Disturbance and Diversity in Low-Productivity Ecosystems

Hugh D. Safford, *Pacific Southwest Research Station, USDA Forest Service*
Chris R. Mallek, *University of California, Davis*

Ecological theory predicts that the amount of resources available in an ecosystem should affect its response and sensitivity to ecological disturbances like fire, herbivory, and soil disturbance. Plant stature and life form, biomass, rates of growth, and plant palatability are all influenced by habitat productivity, and these factors play key roles in determining disturbance frequencies and intensities (Pickett and White, 1985; Bond and van Wilgen, 1996; Grime, 2001; Table 12.1). Theory and empirical investigations find that site quality is often related to rates of competitive displacement, with relatively unproductive, less competitive environments less reliant on disturbance for diversity regulation (Huston, 1994; Grime, 2001). Because the most significant direct effect of disturbance on vegetation is to increase available space and light (Grace, 1999), the effects of disturbance on plant diversity should correlate positively with productivity, since more productive plant communities are more limited by above-ground competition (Tilman, 1982). Ecologically, a disturbance of a given intensity will cause more change in space and light availability in dense vegetation than in open habitats, where these resources are already more abundant. On evolutionary time scales, species are less likely to specialize on regenerating after disturbance in communities where space and light are less limiting (Grubb, 1977; Bond and van Wilgen, 1996).

Given the great differences in productivity between serpentine and nonserpentine habitats, coupled with the heightened presence of endemics and species of

TABLE 12.1 "Contextual" Features of Serpentine Soil and Vegetation That Influence the Relationship between Disturbance and Plant Diversity

Feature	Serpentine Effect
Ecosystem structure	Stunted vegetation; relatively sparse, heterogeneous plant cover; low stem density and woody plant cover; relatively low bio-mass; significant areas of exposed soil; low canopy height; greater development of understory vegetation.
Resource base	Infertile soils with high Mg; low Ca, N, P, and K; high heavy metals (Cr, Ni). Available water capacity (AWC) can be higher or lower than normal soils, but many authors refer to low soil moisture of serpentine soils.
Species traits	Relatively slow growth rates, compared to conspecifics or congeners on more fertile soils. Stress-tolerant life history strategies common. Many endemic plant species. Serpentine plants often exhibit xeromorphic traits traits such as small, thick, hairy, and/or evergreen foliage. In some regions (mostly humid, warm climates), some species hyperaccumulate heavy metals (Cr, Ni, Co), which may act as an herbivore defense. In California, some evidence of *higher* palatability of serpentine versus nonserpentine grasses. Root systems often deeper and better-developed than on more fertile soils. Often higher dominance of perennial forbs and grasses than on more fertile soils. In California, woody plants with postfire seeding strategy (serotiny and obligate seeders) are relatively more abundant in serpentine chaparral than in nonserpentine chaparral. Fire-dependent herbs (e.g., fire-cued germination) less common in serpentine than nonserpentine vegetation.
Landscape characteristics	Soils sometimes bare and rocky, often with relatively low litter cover. In humid climates, serpentine areas often support lower topographic relief than other substrate types. In drier climates, serpentine areas can be steep and rocky. Soil nutrient effect of serpentine can diminish effects of slope and aspect on vegetation development, leading to landscape vegetation pattern that is less patchy at the coarse scale. Relatively lower levels of tree and shrub cover on serpentine soils can enhance effects of wind and sun on soil and fuel drying and heating, and fire propagation.

NOTE: Also see Figure 12.5.

SOURCES: Kruckeberg 1984, 2004; Brooks 1987; Baker et al., 1992; Safford & Harrison, 2004; Alexander et al., 2007.

conservation concern in the former, it would seem that ecologists interested in studying the factors regulating diversity would gravitate to field and laboratory comparisons across this natural productivity gradient. However, such comparative studies remain rare, even in places where serpentine soils are a common part of the landscape. In the past two decades or so, the value of the serpentine–nonserpentine productivity gradient as a model system has become more apparent to community and landscape ecologists, and the number of studies investigating classic questions relating to biodiversity regulation has increased, especially in California. In this chapter, we carry out the first review of ecological studies of disturbance in serpentine vegetation, focusing on general patterns in the responses of plant species diversity to large ungulate herbivory, fire, and soil disturbance.

THE INTERACTING ROLES OF DISTURBANCE AND PRODUCTIVITY IN BIODIVERSITY REGULATION: THE THEORETICAL BACKGROUND

The modern synthesis of equilibrial and nonequilibrial theories for biodiversity regulation began in the mid-1970s, with recognition that competitive exclusion is often prevented in natural communities by factors like predation and harsh physical conditions. Connell's intermediate disturbance hypothesis (IDH) proposed that community structure is the product of three factors: disturbance; environmental heterogeneity, which is created and modified by disturbance; and recruitment, which is dependent on both of the former (Connell, 1978; Petraitis et al., 1989; Reice, 1994). The chief prediction of the IDH is that there is a unimodal relationship between diversity and disturbance, such that diversity is high at "intermediate" levels of disturbance (size or intensity or frequency) and lower at both lower and higher rates of disturbance (see Figures 12.1 and 12.2). At low levels of disturbance, equilibrial processes dominate community interactions, and superior competitors reduce diversity by eliminating inferior species. At high levels of disturbance, diversity drops as species with low recruitment rates disappear from the community.

