1973; Kilgore & Taylor, 1979; Parsons, 1981; Pyne, 1984; Taylor, 2000): (1) changes in species composition and/or vegetation community structure, and (2) a build-up of fuel to unnaturally high levels, resulting in more severe and costly wildfires (Skinner & Chang, 1996; Taylor, 2000). There is now a general consensus that fire suppression policies need to be greatly modified (Conrad & Weise, 1998; Stephenson, 1999; Veblen, 2003) and many ecologists and resource management organizations believe that restoring fire regimes to historical patterns is necessary for the proper management of those systems (Parsons *et al*., 1986; Parsons & Swetnam, 1989; Keeley & Stephenson, 2000). However, the use of fire to achieve ecological and conservation goals is not without complications, and it is unclear exactly what the implications of restoring historical fire regimes are (Keeley & Stephenson, 2000). First, how ecosystems now respond to fire relative to historical conditions is unclear (Stephenson *et al*., 1991; Stephens, 1998; Stephenson, 1999). Second, disturbance is considered to be one of the most important processes for establishment and spread of invasive plant species (Hobbs, 1991; Hobbs & Huenneke, 1992; Mack & D'Antonio, 1998; Byers, 2002). More specifically, over the last 15 years there has been increasing evidence that many non-native plant species can invade and eventually dominate burnt areas (D'Antonio & Vitousek, 1992; Hobbs & Huenneke, 1992). Not only has this altered succession patterns, but by changing

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fuel structure and fuel loads invasive plants have transformed entire fire regimes (D'Antonio, 2000).

Invasive non-native plants are considered one of the primary threats to biological diversity and ecological integrity of many ecosystems (Mooney *et al.*, 1989; Pysek *et al.*, 1995; Child *et al.*, 2003). Ecosystems with mediterranean-type climates have been particularly vulnerable to invasions (Groves & DiCastri, 1991). This pattern is especially apparent in California, where non-native plant invasions have had a rapid and disproportionate effect on plant communities throughout the state (Rejmánek *et al.*, 1991; Schierenbeck, 1995). Of the approximately 5800 species of vascular plants in California growing out of cultivation, 1020 are considered non-native (Hickman, 1993; Rejmánek & Randall, 1994). This has resulted in the wholesale transformation of species composition in some communities (Heady, 1988; Huenneke *et al.*, 1990) and alteration of ecosystem processes in others (Bell, 1997).

The most extensive and severe effects of invasive plants in California have occurred in ecosystems at low elevations (Randall *et al.*, 1998). Although invasive plant species occur in higher elevation ecosystems, they are less abundant and have had less affect than those at lower elevations (Mooney *et al.*, 1986). However, there is concern that impacts from invasive plant species may begin to become more severe in higher elevation ecosystems (Schwartz *et al.*, 1996) and that fire management programs could be an important contributing factor. Of particular concern are plant communities on the west slope of the Sierra Nevada mountain range (Keeley, 2001). Non-native plant species are known to invade burnt areas across an entire spectrum of community types and fire regime characteristics (D'Antonio, 2000; Brooks *et al.*, 2004), and the west slope of the Sierra Nevada consists of a mix of public (e.g. national park and national forest) and private lands that are subject to both prescribed fires and large intense wildfires. Some non-native species that occur in the Sierra Nevada have been responsible for transforming fire regimes in other ecosystems (Whisenant, 1990), and there is evidence that the abundance of non-native plants can increase in burnt areas in some western montane ecosystems (Crawford *et al.*, 2001; Keeley *et al.*, 2003).

Despite the potential threat, it is unlikely that fire in and of itself will be a simple deterministic process that results in increased rates of invasion by non-native species into burnt areas in the Sierra Nevada. Invasion rates of non-native species can vary substantially along environmental gradients (Fornwalt *et al.*, 2003) and plant communities in the Sierra Nevada occur in mosaics along gradients of topography, soil, and moisture (Vankat, 1977; Parker, 1989). In turn, fire behaviour and fire regimes vary along these gradients (Caprio & Swetnam, 1995; Keeley & Stephenson, 2000), which suggests that variation in fire regimes could result in different patterns of invasion by non-native species (Keeley, 2001). The effect of these interactions and whether they would result in higher or lower rates of invasion is largely speculative though. For instance, data on the relationship between elevation and invasion rates suggest that burns in higher elevation areas would be less susceptible to invasion. However, these data have come primarily from unburnt sites (Mooney *et al.*, 1986; but see Keeley *et al.*, 2003), and there is evidence from other western montane ecosystems that burning can alter this relationship (Turner *et al.*, 1997; Crawford *et al.*, 2001).

Rates of invasion may also depend on the pool of non-native species that could potentially invade burnt sites. Because they vary in life-history characteristics, dispersal capabilities and adaptations to fire, only a subset of the local non-native species pool is likely to become established in burnt sites. This implies that there may be different assemblages of non-native species in burnt and unburnt areas (Boyd *et al.*, 1993; Giessow & Zedler, 1996; Crawford *et al.*, 2001; Klinger & Messer, 2001), that these assemblages may change over time (Keeley *et al.*, 2003), or that only a very limited number of species become abundant in burnt sites (Turner *et al.*, 1997).

Characteristics of the fire itself, such as size, return interval and severity, will likely influence invasion rates as well (Crawford *et al.*, 2001; Keeley *et al.*, 2003). The size of burns varies substantially in the Sierra Nevada (McKelvey & Busse, 1996; Skinner & Chang, 1996), but it is difficult to predict how this affects invasion rates. Large burns (Skinner & Chang, 1996) could potentially result in high invasion rates because of the proportionally large disturbed area for non-native species to exploit. However, because of the large ratio between the area of a burn and its perimeter, invasive non-native species may not be able to disperse much beyond the edge of a burn or in great enough numbers to compete with native species in the interior. Alternatively, the low area/perimeter ratio in small burns (McKelvey & Busse, 1996) could lead to high rates of invasion into the interior of the burn unit, increasing the density of potential non-native propagules (Turner *et al.*, 1997). This could lead to increased non-native propagule sources as the number of heavily invaded small burns increases.

Determining the relative importance of environmental gradients and fire on patterns of distribution and abundance of invasive non-native species would provide both insight into basic ecological processes and useful information for designing fire management programs. However, there have been few studies on invasion by non-native species into burnt sites in montane ecosystems (Turner *et al.*, 1997; Crawford *et al.*, 2001; Fornwalt *et al.*, 2003; Keeley *et al.*, 2003). Consequently, the extent, magnitude and effects of invasion by non-native species into burnt areas in these systems are poorly understood. Therefore, our objectives in this study were to: (1) compare the level of invasion of non-native plants into burnt and unburnt areas along an elevation gradient in Yosemite National Park, California, and (2) determine the degree to which distribution and abundance patterns of non-native plants were influenced by fire relative to other physiographical factors (e.g. slope, soils). We hypothesized that: (1) levels of invasion by non-native plants in burnt and unburnt areas would decrease along a gradient of increasing elevation, (2) there would be greater species richness and abundance of non-native plants in burnt than unburnt areas, (3) species richness and abundance of non-native plants would be greater in smaller burns than larger burns and would decrease with time since an area burnt, and (4) there would be distinct assemblages of non-native species in burnt and unburnt areas.