Many studies have sought to evaluate the universality of the IDH, with varying results. Some authors have underscored the fact that different types of disturbance are not equivalent, and in many systems different disturbances interact to generate complex outcomes (Collins, 1987; Noy-Meir, 1995). Others have found that the unimodal disturbance–diversity relationship is dependent on, among other things, the type of disturbance, the sample size area, and productivity of the study system (Huston, 1994; Mackey and Currie, 2000, 2001). Proulx and Mazumder (1998) reviewed herbivory studies and found that all the studies from nutrient-poor ecosystems showed declines in species richness under heavy grazing, whereas 60% of
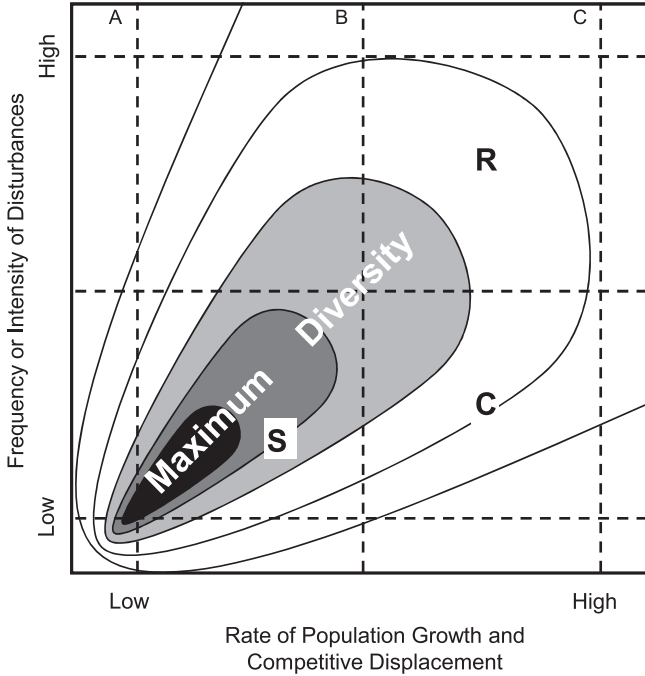
FIGURE 12.1. Effects of productivity (growth rate) and disturbance on local plant diversity, as predicted by the dynamic equilbrium model (DEM; Huston, 1994). Transects A through C represent cross-sections across the disturbance gradient at low, intermediate, and high productivity. The centroids of Grime's (2001) fundamental plant strategies (C, S, R) are also plotted. Figure altered and redrawn from Huston (1994).

studies from nutrient-rich systems showed increases in richness under heavy grazing.

The relationship between ecosystem productivity and species diversity has itself been the subject of intense debate for many years. Primary productivity—our focus—is the rate of change in plant biomass per unit area over time (Barbour et al., 1987). Numerous researchers have found broadly unimodal patterns relating species diversity to different (imperfect) surrogates for primary productivity (e.g., biomass, soil resource availability, precipitation) where diversity is maximized at intermediate productivity (Huston, 1994; Grace, 1999; Grime, 2001). It is generally thought that environments are too nutrient-poor at the low end of the productivity gradient for most species to survive. The often observed decline in diversity at the high end of the productivity gradient may be driven by local biotic processes like competitive exclusion, regional and historical processes, or both
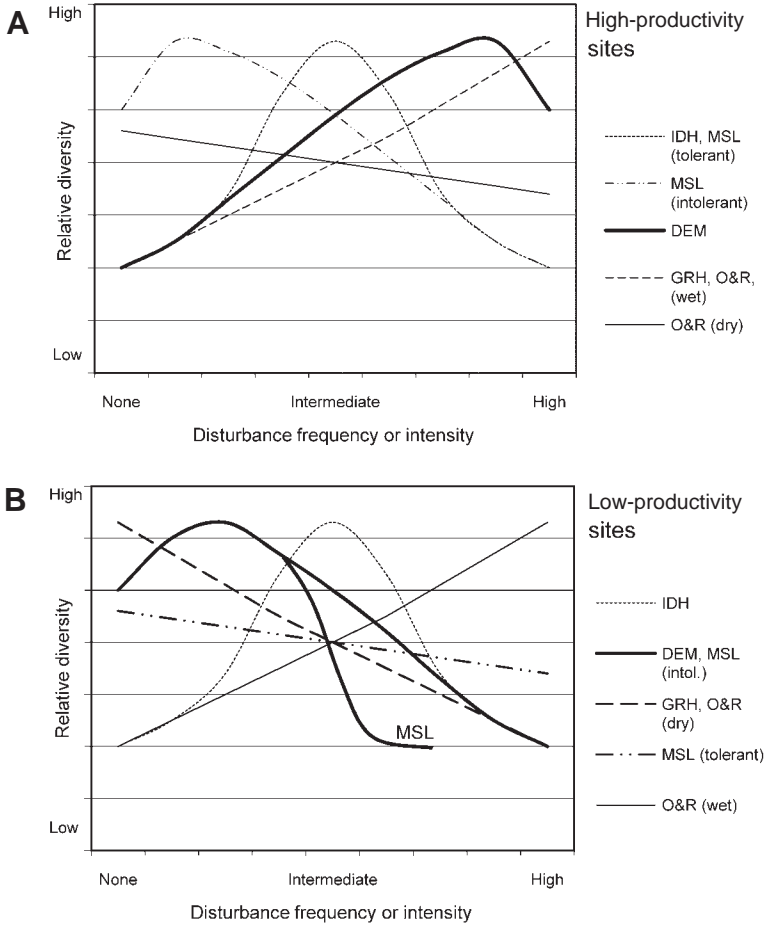
FIGURE 12.2. Theoretical disturbance-diversity curves for (A) high-productivity sites (see transect C in Figure 12.1); (B) low-productivity sites (see transect A in Figure 12.1). Diversity curves refer to relative (not absolute) diversity, and diversity levels should not be compared between curves. IDH = intermediate disturbance hypothesis (Connell, 1978); MSL = Milchunas, Sala, and Lauenroth (2003) (for disturbance-tolerant and -intolerant species); DEM = dynamic equilibrium model (Huston, 1994); GRH = grazing reversal hypothesis (Proulx and Mazumder, 1998); O&R = Olff and Ritchie (1998) (for wet and dry climates, large herbivores only). In (B), MSL differs from DEM in predicting that intolerant species in low-productivity sites cannot support high disturbance intensities or frequencies.

(Ricklefs and Schluter, 1993). Like the disturbance–diversity relationship, the unimodal productivity–diversity relationship may not be universal, and theoretical and empirical studies have also found support for positive and negative relationships (Rosenzweig and Abramsky, 1993; Abrams, 1995; Mittelbach et al., 2001).

A number of authors have suggested that species diversity patterns are best understood when the disturbance–diversity and productivity–diversity relationships are jointly considered as part of the same theoretical framework (e.g., Grime, 1977; Huston, 1994). Grime's 1979 CSR theory (Grime, 2001) and Huston's (1994) dynamic equilibrium model (DEM) are both based on a disturbance-by-productivity matrix (Figure 12.1). Grime (2001) described three primary plant strategies (C = competitors, S = stress tolerators, R = ruderal species) that result as evolutionary solutions to different permutations of the matrix, reasoning that a fourth strategy (for the extreme low-productivity/high-disturbance condition) was not viable in nature. Huston (1994) retained the fourth ecosystem condition, but otherwise CSR and the DEM make many of the same predictions. In this contribution, we focus our consideration on the DEM, because its retention of separate axes of productivity and disturbance (which are not truly independent) makes comparison of disturbance effects on serpentine and nonserpentine ecosystems more tractable (Figure 12.1).

Because increased ecosystem productivity usually leads to increased growth rates of individuals and populations, the DEM (and CSR) predicts that more frequent or severe disturbance is required to prevent competitive exclusion in highly productive habitats; highly productive, highly disturbed sites are dominated by "weedy" ruderal species, often at high species densities. At low productivity, high disturbance creates conditions where few species can survive. The DEM predicts maximal diversity where disturbance and productivity are balanced (Figure 12.1), because in these conditions the roles of local processes that drive mortality and competitive exclusion are either minimized (low ends of both gradients) or they offset one another (high ends), and larger scale factors that influence the size of the regional species pool (landscape heterogeneity, rates of immigration and speciation, etc.) come into play (Huston, 1994). Because conditions of low productivity and low disturbance allow the coexistence of many life history strategies, the DEM expects the highest diversity to occur in this region of Figure 12.1. Under high productivity, the DEM expects more or less monotonic increases in diversity as disturbance levels rise, whereas under low productivity, the model predicts diversity to generally decrease (Figure 12.2). Unimodal relationships between diversity and disturbance are only expected under intermediate conditions of productivity.

In their grazer reversal hypothesis (GRH), Proulx and Mazumder (2001) make broadly similar predictions to the DEM, with herbivore effects expected to

increase diversity monotonically in high-productivity ecosystems and decrease diversity in low-productivity ecosystems (Figure 12.2). The GRH suggests that resource availability on its own is largely sufficient to explain these patterns, with some contribution from evolved grazing tolerance. Olff and Ritchie (1998; O&R) posit that precipitation and herbivore size interact with productivity to drive plant diversity responses to disturbance. For large ungulates, O&R predict a negligible to moderate loss in diversity in dry sites but a moderate to major gain in diversity for wet sites, depending on nutrient availability. The strongest disturbance-driven decrease in diversity is expected for low-fertility soils in dry climates, and the strongest increase for low-fertility soils in wet climates (Figure 12.2).

A number of authors have noted that changes in species diversity due to disturbance may depend on the historic relationship between the studied ecosystem, its component species, and the disturbance in question (Denslow, 1985; Milchunas et al., 1988; Huston, 1994; Olff and Ritchie, 1998). Organisms that have long been subject to a particular disturbance regime (e.g., certain patterns in frequency, size, or intensity) will adapt to that regime or leave the ecosystem. Milchunas, Sala, and Lauenroth (1988; MSL) developed a theoretical framework for understanding the responses of grasslands to grazing based on their evolutionary exposure to herbivory. In floras long associated with herding ungulates, the interaction between moderate grazing and high community productivity is likely to induce strong increases in diversity and large changes in composition; in floras lacking this long association with large herbivores, however, diversity may drop strongly (Milchunas et al., 1988; Figure 12.2). A similar example can be drawn for fire. Ecosystems that rarely experience wildfire are unlikely to support many taxa that possess adaptations for rapid recolonization of burned areas, whereas ecosystems that do experience frequent fire will have many niches for postfire specialists (Grubb, 1977; Denslow, 1985).

All of these predictions concern local-scale diversity, but disturbance–diversity theory also makes predictions about regional diversity. If we assume a landscape is homogeneous (in soil, weather, topography, etc.), then theory predicts that a given disturbance regime will generate a certain range of species diversity at the local scale. If the entire landscape is disturbed at the same time by a disturbance of homogeneous intensity, as it will be if conditions are perfectly homogeneous, then the diversity of the region will be equal to the diversity of the local site. Subjecting a homogeneous landscape to a series of spatially and temporally discontinuous disturbances would generate a patchwork of different successional stages, which might lower the average local diversity (depending, e.g., on productivity) but increase beta diversity among sites and therefore regional diversity as well. Still higher regional diversities would be generated in complex landscapes, where localities of differing productivities are subjected to differing regimes of disturbance (Ricklefs and Schluter, 1993; Huston, 1994; Grime, 2001).

SERPENTINE ECOSYSTEMS AND DISTURBANCE: A REVIEW

Although ecological disturbances are ubiquitous (Pickett and White, 1985; Huston, 1994), and some serpentine ecosystems are clearly structured by disturbance (e.g., Safford and Harrison, 2004; Grace et al., 2007), research into the effects of disturbance on plant diversity in serpentine ecosystems remains rare. In our literature review, we found fewer than 50 published studies containing information relating to the diversity–disturbance relationship in serpentine vegetation, with few of these studies actually focused on disturbance itself and even fewer treating the subject quantitatively or statistically. To this point, disturbance research on serpentine habitats has focused on three types of ecological disturbance: herbivory, fire, and soil disturbances. For these three disturbance types, we summarize the results of our review.

Herbivory

Theory and empirical evidence suggest that grazing may either increase or decrease plant diversity, in the former case by reducing the dominance of superior competitors, in the latter by reducing the diversity of grazing-intolerant species (Collins et al., 1998; Gough and Grace, 1998; Olff et al., 1999; Grime, 2001). Because resource availability limits population growth, the direction of the plant diversity response to herbivory is widely thought to depend on ecosystem productivity (Huston, 1994; Olff et al., 1999; Grime, 2001). Generally speaking, grazing is expected to affect diversity positively in resource-rich ecosystems and negatively in resource-limited ecosystems, although evolutionary exposure to grazing and other factors may modify this relationship (Milchunas et al., 1988; Huston, 1994; Olff and Ritchie, 1998; Proulx and Mazumder, 1998; Figure 12.2).

Although many serpentine areas support grasslands, and although these grasslands are an important source of livestock forage in many parts of the world (Borhidi, 1988; Harrison, 1999; McCallum, 2006), there have been surprisingly few studies of the effects of grazing on serpentine plant diversity. Almost all of these have taken place in California, where research has been largely motivated by the desire to understand how herbivory and other disturbances relate to the persistence of a rapidly diminishing native grassland flora. In California, infertile substrates like serpentine are much less invaded than other substrates and provide a critical refuge for many native grassland species. Most non-native grassland species in California evolved in ecosystems subject to heavy pressure by herding ungulates; however, ungulate densities in California have been relatively low since the early Holocene extinctions, and grazing selection has likely been less important in the development of California's native grassland flora (Kimball and Schiffman,

2003). Serpentine/nonserpentine comparisons in California—and other similarly invaded regions—are thus uniquely well positioned to empirically examine the interactive effects of disturbance, productivity, soil type, and floral ancestry on plant diversity.