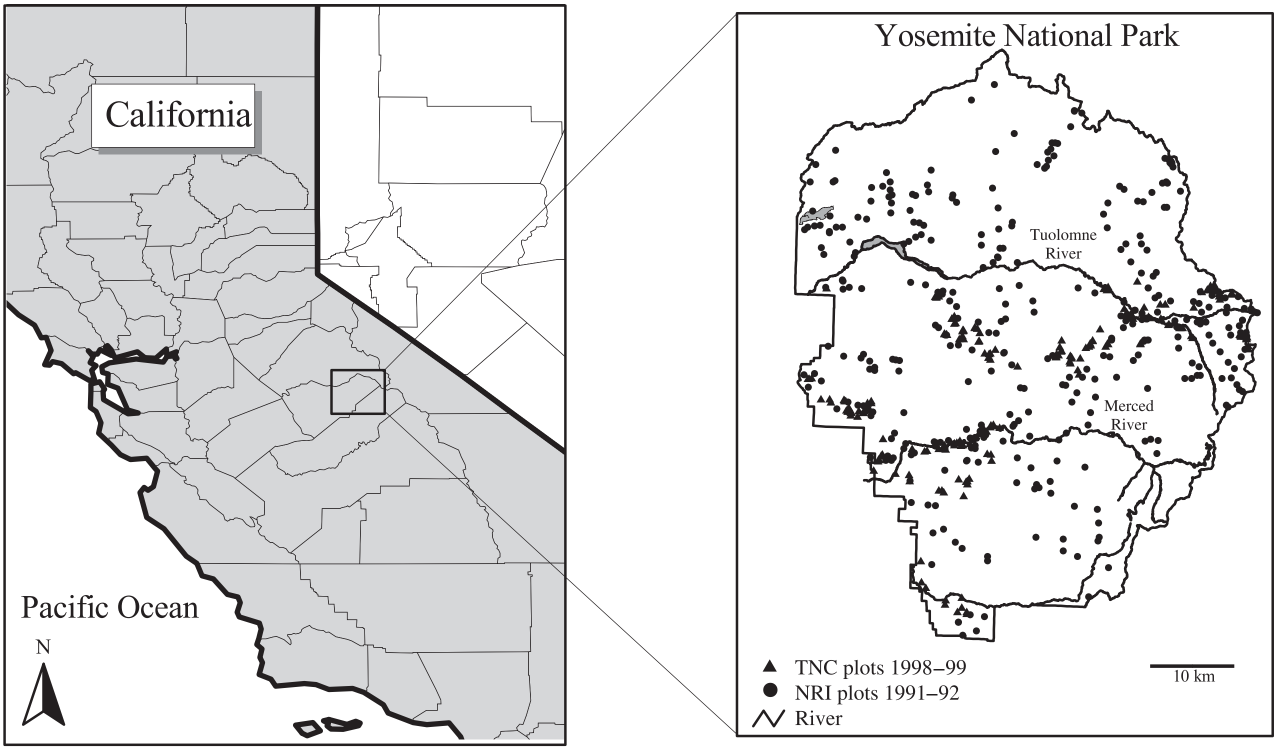

Figure 1 Yosemite National Park, California, and the location of sampling plots used in two plant surveys conducted in the park.

Yosemite National Park (YNP) provided a unique opportunity to test these hypotheses. Because of the parks size and topographical diversity, environmental gradients (e.g. elevation, slope, aspect, soils) are very pronounced. There is a relatively large number of plant communities within the boundaries of YNP (Botti, 2001), and the US National Park Service (NPS) has compiled records of the physical (e.g. size, arrangement) and temporal (e.g. years since fire) characteristics of all fires dating back to 1930. In addition, two comprehensive vegetation surveys had been completed in the park over the last decade and many of the sample plots in these surveys had been located in burnt areas that spanned a range of environmental conditions and fire characteristics (e.g. burn size, years since fire). This allowed us to not just analyse invasion patterns at a relatively large spatial scale, but also the temporal scale to determine how long these patterns could be expected to persist.

STUDY SITE

YNP is located in central California on the western slope of the Sierra Nevada mountain range (37°29′ N 119°13′ W; Fig. 1). Humans first settled in the Yosemite area approximately 8000 yr BP. European and American settlers conducted livestock and limited farming operations throughout the region for several decades in the mid-19th century (Greene, 1987). In 1890, Yosemite was designated a national park and a World Heritage Site in 1984 (Greene, 1987). It is one of the most visited parks in USA, with over 3.5 million visitors/year.

YNP comprises an area of 3032 km^2 and encompasses an elevation range of 524 m to 3998 m (Botti, 2001). Parent rock in YNP is primarily granite, with intrusions of other plutonic igneous forms and pockets of basalt and metamorphic rock. Much of the underlying rock has been exposed by glaciation, so soils outside of the larger valleys tend to be thin and relatively nutrient poor. Two major rivers (Tuolumne and Merced) flow through the park in an east–west direction (Fig. 1). The climate of YNP is distinctly mediterranean, with a hot dry season (May–September) and a cool wet season. Temperature and precipitation vary with elevation; mean annual precipitation ranges from 900 mm at lower elevations to 1200 mm at upper elevations. Mean daily summer temperatures range from 12 °C to 33 °C, and mean daily winter temperatures range from 8 °C to −4 °C for lower to upper elevations, respectively.

Five general terrestrial vegetation zones occur within YNP; chaparral/oak woodland, mixed conifer, montane, subalpine and alpine (Botti, 2001). Species composition of different plant communities within these vegetation zones varies with the influence of different abiotic factors, including temperature, soil moisture, soil structure, aspect, light environment and fire history (Parker, 1982; Botti, 2001). There are 1338 species of vascular plants in the park, of which 130 (9.5%) are non-native (Botti, 2001; Gerlach *et al*., 2001). Three of the non-native species are listed by the California Invasive Plant Council as being among the most widespread and invasive non-native plant species in the state (Anderson *et al*., 1999).

Burnt areas in YNP consist of a complex mosaic of human and naturally ignited fires of varying size, distribution and shape. Prior to 1968, fire suppression was the focus of NPS fire management policy. The suppression policy changed in 1968 to one recognizing fire as a natural process and a prescribed fire program was implemented in 1970. Prescribed burning is done to reduce fuel loads and to create or maintain desirable ecological conditions in wildland areas of the park, while wildfires are allowed to burn in designated areas under certain defined conditions. From 1970 to 1999, a total of 550 wildland fires burnt 28,056 ha, while 197 prescribed fires burnt 17,280 ha. Suppression practices continue in certain circumstances, primarily to protect cultural sites and areas of human use.

METHODS

Data collection

Two different sources of data on the distribution and abundance of non-native plants in YNP were available:
(1) A vegetation inventory and mapping program (Natural Resources Inventory program) conducted from 1989 to 1993 (NRI plots; $N = 362$ plots).
(2) A vegetation community classification and mapping program conducted in 1998 and 1999 by The Nature Conservancy (NatureServe, 2003), the NPS and the US Geological Survey (TNC plots; $N = 236$ plots).

Plots in both the NRI and the TNC surveys were located in all seven of the major vegetation formations throughout the park (Moore, 1993). Plots in the NRI surveys were stratified by vegetation type and elevation. Plot locations in the TNC surveys were stratified across seven environmental characteristics that affect the distribution of plant species: elevation, slope, aspect, geology, hydrology, the east–west gradient in climate and fire history. Spatial data were used to divide the sampling area into six elevation zones (< 900 m, 900–1500 m, 1500–2100 m, 2100–2700 m, 2700–3300 m, > 3300 m), five broad surficial geology classes (plutonic, alluvium, morainal, metamorphic, volcanic), five aspect classes (flat, NE, SE, SW, NW), two slope classes (< 3°, 3°–35°), two hydrology categories (hydric, nonhydric) and two fire-history categories (burnt, unburnt since 1930).

All species present in the NRI plots (0.1 ha) were recorded (Hickman, 1993). Each herbaceous species was given a visual estimate of cover in each of six randomly located 1-m^2 quadrats within each plot. The mean of the six visual estimates was used as the cover estimate for the species within the 0.1 ha plot. Line intercept sampling along two randomly located 18-m transects was used to estimate the cover of shrubs and trees within each plot (Bonham, 1989). Species that occurred in the plot but not in the quadrats or the line transects were given an arbitrary cover value of 0.1%. Besides species data, the overall cover of the herbaceous, shrub and tree layers within each plot was estimated.

Plots in the TNC survey were scaled to the physiognomy of the vegetation so that plot size varied by plant community type (0.01 ha for herbaceous, 0.04 ha for shrub or 0.1 ha for forested stands). Plot shape varied within communities, with both square and rectangular plots being used in each size class depending on topographical configuration. Data were collected at each plot on species identity (Hickman, 1993), coded as non-native or native, and a visual estimate was made of percentage cover for each species. Data were also collected at each plot for three vegetation structure variables: the total percentage cover of trees, shrubs and herbaceous species in each plot (estimated visually). To improve consistency in estimates between observers, cover was collected in six cover classes (< 1%, 1–5%, 5–25%, 25–50%, 50–75% and > 75%).

Data inspection and synthesis

Six plots in the NRI data set were excluded from the analysis because they consisted almost entirely of rock slab and had no native or non-native species. The total number, percentage and absolute and relative cover (%) of non-native and native species were calculated for all plots in both data sets. Nomenclature followed Hickman (1993) and Botti (2001).

The geographical coordinates of the TNC and the NRI plots were imported into a geographical information system (GIS; ARCVIEW version 3.2) and assigned spatial attributes from vector and raster spatial data layers (Underwood *et al.*, 2004). The raster spatial data, at 30 m resolution, included elevation (metres), slope (degree), aspect (degree), years since fire and Fuel Model class (Rothermal, 1983). A number of derived secondary data layers were also created for the analysis including distance to roads, trails and campgrounds (metres) and soil composition (percentage of stone, silt, clay, sand, loam, gravel, boulder and cobble) calculated on the State Soil Geographic (STATSGO) data base, developed by the US Department of Agriculture's (USDA) Natural Resources Conservation Service.

Two vegetation classifications have been developed for YNP; one in 1937 and another by Moore (1993) who developed a plant community classification for the Yosemite region that was based on Holland (1986). Each of the TNC and the NRI plots was assigned to one of seven vegetation types using the latter classification (Moore, 1993): grassland/meadow, broadleaved upland forests and woodlands, chaparral/scrub, lower montane conifer forest, upper montane conifer forest, subalpine conifer forest and barren areas.

Preliminary analysis

All known fires regardless of size have been mapped in YNP since 1930. Maps from 1930 to 1950 were hand-drawn and transferred to GIS format after 1995. Although the hand-drawn maps were less detailed than maps created on 15-min quadrangles from 1950 to 1995 and after 1995 using Global Positioning System units, their accuracy with respect to fire size and burn perimeter was adequate. There were 149 plots in the two data sets that were in burnt sites. Since only five sites were burnt prior to 1960 when techniques for mapping burns were less developed, we considered the effect of mapping error on the results of our analysis to be insignificant.

Non-native species were relatively uncommon in both data sets (see Results), so we felt that pooling the two data sets would increase the effectiveness of some analyses, particularly ordination. However, because the plots in the TNC study varied in size and shape, we conducted a preliminary analysis to determine if apparent patterns of non-native species richness, diversity, and composition were in reality artefacts of the sampling design.

Analysis of covariance (ANCOVA) was used to test for differences in species richness between square and rectangular plots of different size. Heterogeneity in species composition was analysed by calculating a simplified Morisita–Horn (M–H) index (Horn, 1966; Wolda, 1981) for all possible pairs of plots within each size/shape category. Analysis of variance (ANOVA) was then used to test if heterogeneity in species composition varied between different size/shape categories.

There was no significant relationship between plot size or shape and the number of non-native species, and there was no significant difference in species composition between different plot shapes within each size class for the TNC data set. Similarity in species composition between the NRI and the TNC data sets was relatively high (mean MH = 0.79). Therefore, we felt there was reasonable justification for combining the two data sets for ordination analysis ($n = 93$ plots with non-native species for the combined data sets). In addition, ordination analyses depend primarily on distribution and abundance patterns between species, plots and/or correlation with environmental variables, and are not particularly sensitive to variation in plot size or shape.

Data analysis

General patterns of non-native species distribution, diversity and abundance

We analysed the degree of aggregation in the distribution of non-native species by fitting their spatial pattern to the negative binomial distribution (White & Bennett, 1996). Failure to reject the null hypothesis of this test indicates support for their spatial distribution being aggregated, with the magnitude of aggregation increasing as the exponent of the distribution (k) → 0 (Bliss & Fisher, 1953).

Three indices of non-native species diversity were calculated for each plot (Magurran, 1988). These included species richness (S, the total number of non-native species in a plot), species diversity ($N_2 = 1/C$, where C = Simpson's index of dominance (Hill, 1973)), and evenness (G = Molinari's index). Molinari's index was used to calculate evenness, since this index has been found to be least affected by the influence of one dominant species (Molinari, 1989). The M–H similarity index was calculated for all possible pairs of plots for burnt and unburnt conditions for each data set. An overall M–H index (plots combined) was also calculated for burnt and unburnt conditions within and between the NRI and the TNC data sets.

A log-likelihood chi-square analysis was used to test if the frequency of non-native species in different vegetation formations was equal to the proportional occurrence of the vegetation formations (Manly *et al.*, 1993). Log-likelihood chi-square analysis was also used to test if the proportion of plots in different vegetation formations was similar between the NRI and the TNC data sets.

ANOVA was used to test for differences in the diversity indices and percentage cover of non-native species between vegetation formations and between burnt and unburnt areas. Residuals were analysed to see if the dependent variables met the assumptions of ANOVA. The data were skewed for all variables, so the number and percentage of non-native species were logarithmically transformed (log + 1) and the absolute and relative cover values were arcsine ($\sqrt{x}$)-transformed. The transformations improved the skewness but the large differences in sample size between vegetation formations led to inequality of variances. Therefore, ANOVA's for the vegetation formations used separate variance calculations. We expected to find a higher number of non-native species in meadows and grasslands, so if the overall test was significant, we used planned comparisons to test for differences between these and the other vegetation formations (Day & Quinn, 1989). ANOVA was also used to test for differences in the size and age of the burns between the NRI and the TNC data sets, and if there were differences in heterogeneity in species composition (based on the M–H index) between burnt and unburnt plots within each data set and between data sets within burnt/unburnt conditions.

Least-squares regression was used to analyse the relationship between years since a plot burnt (1–44 years) and the cover and number of non-native species. Cover was arcsine ($\sqrt{x}$)-transformed and species richness was $\log_{10}$-transformed to meet the assumptions of parametric regression. The analysis used only the TNC data because of the small number of burnt plots with non-native species in the NRI data set.

Non-native species and physiographical variables

Values for 21 environmental variables were determined for each plot in the NRI and the TNC data sets. Data for some of these variables were collected in the field, but the majority were generated by conducting a spatial join between the plot locations and the physiographical layers in the GIS. The environmental variables were grouped into five general categories: (1) topographical (elevation, slope, aspect (calculated as degrees deviance from true north)); (2) vegetation structure (the percentage cover of trees, shrubs and herbaceous species; the number of species of trees, shrubs and herbaceous species); (3) soil texture (the percentage of stone, sand, loam, gravel, boulder and cobble in the soil); (4) burn configuration (burn size (ha), the ratio of perimeter to area of the burn, and the number of years since the last burn); and (5) anthropogenic use (distance (metre) from a stream, road, trail or campground).

Logistic regression was used to select the best subset of the 21 environmental variables that predicted the occurrence (presence/absence) of non-native species in the NRI and the TNC plots. Separate analyses were run for each data set. Forward stepping multiple linear regression was then used to analyse the correlation of species richness (absolute and percentage of all species) and cover (absolute and relative) of non-native species with the variables from the logistic regression that had a significant correlation with the presence of non-native species in a plot.

Ordination of physiographical and vegetation formation variables

Canonical Correspondence Analysis (CCA; ter Braak, 1995) was used to determine the major gradients correlated with distribution

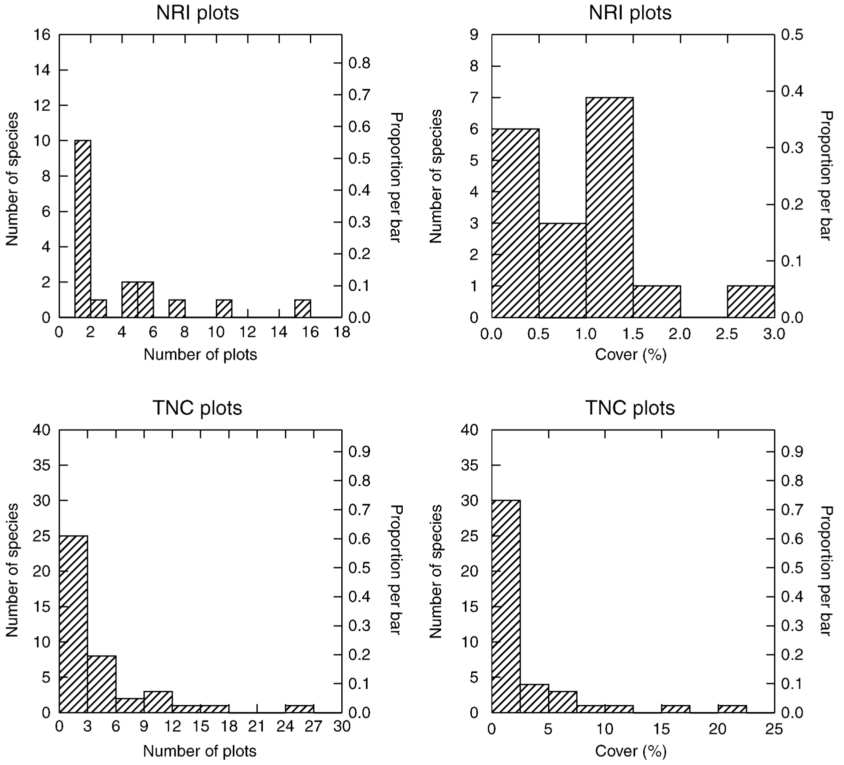

Figure 2 Distribution and abundance patterns of non-native species recorded in NRI and TNC plots at Yosemite National Park, California. NRI plots sampled from 1989 to 1993 and TNC plots sampled in 1998 to 1999.

and abundance patterns for non-native species. Variables used in the ordinations included those in the four general physiographical categories; topography, vegetation structure, soil and burn configuration. There was a strong correlation ($r = 0.87$) between cover and the number of species of trees, shrubs and herbaceous plants, therefore we selected cover variables for the analysis because we felt these were most representative of the vegetation structure in the different formations. Anthropogenic use variables were not included because they were not important predictors of non-native species occurrence, richness or cover in other analyses of this data set (Underwood *et al*., 2004).