Herbivory Summary.   We found eight studies that statistically assessed the effects of ungulate grazing on species diversity in serpentine grassland (Huenneke, unpublished data, cited in Hobbs and Huenneke, 1992; Harrison, 1999; Safford and Harrison, 2001; Gelbard and Harrison, 2003; Harrison et al., 2003; McCallum, 2006; Niederer and Weiss, 2007; Safford, unpublished data), and one that had qualitatively assessed disturbance effects in a shrubland–grassland transition (Spence, 1957). Of the statistical assessments, seven conducted analysis at the local scale (<10 m^2), and all seven were in California. One study in South Africa evaluated grazing impacts at a broader spatial scale (1000 m^2; McCallum, 2006). Only two included analysis of the effects of varying disturbance levels (Safford and Harrison, 2001; Safford, unpublished data).

Our review suggests that low to moderate levels of ungulate (livestock) grazing in California annual grasslands tend to increase local species richness. On serpentine soils, the effect is primarily mediated through an increase in native species; richness increases on nonserpentine soils are more likely to be driven by increases in the non-native species component (Figure 12.3). Only two studies (Safford and Harrison, 2001; Safford, unpublished data) collected data from paired grazed–ungrazed plots, which allow unbiased measurement of grazing intensity and productivity. Both studies found evidence of decreased diversity at higher levels of grazing intensity (Figure 12.4). These studies also document interactions between productivity and grazing such that changes in diversity and composition due to grazing are greater in higher biomass sites.

In the reviewed studies, beta diversity in serpentine (and nonserpentine) grasslands was either unchanged or decreased by grazing; this appears to primarily be a result of floristic homogenization due to loss of grazing-intolerant taxa. Of four studies with explicit or inferred measurements of regional diversity in serpentine grassland, grazing drove an increase in one (Safford and Harrison, 2001), a decrease in one (McCallum, 2006), and no change in two (Gelbard and Harrison, 2003; Harrison et al., 2003). Three studies included regional measures from nonserpentine sites; two of them showed increases in regional diversity due to grazing (Safford and Harrison, 2001; Safford, unpublished data), one measured no change (Harrison, 1999).

The productivity of serpentine grassland is indisputably low on a global scale, but most of the reviewed studies find either a positive or negligible effect of grazing on local richness, which appears to contradict most theoretical expectations
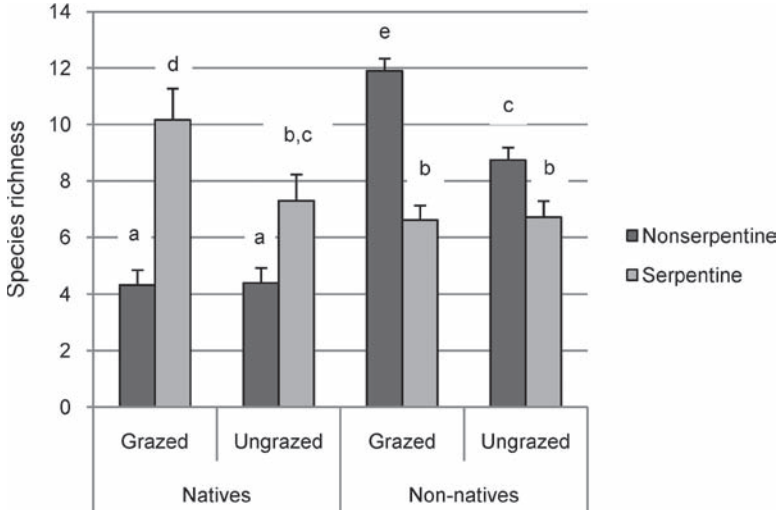
FIGURE 12.3. Effects of grazing and soil type on native and non-native species richness in serpentine and adjacent nonserpentine grasslands in northern California (Safford and Harrison, 2001).

(Figure 12.2). Most of the reviewed studies reported that they sampled areas subject to low to moderate grazing intensities (without providing actual measures of intensity). The two studies that included complete gradients of disturbance showed moderate increases in richness but negative effects on diversity as grazing intensity rose (Safford and Harrison, 2001; Safford, unpublished data). One study showed stronger losses in diversity on serpentine than on nonserpentine soils (Figure 12.4). Overall, the best theoretical match for these results is provided by the DEM and MSL (grazing-intolerant species) predictions for low-productivity soils, both of which predict an initial rise in diversity with disturbance, followed by a strong decrease at intermediate to high disturbance levels (Figure 12.2). At the moderately low levels of productivity that characterize serpentine grasslands in California (which is the only place where statistical assessment of grazing effects on plant diversity has been performed), low to moderate levels of herbivory reduce the biomass and thatch of the dominant species, which are often non-natives, providing competitive release for a suite of mostly native forbs and grasses (Hobbs and Huenneke, 1992; Weiss, 1999; Safford and Harrison, 2001; Harrison et al., 2003). At higher levels of herbivory, low levels of soil fertility and intrinsically slow growth rates of many serpentine species can result in their exclusion from the landscape. This pattern is exacerbated by the general grazing intolerance of many California species (Safford and Harrison, 2001; Kimball and Schiffman, 2003).
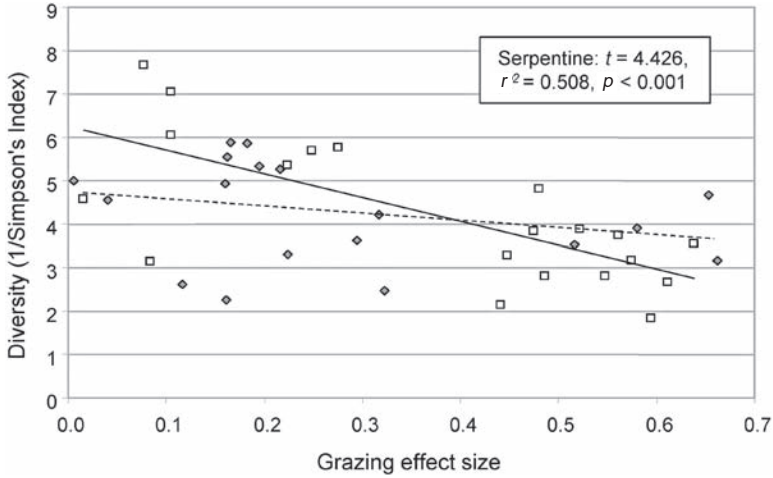
FIGURE 12.4. Local diversity versus grazing intensity for 18 nonserpentine (dotted line and diamonds) and 21 serpentine (solid line and squares) grassland sites across northern and central California. Diversity measured as 1/Simpson's Index, which measures the number of highly abundant species (lower diversity thus means that fewer species are dominating the plot and more species are becoming rare). Species richness is (weakly) lower under higher grazing intensities at serpentine sites but not at nonserpentine sites. With soil types pooled, $r^2 = 0.281$ ($p < 0.01$). Nine sites with < 0 effect size are excluded from this graph (overall regression $r^2 = 0.278$ with them).