The CCA was based on the linear combination of plot scores. Forward-stepping multiple regression was used to select the environmental variables that contributed significantly to the ordinations (ter Braak, 1995). Permutation tests were used to test the significance of the multiple regression analyses, the first ordination axis and the overall ordination (ter Braak, 1995). A total of 499 permutations were used to calculate significance levels. Cover values for the species were transformed (log + 1), and rare species were downweighted (ter Braak, 1995). The program CANOCO 4.5 (ter Braak & Smilauer, 2002) was used to perform the CCA.

RESULTS

Distribution and abundance patterns of non-native species

A total of 17 non-native species were recorded in the NRI plots and 41 in the TNC plots, with a total of 46 between the two data sets (Appendix 1). This represented 2.7% of the total number of species (native + non-native) recorded in the NRI plots and 5.4% in the TNC data set. Twenty-one of the non-native species were grasses and the rest forbs. *Bromus tectorum*, *Vulpia myuros* and *Poa pratensis* were the most widely distributed and abundant species. Collectively, these three species had mean cover values of < 6%.

Non-native species occurred in only 10.1% of the NRI plots ($n = 36$; Appendix 1), and their distribution was highly aggregated (negative binomial $k = 0.114$, $P = 0.54$). Ten of the 17 species occurred in only one plot, and none of the species had mean cover values > 3.0% (Fig. 2). The mean number of non-native species/plot in the NRI data set was 0.17 (95% CI 0.10–0.24), with a mean cover value of 0.22% (95% CI 0.12–0.32). Burnt plots comprised 12.3% ($n = 44$) of the total NRI plots, but of these only five had non-native species (1.4%).

Non-native species occurred in 24.2% of the TNC plots ($n = 57$; Appendix 1), and their distribution was also highly aggregated (negative binomial $k = 0.168$, $P = 0.17$). Nine of the 41 non-native species in the TNC data set occurred in only one plot, and > 70% of the species had mean cover values < 3.0% (Fig. 2). The mean number of non-native species/plot in the TNC data set was 0.69 (95% confidence intervals 0.47–0.91). Mean non-native cover was 2.8% (95% CI 1.4–4.2). In contrast with the NRI data set, 26.3% of the TNC plots occurred in burnt areas ($n = 62$). Thirty-one of these burnt plots had non-native species present (50.0%).

There was a significant difference in the proportion of plots in different vegetation formations between the two data sets ($\chi^2 = 38.5$, d.f. = 6, $P < 0.0001$). This was due to only 7.8% of the

NRI plots in the grassland/meadow formation, compared to 22.5% of the TNC plots (Appendix 2).

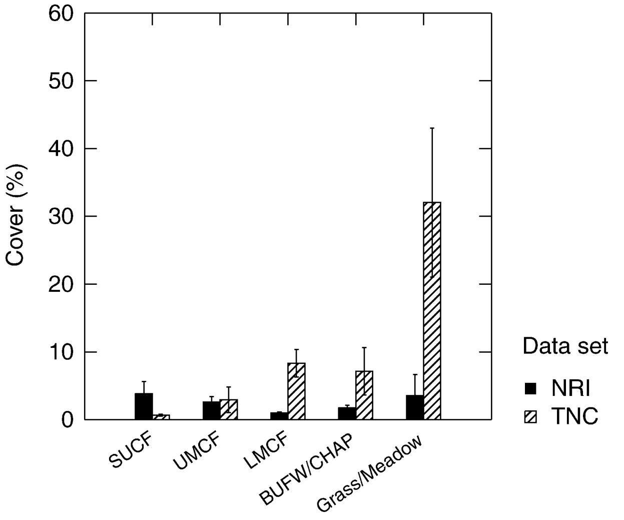

Figure 3 Mean cover (± 1 standard error) of non-native species in vegetation formations in Yosemite National Park, California. The data are from NRI plots sampled from 1989 to 1993 and TNC plots sampled in 1998 to 1999. Vegetation formation codes are SUCF = subalpine conifer forest, UMCF = upper montane conifer forest, LMCF = lower montane conifer forest, BUFW = broadleaf upland forest and woodland, CHAP = chaparral, and Grass/Meadow = grasslands and meadows.

Non-native species in the NRI data set occurred proportionally less than expected in chaparral and subalpine conifer forest plots and proportionally more than expected in broadleaf upland forests and woodland plots ($\chi^2 = 282.1$, d.f. = 6, $P < 0.0001$; Appendix 2). The results for chaparral and broadleaf woodland must be interpreted very cautiously though, because the small number of plots may seriously bias the analysis for these formations (Manly *et al*., 1993). There was no significant difference in the three species diversity indices (S, N_2, G) or cover of non-native species between the vegetation formations ($P > 0.098$).

Non-native species in the TNC data set occurred less frequently than expected in subalpine conifer forest plots and more frequently than expected in lower montane conifer forest plots ($\chi^2 = 694.6$, d.f. = 6, $P < 0.0001$; Appendix 2). The cover of non-native species was significantly greater in grassland/meadow than the other vegetation formations ($P = 0.004$; Fig. 3). There was no significant difference in the three diversity indices between the different vegetation formations.

Similarity in non-native species composition between the total sample and unburnt plots within each data set was extremely high (Table 1). Similarity between the total sample and burnt plots was lower in the NRI data set than the TNC data set (Table 1). M–H-values between burnt and unburnt plots within each data set were 0.59 for the NRI data and 0.89 for the TNC plots (Table 1). There was no significant difference in heterogeneity between burnt and unburnt plots within either data set ($P \geq 0.336$), or between data sets within burnt/unburnt conditions ($P \geq 0.138$).

There were no significant differences in the species diversity indices or cover of non-native species between burnt and unburnt plots in the NRI data set. Only seven species occurred in burnt plots, and of those none occurred in > 2 plots and all had cover values < 4.0%.

There were no significant differences in species richness, N_2 and cover of non-natives between burnt plots and unburnt plots in the TNC data set ($P > 0.427$). Mean evenness (G) was 0.559 in burnt plots and 0.800 in unburnt plots ($F = 6.291$, d.f. = 1,55, $P = 0.015$). Mean absolute and relative cover in burnt areas was < 15%, and there were on average < 4 non-native species/burnt plot. Three burnt plots had seven to 10 non-native species recorded in them, but 24 of the burnt plots had < 4 non-native species (77.4%). Mean cover of non-native species in burnt grassland plots was 33.5% with a maximum of 68.5%. The mean cover of non-native species in the other burnt vegetation formations ranged from 0.5% to 10.5%, with maximum values from 1.5% to 38.5%. The most widespread and abundant species in burnt plots were *P. pratensis*, *Rumex acetosella*, *B. tectorum*, *V. myuros*, *Cirsium vulgare* and *Holcus lanatus* (Appendix 1). The maximum cover value for any non-native species in the burnt TNC plots was 38%, and 87.3% of the cover values were ≤ 2.5%.

Mean burn size for plots with non-native species present in the NRI data set was 3794 ha (range 466–7191 ha) and 3035 ha (range 2.3–24,000 ha) for the TNC data set ($F = 3.58$, d.f. = 1,33, $P = 0.067$). For burnt plots with non-native species present, mean time since the burn in the NRI data set was 22.6 years and

Table 1 Similarity in species composition between burnt and unburnt plots from NRI and TNC data sets at Yosemite National Park, California. Total = total number of non-native species (burnt + unburnt) in each respective data set. Morisita–Horn is the modified Morista–Horn index of similarity. Species First = number of species in the first sample, Species Second = number of species in the second sample and Shared Species = number of the same species in common between both samples

First Sample	Second Sample	Species First	Species Second	Shared Species	Morisita–Horn index
NRI total	NRI unburnt	17	14	14	0.99
NRI total	NRI burnt	17	7	7	0.67
NRI unburnt	NRI burnt	14	7	4	0.59
TNC total	TNC unburnt	41	31	31	0.97
TNC total	TNC burnt	41	32	32	0.98
TNC unburnt	TNC burnt	31	32	22	0.89
NRI unburnt	TNC unburnt	14	31	9	0.59
NRI burnt	TNC burnt	7	32	6	0.71
NRI total	TNC Total	17	41	12	0.72
Mean					0.79