High-intensity, long-term grazing may be more likely to reduce diversity in serpentine grassland than in nonserpentine grassland (e.g., Dennis, 1989; Huntsinger et al., 1996), but species turnover due to grazing is likely to rise as productivity increases (Safford, unpublished data). The latter effect may be independent of soil type.

Community response to disturbance is highly dependent on the life histories of the species that are there to respond. In California, native species tend to respond most strongly to grazing on serpentine soils, whereas non-natives respond most strongly on nonserpentine soils (Safford and Harrison, 2001; Gelbard and Harrison, 2003; Harrison et al., 2003; Safford, unpublished data). The richness of non-natives appears to rarely (if ever) increase on serpentine soils as the result of low- to moderate-intensity grazing. Limited data from one ongoing California study suggest that grazing-tolerant species may be equally common in serpentine and nonserpentine grassland, with their contribution to biomass surprisingly high in the former (Safford, unpublished data).

The strength of the floristic homogenization effect of grazing may generally be stronger in more productive and nonserpentine sites, but some serpentine species

may be resistant to herbivory for reasons not linked to herbivory itself (life form, magnesium content, leaf constitution). Herbivore pressure is not uniform across the landscape, and outcomes may differ based on whether grazing is light, moderate, or heavy. Although one study documented an increase in grazing effect with productivity (Safford, unpublished data), herbivore pressure may not necessarily be lower in serpentine grasslands. One California study found that the nutritional value of serpentine grass forage was actually higher than forage on adjacent nonserpentine soils (Rosiere and Vaughn, 1986).

Fire

For fire to occur, heat must be applied to fuel in the presence of oxygen. Once ignition has taken place, the behavior of fire (its intensity, rate of spread, etc.) is driven primarily by fuel characteristics, weather, and topography (Bond and van Wilgen, 1996; van Wagtendonk, 2007). The major difference between many serpentine habitats and nearby nonserpentine habitats is the amount and arrangement of biomass (fuel). In general, most serpentine vegetation is characterized by low rates of biomass accumulation. Compared to more fertile substrates, the vegetation of ultramafic soils is often of lower stature and cover, stands of woody plants are more open, soils are often rockier and frequently free of vegetation cover, and there is relatively high light and wind incidence at the ground (Table 12.1). Broad-scale weather patterns do not differ between serpentine and adjacent nonserpentine habitats, but the differing arrangements of biomass in the two habitats can lead to different effects of sun and wind on fuel drying and fire propagation. In some cases, topographic differences can also exist between serpentine areas and the nonserpentine matrix (Takaoka and Sasa, 1996).

In many parts of the globe, fire plays an important role in structuring ecosystems, but ecosystems themselves also play a role in structuring fire. In Mediterranean climate regions, islands of serpentine soils can support populations of regionally or locally rare plants that appear to be escaping competition and/or frequent fire (Vogl et al., 1977; Safford and Harrison, 2004). These taxa include species that are adapted to fire-driven reproductive cycles but require sufficient time between fires to generate adequate germplasm to guarantee population persistence (e.g., serotinous conifers). The ameliorating effect of open serpentine vegetation on wildfire spread is well known to firefighters in California, and forest fuel treatment plans sometimes incorporate natural serpentine fuel breaks. To this point, however, little is known about the role of fire in serpentine ecology or the relationship between fire and plant diversity in serpentine vegetation. Fire, fuel, and resource management in serpentine vegetation must be prosecuted almost entirely based on inference from contextual features, such as those in Table 12.1.

Fire Summary.   We reviewed the results of 21 fire studies in serpentine vegetation (Coombes and Forst, 1956; Wells, 1962; Miller, 1981; Knox, 1984; Borhidi, 1988; Parker, 1990; Tyndall, 1992, 1994; Takaoka and Sasa, 1996; McCoy et al., 1999; Arabas, 2000; Matos Mederos and Torres Bilbao, 2000; Chiarucci et al., 2001; Chiarucci, 2003; Harrison et al., 2003; Safford and Harrison, 2004; CAPO, 2007; Tolman, 2007; Safford, 2008; EBRPD, 2009; Reddy et al., 2009). Only four studies provided quantitative data on the effects of fire on local diversity (McCoy et al., 1999; Matos Mederos and Torres Bilbao, 2000; Harrison et al., 2003; Safford and Harrison, 2004), and only two carried out formal statistical analysis of those effects. Both of these latter studies were in California, and both investigated interactions with productivity and species provenance (Harrison et al., 2003; Safford and Harrison, 2004).

In California and other Mediterranean climate regions, fire has a strong positive effect on diversity in productive vegetation but less effect in unproductive (e.g., serpentine) sites, where space and light are less limiting in the undisturbed landscape (Harrison et al., 2003; Safford and Harrison, 2004, 2008). During postfire succession, diversity drops more rapidly in more productive sites (Figure 12.5). Safford and Harrison (2004) found an increase in local diversity in serpentine chaparral (sclerophyllous shrubland) due to fire (Figure 12.5), whereas Harrison and colleagues (2003) found no overall diversity effect of a late dry season fire in a serpentine grassland. In the latter, fire increased the number of native species in serpentine vegetation but not the number of non-natives. In both studies, the number of non-native weedy species in the postfire flora was disproportionately enhanced in nonserpentine versus serpentine chaparral. The effects of fire on beta and regional diversity were only statistically assessed in one study in California (Safford and Harrison, 2004). Beta diversity did not respond to fire in serpentine chaparral, but it rose in nonserpentine chaparral. Both chaparral types saw an increase in regional diversity due to the effects of fire.