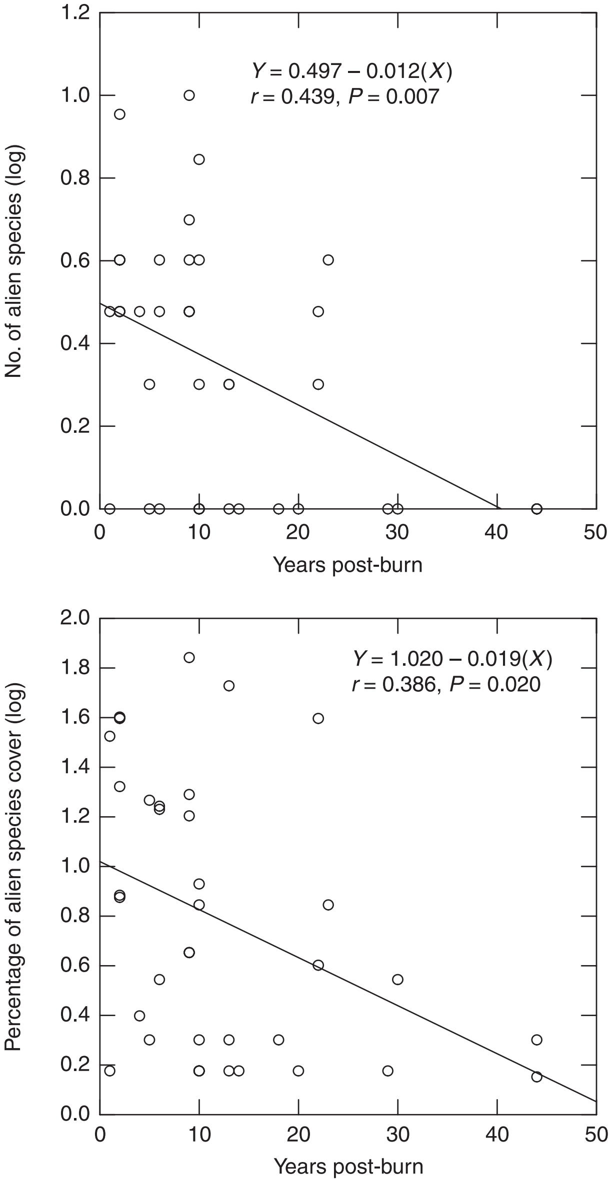

Figure 4 The relationship between the number of years a plot previously burnt and the percentage of absolute cover and number of non-native species/plot. Absolute cover and the number of non-native species/plot are on a log scale. The data were collected in TNC plots in 1998–99.

10.3 years for the TNC data set ($F = 6.12$, d.f. = 1,32, $P = 0.019$). There was a significant negative relationship between the number of non-native species/plot and the number of years post-burn (Fig. 4). Burnt plots had < 2 non-native species and mean cover values < 4% after 25 years of being burned (Fig. 4).

Correlation of non-native species distribution and abundance with biological and physiographical variables

The occurrence of non-native species in the NRI data set had significant odds ratios for six variables: elevation, the number of tree, shrub and herbaceous species, and the percentage of sand and loam in the soil (Table 2). Plots with higher numbers of non-native species tended to occur most frequently at relatively low to mid-elevations (range = 1060–3300 m; median = 1500 m), in areas with loam soil and a high proportion of herbaceous species. The classification success of plots with non-native species was only 53%, but the classification success of plots without non-native species was 95%. The overall classification success was 90.4% (McFadden's rho^2 = 0.481; $P < 0.0001$).

The occurrence of non-native species in the TNC data set had significant odds ratios for four variables: elevation, slope, the number of herbaceous species and the percentage of cobble in the soil (Table 2). Plots with relatively high numbers of non-native species tended to occur most frequently at lower elevations, in areas of low to moderate slope, with fine soils, and a high proportion of herbaceous species. The classification success of plots with non-native species was 65%, and for plots without non-native species it was 89%. The overall classification success was 83.5% (McFadden's rho^2 = 0.515; $P < 0.0001$).

Multiple linear regression analysis indicated that elevation and the number of herbaceous species were significantly correlated with non-native species richness for the NRI data set (Table 3). Seventy-two percent of the plots with non-native species in the NRI data set were below 1800 m. There was a mean of 2.0 non-native species/plot below 1800 m (range = 1–7), while above 1800 m there was only a mean of 1 non-native species/plot (range = 1–4 species). There was no significant relationship between cover of non-native species and any of the independent variables for the NRI data set (Table 3). Similarly, species richness and cover of non-native species in the TNC data set had significant correlations with elevation and herbaceous cover (Table 3). Eighty-two percent of the plots with non-native species in the TNC data set were below 1800 m. Below 1800 m there was a mean of 3.2 non-native species/plot (range = 1–10), while above 600 m there was a mean of 1.1 species/plot (range = 1–2). No non-native species were recorded above 2950 m in the TNC data set.

Ordination of species and plots and correlation with environmental variables

The distribution and abundance of non-native species varied along gradients of vegetation and soil characteristics, but burn configuration variables did not contribute significantly to the ordination (Table 4). The first axis was a gradient from steep sites with a high proportion of shrubs to flatter sites with a high proportion of herbaceous species (Fig. 5). The second axis was a soil gradient from areas with a high proportion of cobble-sized stones to those with fewer large stones (Fig. 5). Cumulatively, the first two axes explained almost 70% of the variation in the non-native species data. Two vegetation structure variables, one topography variable, and one soil variable had significant correlations with the first two axes (Table 4).

The CCA indicated that there were three groups of co-occurring non-native species (Fig. 5). One group consisting of 18 species was found most typically on steeper, shrub-dominated slopes. The most common species in this group were *B. tectorum*,

Table 2 Results of logistic regression analysis of the occurrence (presence/absence) of non-native plant species in NRI and TNC plots at Yosemite National Park, California. t = standardised logit coefficient

Regression statistics — NRI data (1989–93)

Parameter	Coefficient	SE coefficient	t	*P*	Odds ratio	95% CI Odds ratio
Elevation	–0.001	0.000	6.03	< 0.001	1.00	±0.001
Tree species	0.495	0.224	2.21	0.027	1.64	±0.740
Shrub species	0.534	0.270	1.98	0.048	1.71	±0.945
Herbaceous species	0.198	0.046	4.31	< 0.001	1.22	±0.105
Sand (%)	–0.315	0.105	3.02	0.003	0.73	±0.151
Loam (%)	0.315	0.144	2.19	0.029	1.37	±0.068

Classification table — NRI data (1989–93)

	Predicted classification		
Non-native species	Present	Not present	Total number of plots
Present	19	17	36
Not present	17	303	320

Regression statistics — TNC data (1998–99)

Parameter	Coefficient	SE coefficient	t	*P*	Odds ratio	95% CI odds ratio
Elevation	–0.004	0.001	5.54	< 0.001	0.996	±0.002
Slope	–0.092	0.043	2.15	0.031	0.912	±0.077
Cobble (%)	–0.409	0.154	2.65	0.008	0.664	±0.204
Herbaceous Cover (%)	0.018	0.009	1.95	0.051	1.018	±0.017

Classification table — TNC data (1998–99)

	Predicted classification		
Non-native species	Present	Not present	Total number of plots
Present	36	20	56
Not present	20	160	180

V. myuros and *Bromus hordeaceous*. There were 24 species in the second group, which occurred most frequently in flatter meadows and grasslands. Although the mean number of plots/species was similar between group 1 and group 2 (5.1 and 5.3, respectively), species in group 2 had > 2× the mean cover (22.1%) than species in group 1 (10.7%). The most common species in group 2 were *P. pratensis*, *R. acetosella*, *H. lanatus* and *C. vulgare* (Appendix 1). There were only four species in the third group and they occurred almost exclusively in areas with a high percentage of cobble-sized rocks (Fig. 5). However, of the four species in the group, three occurred in only one plot and the other in only three plots (Appendix 1). Thus, the loose affinity of the species in this group could have been due as much to an artefact of sampling as to any ecological relationships.

DISCUSSION

Our analysis suggests that a potentially strong response to fire by non-native plants in YNP is being mediated to a great extent by physical and biotic factors. We were not surprised to find support for our hypothesis that levels of invasion would decrease with increasing elevation, regardless of whether a site had burned or not (Mooney *et al*., 1986). There was also support for our hypothesis that the number and cover of non-native species in burnt areas would decrease over time. However, while distinct assemblages of non-native species occurred in YNP, there was little evidence their occurrence was related to burning. We could also find no support for our hypotheses that species richness and abundance of non-native species would be greater in burnt areas than in unburnt areas, or in smaller burnt areas than larger burnt areas. The patterns of non-native species distribution and abundance in YNP indicated that they were responding to a series of complex environmental gradients that overrode fire effects at the local scale. Species composition, richness and cover of non-natives were more strongly affected by topography, vegetation structure and soil texture than by disturbance from fire, and there was no evidence that non-native species would dominate burnt sites in any vegetation community.

Table 3 Multiple regression statistics of the relationship between non-native species richness and cover and environmental variables that had a significant correlation with occurrence (presence/absence) of non-native species (see Table 2 and text) from NRI and TNC data sets at Yosemite National Park, California

NRI data — species richness

Adjusted $R^2 = 0.391$, d.f. = 6.29, $P = 0.002$

Variable	Coefficient	Coefficient SE	t	*P*
Elevation	–0.001	0.0001	2.420	0.022
Tree species	–0.025	0.0150	1.730	0.094
Shrub species	–0.005	0.0200	0.238	0.814
Herbaceous species	0.020	0.0040	4.396	0.000
Sand (%)	0.001	0.0110	0.069	0.945
Loam (%)	–0.002	0.0120	0.132	0.896

NRI data — % cover

Adjusted $R^2 = 0.063$, d.f. = 6.29, $P = 0.251$

Variable	Coefficient	Coefficient SE	t	*P*
Elevation	0.000	0.0000	0.103	0.919
Tree species	–0.028	0.0270	1.041	0.307
Shrub species	0.008	0.0360	0.225	0.823
Herbaceous species	0.015	0.0080	1.845	0.075
Sand (%)	–0.033	0.0190	1.673	0.105
Loam (%)	0.031	0.0210	1.450	0.158

TNC data — species richness

Adjusted $R^2 = 0.242$, d.f. = 4.51, $P = 0.001$

Variable	Coefficient	Coefficient SE	t	*P*
Elevation	–0.001	0.0001	4.540	0.000
Slope	0.006	0.0050	1.099	0.277
Cobble (%)	0.007	0.0170	0.431	0.668
Herbaceous cover	0.002	0.0010	1.940	0.058

TNC data — % cover

Adjusted $R^2 = 0.324$, d.f. = 4.51, $P = 0.000$

Variable	Coefficient	Coefficient SE	t	*P*
Elevation	–0.001	0.0001	4.965	0.000
Slope	0.004	0.0120	0.352	0.727
Cobble (%)	–0.008	0.0400	0.204	0.840
Herbaceous cover	0.007	0.0020	3.417	0.001

Physical factors and the distribution and abundance of non-native plants in YNP

Physical factors, such as elevation, topography and soil characteristics, have direct and indirect effects on the physiological tolerances and hence the range of invasive non-native species (Rejmánek, 1989) and are known to have a strong effect on species composition in montane ecosystems (Arkley, 1981; Parker, 1982). A consistent pattern in our analysis was the negative correlation of elevation with non-native species richness and abundance. Elevation *per se* may not have strong direct effects on species distributions, but more likely represents a complex gradient comprised of a number of different variables that do, including temperature, light, moisture and nutrients (Stevens, 1992). Although non-native plants in YNP occurred sporadically at higher elevations, most were found < 2000 m and with far greater cover estimates than in higher elevation areas. Non-native species in YNP are primarily of Mediterranean origin and do not occur at high elevations in their native range (Tutin *et al.*, 1964; Hickman, 1993). Although it makes intuitive sense that their range in YNP reflects patterns from their native range, there have been no studies that have confirmed this hypothesis (Keeley *et al.*, 2003).

The number of non-native species in YNP appeared not to be related so much to any particular vegetation type but to physical gradients that occur across vegetation types. Broadleaf woodlands and chaparral occur most commonly in the lower elevations of YNP, and we found evidence that non-native species may occur more frequently than expected in broadleaf woodland relative to its area in the park. However, non-native species occurred less frequently than expected in chaparral stands. While these patterns are tenuous because of the small number of plots located in each formation, they do indicate that non-native species in YNP are not uniformly more abundant simply because of low elevation but are likely responding to other variables related to elevation.

The relationship between non-native species distribution patterns and soil properties is not well-understood, especially in montane ecosystems (Sanders, 1976; Chicione *et al.*, 1985; Williamson & Harrison, 2002). We found that soil texture was useful for predicting where non-native species occurred, but with the exception of several uncommon species that appeared to be restricted to rocky areas, it had little predictive power for distinguishing major differences in non-native species assemblages. However, the scale of the soil texture data from the GIS was relatively coarse. Finer resolution data, along with additional data on soil chemistry (Parker, 1989), might have resulted in a much stronger correlation of non-native species assemblages with soil properties.

Similar to elevation, vegetation structure and slope steepness were likely indirect gradients (Austin, 2002). Physical gradients most likely to be affected by vegetation structure in the Sierra Nevada are light and moisture. All of the non-native species recorded in the surveys were herbaceous, so it was not surprising that they tended to be most abundant in grassland/meadow and lower montane conifer forest communities where there are relatively high levels of light and moisture. We hypothesize that there is a correlation between slope steepness and soil moisture in YNP, but confirmation of this hypothesis will require further study.

Biotic factors and the distribution and abundance of non-native plants in YNP

Biotic interactions, such as competition, herbivory and seed dispersal, can act to limit distribution and abundance of non-native species once they are established within their range (Bossard, 1991). Biotic factors that may have limited the distribu-

Table 4 Canonical Correspondence Analysis intraset correlations, multiple regression statistics and summary statistics for the relationship between environmental variables and the distribution and abundance of non-native plant species in NRI and TNC plots in Yosemite National Park, California. Variables in bold had a significant correlation ($P < 0.05$) with distribution and abundance patterns of species. S_r is the additional variation explained by a variable when included with the other variables already in the model. F is the test statistic based on Monte Carlo permutation tests and P is the significance of the test. λ = eigenvalue, and Species/Environment Correlation is the correlation (Pearson) between sample scores that are linear combinations of the environmental variables and sample scores derived from the species data

Variable	Axis 1	Axis 2	Axis 3	S_r	F	P
Slope	0.733	0.020	0.154	0.36	3.49	0.002
% cobble	−0.061	0.884	−0.123	0.31	3.10	0.042
Herbaceous cover (%)	−0.621	−0.065	0.463	0.26	2.57	0.002
Shrub cover (%)	0.650	0.177	−0.040	0.21	2.13	0.046
% boulder	−0.098	0.098	0.706	0.23	2.41	0.072
Burn area (ha)	0.335	0.079	0.211	0.15	1.59	0.112
Elevation	0.035	−0.184	−0.007	0.13	1.45	0.096
Tree cover (%)	−0.122	0.083	−0.409	0.12	1.24	0.234
Aspect	0.317	0.024	0.100	0.10	1.07	0.352
Years post-burn	−0.082	0.043	0.202	0.11	1.08	0.310
% Sand	0.108	−0.158	0.090	0.09	0.98	0.412
% Gravel	0.209	−0.021	−0.156	0.09	1.02	0.428
% Stone	0.182	0.354	−0.158	0.07	0.66	0.760
% Loam	−0.310	−0.169	−0.014	0.06	0.67	0.854
Burn area/perimeter	−0.275	−0.063	−0.092	0.05	0.51	0.630
λ	0.478	0.309	0.219			
Species/Environment Correlation	0.798	0.855	0.675			

tion of non-native species in YNP include propagule pressure and a relatively small species pool. Propagule pressure is considered to be an extremely important factor in the establishment and spread of invasive species; the greater the potential pool of invasive species, the greater the likelihood some will become established into areas where they disperse (Lonsdale, 1999; Mack *et al.*, 2000). Gerlach *et al.* (2001) recorded 130 non-native species in areas of anthropogenic use in YNP, and these species tended to be more common near areas of human disturbance (Moore & Gerlach, 2001). In contrast, only 35% of the species recorded by Gerlach *et al.* (2001) and Moore and Gerlach (2001) were found in the NRI and the TNC surveys. Most occurred only sporadically across the landscape, and, with the exception of some grasslands and meadows, they comprised a low proportion of the species and relative cover in all vegetation formations. We hypothesize that this is due primarily to the NRI and the TNC plots not being close to areas of heavy anthropogenic use, such as roads and trails. The relatively small species pool and apparently low propagule pressure have likely resulted in low rates of dispersal of non-native species in the wilderness of YNP. If the NRI and the TNC plots were located in areas that were not so isolated, we expect that we would have found a far greater number of non-native species.