Three publications from the wet tropics provided sufficient data to allow for a post facto evaluation of fire-diversity patterns (Borhidi, 1988; McCoy et al., 1999; Matos Mederos and Torres Bilbao, 2000). In Cuba and New Caledonia, local and regional diversity were both strongly reduced due to fire; in the latter, beta diversity among plots was enhanced in early successional habitats.

The effects of fire on diversity in serpentine ecosystems appear to be strongly dependent on ecological and evolutionary context. Data and anecdotes from areas of humid climate suggest that fire tends to have a negative effect on both local and regional diversity of serpentine vegetation (Coombes and Forst, 1956; Proctor and Woodell, 1971; Borhidi, 1988; McCoy et al., 1999; Matos Mederos and Torres Bilbao, 2000), although rare species may benefit from fire in some cases (Miller, 1981; Tyndall, 1992). Data from California and observations from Italy suggest that fires
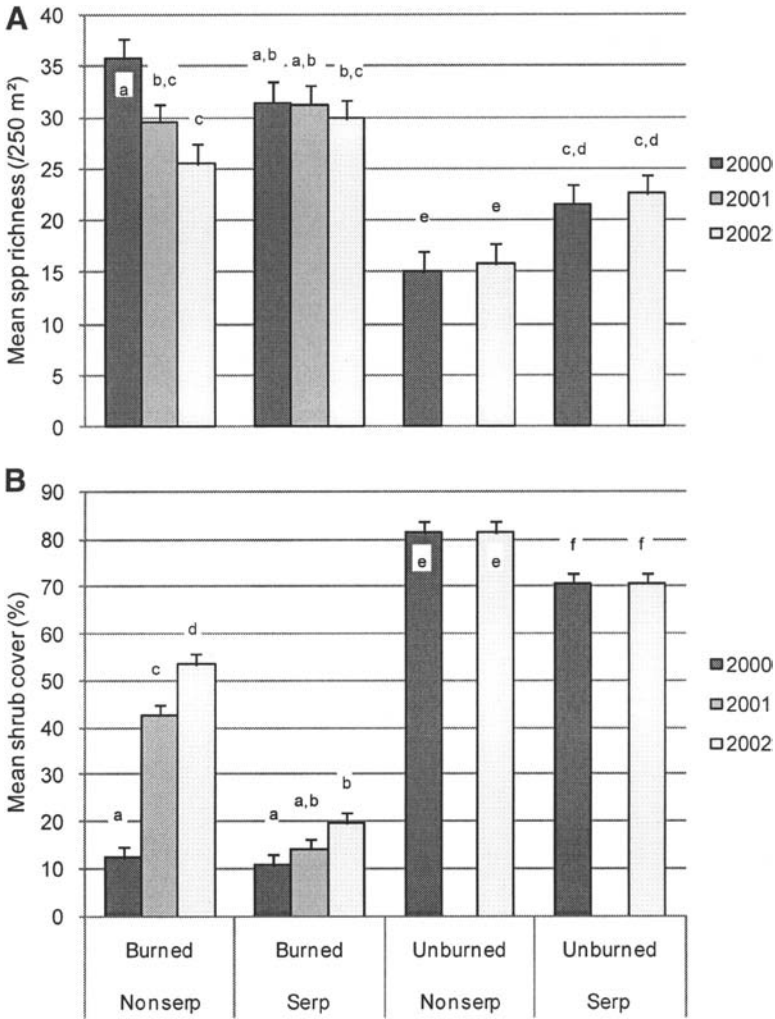
FIGURE 12.5. Postfire recovery of (A) local species richness and (B) woody cover on serpentine and sandstone chaparral sites burned in 1999 in northern California. Lowercase letters indicate significantly different means. Figure redrawn from Safford and Harrison (2004).

on serpentine in Mediterranean climate regions are more likely to increase local and regional diversity, although not as strongly as on more productive soils. Patterns in the reviewed studies support the existence of a peak in local diversity somewhere in the low to moderate disturbance intensity/frequency range. This would appear to best support the IDH, DEM, or MSL models (for disturbance-intolerant

species). These patterns may be best explained by the relative rarity of natural (nonanthropogenic) fire in most humid landscapes, and its commonness in Mediterranean climates. Areas without evolutionary exposure to frequent fire are unlikely to evolve many species that fill fire-related niches (Grubb, 1977; Denslow, 1985), and modern increases in fire frequency due to human causes in these ecosystems are likely to have largely deleterious outcomes for plant diversity. On the other hand, the successful long-term suppression of fire in many semiarid areas of the planet has reduced plant diversity in many places (Hobbs and Huenneke, 1992; Sugihara et al., 2007), but this is probably not so much the case in vegetation on serpentine soils, where all signs point to a much looser relationship with fire than in most types of nonserpentine vegetation (Safford and Harrison, 2004, 2008; Safford, 2008).

The effects of fire on serpentine vegetation are longer lasting than they are on nonserpentine vegetation, probably due to lower productivity as well as slower intrinsic growth rates of many serpentine plant taxa (Proctor and Woodell, 1971; O'Dell et al., 2006). Postfire vegetation succession is a much slower process on serpentine soils, and therefore—even though the diversity effects of fire are not as strong—the vestiges of fire in serpentine community structure are longer lasting than on more productive soils.

Generally lower frequencies of fire in serpentine habitats have led to an association of fire-sensitive taxa with serpentine soils. In Mediterranean climate regions, woody species with fire-adapted regeneration strategies (serotiny, obligate seeding shrubs) that require longer fire-free periods (and less competition for resources) are disproportionately common on serpentine soils (Vogl et al., 1977; Safford and Harrison, 2004, 2008). In California, many of the herbaceous taxa requiring fire to cue germination are found in serpentine as well as nonserpentine sites, but their overall abundance and contribution to biomass is much lower in the serpentine vegetation (Safford and Harrison, 2004).

There are soil and geomorphology feedbacks between serpentine soils, climate, and disturbance. For example, more humid areas can break down more weatherable ultramafic rocks into less defined topography, which may lead to more rapid fire spread and more homogeneity in burn severity (Takaoka and Sasa, 1996). Drier climates leave much serpentine bedrock at the surface and increase burn heterogeneity and decrease fire spread (Safford and Harrison, 2004).

Compared with more productive soil types, vegetation on serpentine soils tends to support low fuel (biomass) loads and highly heterogeneous fuel structure. In drier regions or in areas with a pronounced dry season (e.g., Mediterranean climates), this leads to relatively low frequencies and intensities of fire in serpentine vegetation (Safford and Harrison, 2004; Safford, 2008). In wetter climatic regions, the lack of a dense woody overstory on serpentine soils may lead to the development of high biomass in the vegetation understory. In such regions, high levels of

understory fuels, coupled with the enhanced influence of sun and wind on fuel moisture in the more open understory, may lead to higher flammability in serpentine vegetation (Proctor, 1999; Safford, 2008).

Soil Disturbance

Unlike herbivory and fire, there have been no grand holistic theoretical treatments of the relationship between soil disturbances and diversity. Short reviews of the effects of soil disturbance on diversity are provided by Hobbs and Huenneke (1992) and Huntly and Reichmann (1994). Considerations of the effects of soil disturbance on serpentine vegetation have focused on ablation by wind (Spence, 1957), frost heave (Rune, 1957; Dearden, 1979), soil movement due to shrink-swell clays (Alexander et al., 2007), precipitation and gravity (Oberhuber et al., 1997), and bioturbation by fossorial mammals (e.g., Hobbs and Mooney 1985, 1991, 1995; Hobbs et al., 1988, 2007). One group of researchers at Stanford University has been carrying out manipulative experiments of gopher disturbance effects on diversity for more than two decades (see Hobbs and Mooney, 1985; Hobbs et al., 2007). Their results underscore the important role that soil disturbance can play in maintaining habitat heterogeneity and regulating species diversity along both spatial and temporal gradients.

Soil Disturbance Summary.   We found more than a dozen studies that either qualitatively or quantitatively treated the subject of soil disturbance and diversity in serpentine vegetation (Rune, 1957; Spence, 1957; Dearden, 1979; Hobbs and Mooney, 1985, 1991, 1995; Hobbs et al., 1988, 2007; Safford and Harrison, 2001; Harrison et al., 2006a, 2006b; Davies et al., 2007; Safford, unpublished data). Only fossorial mammal disturbance was assessed statistically or experimentally, and then only in studies carried out in California. Only one study explicitly compared serpentine and nonserpentine soils (Safford and Harrison, 2001).

Our review suggests that the effects of soil bioturbation on local richness in herbaceous serpentine vegetation are nearly uniformly negative, although one set of studies found a unimodal response (Harrison et al., 2006a, 2006b; Davies et al., 2007; Safford, unpublished data). Beta diversity among plots appears primarily to be enhanced by soil disturbance (e.g., Hobbs and Mooney, 1985, 1991; Safford, unpublished data). The summed effect on regional diversity may be positive or negligible. These results more or less conform to expectations of five of six of the disturbance–diversity theories. This includes the unimodal response seen in one of the California studies, which is predicted by the DEM and MSL. Only the IDH is unsupported by the serpentine soil disturbance results we reviewed. It has been hypothesized that low-fertility ecosystems are characterized by lower levels of competition and/or shifting of competition from shoots to roots because of the relative

abundance of light and scarcity of soil nutrients (Tilman, 1982; Huston, 1994; Grime, 2001). If serpentine grassland plants compete primarily for below-ground resources, then disturbances like tunneling, mounding, and underground herbivory, which affect root systems, may be especially deleterious to local richness. At the same time, these locally destructive activities may promote beta diversity by increasing habitat heterogeneity and providing colonization sites for disturbance-tolerant species whose habitat requirements are not met in undisturbed vegetation (Hobbs and Mooney, 1985, 1991, 1995; Hobbs and Huenneke, 1992).

Tunneling and mound-building animals like gophers can greatly increase spatial and temporal heterogeneity in areas with sufficiently deep soil and herbaceous vegetation (Hobbs and Mooney, 1985, 1991). This creates niche opportunities for many relatively uncompetitive species. Locally, gopher disturbance may be an important driver of rare species richness and abundance on serpentine soils, but common species are better buffered against the stochasticities in population size caused by soil disturbance and may react more strongly to broad-scale drivers like variations in climate (Hobbs et al., 2007).

Depending on the species that can get propagules to the site, a disturbance may either expand or decrease niche space. There are important feedbacks between the life histories of resident species and the type of disturbance. The timing of the disturbance is of major importance. Climatic conditions before, during, and after a disturbance are critical to determining the ultimate outcome, as is the timing of the disturbance relative to plant life cycles. Species that disperse seeds at the time of the disturbance are more likely to benefit (Hobbs and Mooney, 1985, 1991, 1995).

Deeper serpentine soils often sustain a high fine clay fraction (Alexander et al., 2007), which may be easier for gophers and other tunneling animals to move through, at least in the growing season before the soil hardens. This high fine clay fraction is also highly erodible when exposed to precipitation on sloping ground (Oberhuber et al., 1997; Alexander et al., 2007). The high content of shrink-swell clay minerals in some deeper serpentine soils can result in high levels of soil movement, restricting the survival of woody plants (Alexander et al., 2007). Shallow soils on ultramafic bedrock in cold climates may be more susceptible to frost heave and similar periglacial phenomena than other soil types (Rune, 1953; Dearden, 1979).

DIVERSITY AND DISTURBANCE ON SERPENTINE SOILS: A SYNTHESIS

Only four published studies, plus one in progress, included serpentine and non-serpentine sites, disturbed and undisturbed controls, and explicit measures and statistical assessment of the effects of productivity (independent of soil type) and

disturbance gradients on species diversity (Harrison, 1999; Safford and Harrison, 2001, 2004; Harrison et al., 2003; Safford, unpublished data). The limited number of disturbance studies in serpentine vegetation makes general conclusions difficult, but the potential for important findings is high. We provide a first-cut synthesis of the extant research.

Disturbance–Diversity Theory and Empirical Evidence from Serpentine Ecosystems

Most ecological theory predicts that disturbance should play a less important role in diversity regulation in low- versus high-productivity ecosystems, and our review supports this prediction. Serpentine studies generally found a negligible to moderate rise in local diversity at lower levels of disturbance on low-productivity sites, with a drop in diversity as disturbance intensity increases, in accordance with the dynamic equilibrium model (Huston, 1994) and the model of Milchunas et al. (1998) for disturbance-tolerant species. Exceptions to this included the studies of soil disturbance and studies of fire in humid climates, which did not detect the initial increase in diversity; although the results were not always conclusive, these studies therefore may better support models predicting monotonic decreases in diversity with disturbance (e.g., Milchunas et al., 1988, for disturbance-intolerant species). In studies that either compared serpentine and nonserpentine sites or analyzed continuous gradients of productivity and disturbance intensity, the general result was that increases in local diversity following disturbance were positively correlated with productivity (e.g., Safford and Harrison, 2001, 2004; Safford, unpublished data). Increasing intensity of disturbance reduced diversity monotonically in the grazing studies but showed a unimodal response in the fire study. These studies clearly indicate the inadequacy of the intermediate disturbance hypothesis, which is insensitive to changes in ecosystem productivity.