The lack of woody species in the NRI and the TNC data sets reflected large-scale patterns within YNP (Gerlach *et al.*, 2001) and the entire Sierra Nevada region (Schwartz *et al.*, 1996). Woody plants comprise a relatively small proportion of the non-native species pool in the Sierra Nevada and are largely confined to lower elevations, especially riparian communities (Schwartz *et al.*, 1996). However, this pattern should not be interpreted to mean that particular non-native woody species could not invade and become established in burnt areas of the Sierra Nevada. Woody non-native species invade and persist in fire-prone ecosystems in other regions with mediterranean climates (Holmes & Cowling, 1997; Holmes *et al.*, 2000; Dodson, 2001; Ruthrof *et al.*, 2003), albeit these have also been in lower elevation ecosystems. There are invasive woody species which have the potential to invade higher elevation ecosystems, especially those in the genus *Pinus* (Richardson & Rejmánek, 2004). If these species became established in the Sierra Nevada it is quite conceivable that they could invade burnt sites and increase at higher rates than closely related species, especially if propagule pressure was high enough (Ruthrof *et al.*, 2003).

Fire and the distribution and abundance of non-native plants in YNP

The scarcity and low cover values of non-native species in burnt areas in YNP largely reflected their overall pattern of low abundance and patchy distribution throughout the park. Very few burnt plots had high cover values of non-native species, which was likely related to low dispersal rates from unburnt areas. But it may also have reflected competition intensity with native species. Although species richness in burnt areas of the Sierra may decrease in the first year after a burn, it increases substantially in the next 3–5 years (Keeley *et al.*, 2003). Most species in burnt areas in montane ecosystems of the western USA are native, and it stands to reason that the competitive environment for non-natives will be high. This is the reverse of the situation in some other ecosystems in California, where a high proportion of species are non-native and competition for native species is high (Dyer & Rice, 1997; Gordon & Rice, 2000).

Non-native species were more common and had greater cover values in the burnt TNC plots than the burnt NRI plots. This was due to two factors. First, a larger proportion of the TNC plots were located in grasslands and meadows where non-native species tended to be most abundant; these plots had far greater mean and maximum cover values of non-natives than in burnt plots in other vegetation formations. The second factor was that two large wildfires (> 90,000 ha) in 1996 and 1998 resulted in a larger proportion of the TNC plots having more recent burns. A particularly important attribute in reducing long-term

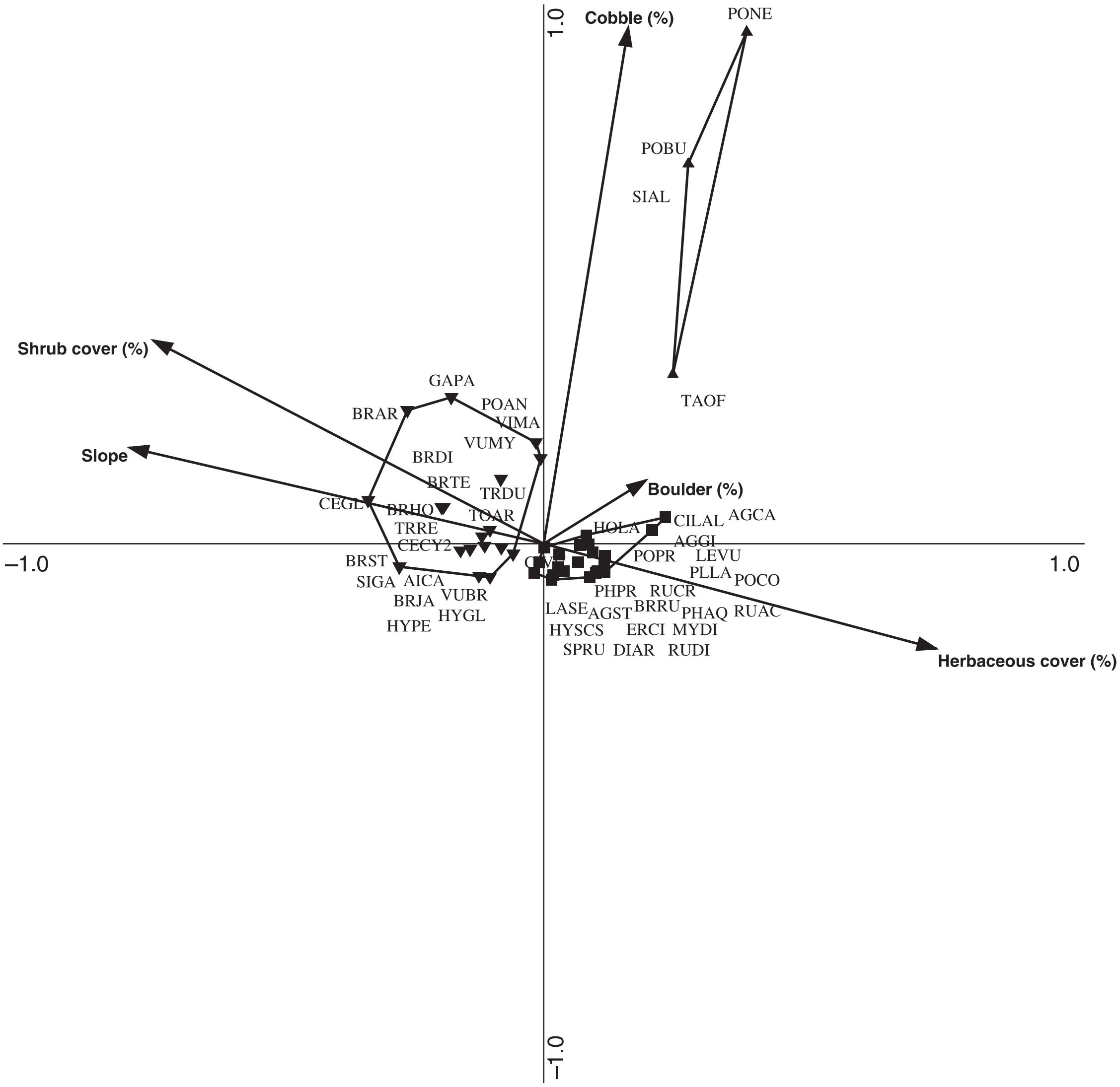

Figure 5 Canonical Correspondence Analysis biplot of the first two ordination axes for three groups of non-native species ($n = 46$) in Yosemite National Park, California. Cover values were estimated for each species in 36 plots sampled from 1989 to 1993 (NRI plots) and 57 plots sampled from 1998 to 1999 (TNC plots; see text). Acronyms for the species are given in Appendix 1. Species within each group are bounded within lines and denoted by the following symbols: down-pointing triangles = Group 1, squares = Group 2, up-pointing triangles = Group 3 (see text for explanation).

establishment by non-native species in burnt sites in the Sierra Nevada appears to be fire return interval (Keeley & Stephenson, 2000; Keeley *et al.*, 2003). Twenty-five years after burning the mean number of non-native species in YNP declined to about half of that found in the first 5 years after the burn. The 1996 and 1998 fires burnt through 28 NRI plots, 12 of which had non-native species present from 1989 to 1992. If these NRI plots were sampled in the same years as the TNC plots, we suspect they would have shown a similar pattern of greater abundance of non-natives species.

Selecting an appropriate temporal scale to evaluate invasion, establishment and persistence by non-native species into burnt areas is critical. Studies by Turner *et al.* (1997), Crawford *et al.* (2001) and Keeley *et al.* (2003) were done within 5 years of burning, and not surprisingly all found that non-native species increased in abundance after the fire and/or were more abundant in burnt than in unburnt sites. In contrast, Fornwalt *et al.* (2003) found no relationship between time since fire and richness or cover of non-native species, but this was likely due to the fact that most sites they analysed had burnt > 20 years previously, with some being centuries old. Studies spanning several decades rather than centuries or just the initial first years after burning would provide a better understanding of persistence of non-native species after burning.

With respect to fire characteristics, it is important to note that we were unable to analyse the relationship between fire return interval or fire severity with non-native species distribution and abundance. Both of these fire regime variables have been shown to be correlated with increased non-native species abundance in burnt areas. The relationship between short fire return intervals and conversion of woody-dominated communities to ones dominated by mostly non-native herbaceous species is well-understood (Zedler *et al*., 1983; D'Antonio & Vitousek, 1992; Zedler, 1995). Fire severity has been found to be important in several other studies on non-native species invasion into burnt areas in montane ecosystems (Turner *et al*., 1997; Crawford *et al*., 2001; Keeley *et al*., 2003). Non-native species appear to be consistently more abundant in high severity burn sites than moderate or low severity sites, at least during the first 5 years after the burn. High severity burn sites in the Sierra have greater levels of light and nutrients in the first years after a fire (Keeley *et al*., 2003). Surface litter is lower but species richness and cover of herbaceous species are also greater in areas of high burn severity (Keeley *et al*., 2003). This indicates the post-fire flush of light and nutrients can be exploited by a variety of native and non-native species. Until the canopy closes in and the nutrients are depleted and become a limiting factor, the relative abundance and proportion of non-native species in high severity burn sites will likely depend on the local species pool and propagule pressure.

CONCLUSIONS

Our analysis indicates that invasion rates by non-native species into burnt areas in higher elevation ecosystems will be low and not lead to alteration of fire regimes or fundamental changes in species composition. However, we want to emphasize that the patterns we observed from YNP are likely a result of restrictive conditions not necessarily found in other ecosystems. Land-use in YNP is highly regulated, and activities known or thought to promote invasion and spread of non-native species such as logging, off-highway vehicle use and grazing do not occur within the park boundaries. The park does not have an extensive road system and it is surrounded by National Forest lands and several wilderness areas, which undoubtedly reduces the rate of spread of non-native plants from adjacent areas (Keeley *et al*., 2003). In the USA these conditions are largely exclusive to National Park lands and some designated wilderness areas. Invasion rates into burnt sites may be considerably higher in other montane ecosystems where levels of human activity and disturbance are greater than or not as regulated as in YNP. In addition, even if most non-native species do not proliferate in burnt areas, fire regimes can still be altered by a single species as well as multiple ones (Whisenant, 1990).

Use of the two pre-existing data sets for this analysis had advantages and disadvantages. Advantages included the large number of plots sampled in each survey and the broad geographical coverage. Disadvantages included the relatively low number of plots in burnt areas (especially in the NRI data set) and some vegetation formations, and the correlation of species distribution and abundance patterns with indirect gradients. The consistency in results between the data sets together with the large sample size and broad geographical coverage are strong indicators that the patterns that emerged in this analysis are ecological and not artefacts of sampling. Nevertheless, surveys and experiments focused specifically on non-native species in burnt and unburnt areas in different vegetation formations would be a considerable contribution to understanding factors directly influencing their distribution patterns. This would lead to a better mechanistic understanding of invasion in montane ecosystems and improve predictive modelling efforts (Underwood *et al*., 2004).

In summary, the strong influence of physical factors has resulted in a limited non-native species pool and reduced propagule pressure for invasion into burnt areas in YNP. It is uncommon for non-native species to be abundant in burnt areas, and they tend not to spread widely or persist in the burnt areas. We conclude that the use of fire as a management tool in montane ecosystems with mediterranean-type climates will likely not lead to high rates of invasion or long-term establishment of non-native species into burnt areas if the sites are isolated from anthropogenic disturbance, fire severity is not high, and fire return intervals remain relatively long.

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Appendix 1 Distribution (number of plots) and abundance (mean cover values) for 46 non-native plant species recorded at Yosemite National Park, California in 356 NRI plots (1989–93) and 236 TNC plots (1998–99)

	NRI plots				TNC plots			
	Burnt		Unburnt		Burnt		Unburnt	
Species (acronym)	Cover (%)	No. of plots	Cover (%)	No. of plots	Cover (%)	No. of plots	Cover (%)	No. of plots
Agrostis capillaris L. (AGCA)					0.50	1	2.50	1
Agrostis gigantea Roth (AGGI)					37.50	1	2.50	1
Agrostis stolonifera L. (AGST)					8.75	2		
Aira caryophyllea L. (AICA)			0.72	3	0.50	3	0.50	1
Bromus arenarius Labill. (BRAR)					1.50	2	0.50	1
Bromus diandrus Roth. (BRDI)			1.00	1	0.50	1	0.50	1
Bromus hordeaceous L. (BRHO)			0.17	2	2.50	1	8.75	2
Bromus japonicus Thunb. ex Murr. (BRJA)			0.17	1			1.50	2
Bromus rubens L. (BRRU)					0.50	1		
Bromus sterilis L. (BRST)							0.01	1
Bromus tectorum L. (BRTE)	1.00	1	0.99	10	4.63	8	1.50	6
Centaurea cyanus L. (CECY)					0.50	1		
Cerastium glomeratum Thuill. (CEGL)							0.50	1
Cirsium vulgare (Savi) Ten. (CIVU)	1.00	2	1.00	2	1.17	6	0.50	3
Citrullus lanatus var. *lanatus* (Thunb.) (CILA)							0.50	1
Dianthus armeria L. (DIAR)					0.50	1	0.50	2
Erodium cicutarium (L.) L'Her. Ait. (ERCI)					0.50	1	2.50	1
Galium parisiense L. (GAPA)					0.50	1		
Holcus lanatus L. (HOLA)	1.67	1	1.67	1	1.30	5	1.00	4
Hypericum perforatum L. (HYPE)					0.50	1		
Hypericum scouleri ssp. *scouleri* Hook. (HYSC)					1.17	3	0.50	2
Hypochoeris glabra L. (HYGL)			0.17	1				
Lactuca serriola L. (LASE)					0.90	5	0.50	2
Leucanthemum vulgare Lam. (LEVU)	0.83	1	0.83	1	0.50	3		
Myosotis discolor Pers. (MYDI)							0.50	2
Phalaris aquatica L. (PHAQ)					2.50	1		
Phleum pratense L. (PHPR)					0.50	3	0.50	4
Plantago lanceolata L. (PLLA)	0.83	1	0.83	1			2.50	1
*Poa annu*a L. (POAN)							0.50	1
*Poa bulbos*a L. (POBU)			1.74	1				
*Poa com*pressa L. (POCO)							2.50	1
*Poa nem*oralis L. (PONE)					15.00	1		
Poa pratensis L. (POPR)	3.33	1	3.75	2	11.27	13	9.73	13
Rubus discolor Weihe & Nees (RUDI)					2.50	1	0.50	1
Rumex acetosella L. (RUAC)			1.00	1	6.86	11	6.00	6
Rumex crispus L. (RUCR)					1.00	4	0.50	1
Silene gallica L. (SIGA)							0.50	1
Sisymbrium altissimum L. (SIAL)			1.33	1				
Spergularia rubra (L.) J. Presl & C. Presl (SPRU)			0.42	1				
Taraxacum officinale G.H. Weber (TAOF)					0.50	2	0.50	1
Torilis arvensis (Huds.) Link (TOAR)					0.50	1	0.50	1
Tragopogon dubius Scop. (TRDU)					0.50	2		
Trifolium repens L. (TRRE)					0.50	1		
Vinca major L. (VIMA)					0.50	1		
Vulpia bromoides (L.) S. F. Gray (VUBR)			0.17	2				
Vulpia myuros (L.) K.C. Gmel. (VUMY)	0.42	1	1.15	10	7.33	6	6.67	3

Appendix 2 Vegetation formations and 95% CI for the occurrence of non-native plant species at Yosemite National Park, California. The data are from 356 NRI and 236 TNC plots sampled from 1989 to 1993 and 1998–99, respectively. O_i = proportional occurrence of plots with non-native species present, A_i = proportion of plots in vegetation formation. Upper and lower 95% CI are for O_i. SUCF = subalpine conifer forest, UMCF = upper montane conifer forest, LMCF = lower montane conifer forest, BUFW = broadleaved upland forest and woodlands, CHAP = chaparral/scrub, GRASS = grassland/meadow, BARREN = barren areas

	Not present		Present					
Vegetation formation	*N*	%	*N*	%	Total	A_i	O_i	95% CI (O_i)
NRI data set								
SUCF	113	31.9	5	1.4	118	0.333	0.139	0.000–0.291
UMCF	65	18.2	8	2.3	73	0.205	0.222	0.039–0.405
LMCF	61	17.1	6	1.7	67	0.188	0.167	0.003–0.331
BUFW	16	4.5	12	3.3	28	0.078	0.333	0.126–0.541
CHAP	9	2.6	0	0	9	0.026	0.000	0.000–0.000
GRASS	26	7.3	2	0.6	28	0.079	0.056	0.000–0.156
BARREN	30	8.3	3	0.8	33	0.091	0.083	0.000–0.205
Total NRI	320	89.9	36	10.1	356			
TNC data set								
SUCF	66	27.9	3	1.3	69	0.292	0.041	0.000–0.101
UMCF	30	12.7	8	3.3	38	0.160	0.108	0.013–0.203
LMCF	23	9.7	31	13.1	54	0.228	0.419	0.268–0.570
BUFW	2	0.8	2	0.8	4	0.016	0.054	0.000–0.123
CHAP	2	0.8	2	0.8	4	0.016	0.054	0.000–0.123
GRASS	43	18.2	11	4.6	54	0.228	0.149	0.040–0.258
BARREN	13	6.0	0	0.0	13	0.060	0.176	0.059–0.292
Total TNC	179	75.8	57	24.2	236			