Several studies of serpentine floras have examined beta diversity (species dissimilarity among plots and sites), which is affected by site heterogeneity, disturbance, and dispersal limitation (e.g., Whittaker, 1960; Harrison, 1997; Freestone and Inouye, 2006). Based on our review, disturbance probably plays a lesser role in determining beta diversity in serpentine than in nonserpentine vegetation. For example, grazing reduces the heterogeneity among grassland plots to a greater degree in more productive sites (Safford, unpublished data).

The Importance of Species Identity and History

Serpentine and nonserpentine soils tend to support markedly different floras and life form spectra, and these dissimilarities undoubtedly play a role in driving differing responses to disturbance and other ecological processes on the two soil types. For example, many studies have noted the higher abundances of prostrate annual forbs, perennial geophytes, and perennial grasses in serpentine versus

nonserpentine grassland, and there are notable differences in dominant plant families and genera as well (Kruckeberg, 1984; Safford et al., 2005; Alexander et al., 2007). Such traits affect ecosystem properties such as resource availability, nutrient cycling rates, soil chemistry and texture, decomposition, invasion, and responses to disturbance (Eviner and Chapin, 2003).

The much lower prevalence of weedy non-native species on serpentine may underlie many of the differences in grazing response in Californian ecosystems, although serpentine tolerance is developing in some non-native species (Harrison et al., 2001), and others have arrived with preadaptation to serpentine (Meimberg et al., 2005). The studies we reviewed from California clearly show that native and non-native species have the capacity to respond differently to herbivory, as is also seen in studies from nonserpentine systems (Kimball and Schiffman, 2003). Natives tended to respond positively to low–moderate grazing intensities on serpentine soils, whereas non-natives were more likely to respond positively to low–moderate intensity grazing on nonserpentine. Floristic differences between serpentine and nonserpentine sites may explain studies that find soil type a better predictor of grazing response than productivity (Harrison, 1999; Safford and Harrison, 2001; Safford, unpublished data).

Species identity and history are also important in the responses of diversity and composition to fire. Herbaceous fire-following species that germinate in response to fire are much more important members of the chaparral flora on nonserpentine than serpentine soils (Safford and Harrison, 2004). This component of the chaparral flora comprises a large portion of the postfire explosion of diversity in herbaceous species and contributes significantly to the differences in relative diversity response between nonserpentine and serpentine soils. Serotinous conifers in fire-prone regions are largely restricted to infertile soils like serpentine and the proportion of obligate seeding shrubs tends to be much higher on serpentine soils than on nearby nonserpentine substrates (Vogl et al., 1977; Safford and Harrison, 2004). The proportion of perennial forb and grass species is also generally higher in the serpentine than the nonserpentine flora (Kruckeberg, 1984; Alexander et al., 2007), and perennials and annuals respond very differently to disturbance.

Differences between Disturbances

Soil disturbances that primarily remove above-ground plant biomass tend to decrease local diversity, increase beta diversity, and benefit ruderal annual species at the expense of perennials (Huston, 1994; McIntyre et al., 1995). However, soil disturbances with strong below-ground effects may have contrasting consequences on plant communities. For example, gopher activity has especially negative effects on geophytes (Hobbs and Mooney, 1985, 1995; Huntly and Reichman, 1994). Gophers and other fossorial mammals also indirectly influence above-ground community structure through mixing unexploited subsoil into upper soil horizons; normally

this increases soil fertility, but in serpentine soils, it may have the opposite effect because subsoils may be low in macronutrients (Hobbs and Mooney, 1991).

Fire and ungulate grazing have many similar effects on plant communities, but there are also important differences. Grazing is always selective, and its effects on plant communities depend on the relative abundances of preferred food species (Huston, 1994; Crawley, 1997). Fire consumes both living and dead material (Bond and Keeley, 2005), and it may be completely unselective in some conditions (e.g., hot, dry, windy weather) and somewhat more selective in others (e.g., moderate weather in low fuel conditions) (Bond and van Wilgen, 1996). In grasslands, effects of recent fire on vegetation cover and diversity can be similar to the effects of grazing, but because grazing continues to selectively reduce living biomass through the growing season, its effects are usually strongly stronger and more pronounced (Collins, 1987; Noy-Meir, 1995; Harrison et al., 2003). Within-study comparisons of grazing and fire show that the two disturbances can differ in, for example, the quantity and quality of biomass removed (Collins and Barber, 1986), traits and species favored (Collins, 1987; Fuhlendorf and Engle, 2004), the effects on community structure and diversity (Collins, 1987; Noy-Meir, 1995; Harrison, et al., 2003), and the spatial and temporal scales of these effects (Collins and Smith, 2006).

The Serpentine "Context": All Serpentine Is Not Equal

Gradients in bedrock and soil can play a major role in modifying vegetation on serpentine soils, thus creating strong variation in disturbance regimes and their effects. Climate can also play a major role in modifying serpentine vegetation and its ecological relationships with disturbance (Kruckeberg, 2004; Grace et al., 2007). In very cold or arid climates, serpentine vegetation may differ insignificantly in structure or composition from the vegetation on neighboring normal soils (McNaughton, 1968; Kruckeberg, 2004; Alexander et al., 2007); in these situations, disturbance factors linked to productivity are unlikely to differ between serpentine and nonserpentine vegetation.

In some humid regions where serpentine supports shrublands and open forest (e.g., Hokkaido, Japan; the wet tropics; the United Kingdom; eastern United States; northwesternmost California), the relatively low woody biomass in the overstory allows for the growth of a dense understory of flammable subshrubs and grasses, and the open vegetation structure also promotes the drying of fuels and wind-driven fire spread. In these situations, fire may be naturally more frequent in serpentine than nonserpentine vegetation (Miller, 1981; McCoy et al., 1999; Proctor, 1999; Arabas, 2000), and managing for an appropriate fire regime to maintain the unique serpentine vegetation is a major concern.

The nutrient factor in serpentine soils can become so dominant in some circumstances that other important drivers of vegetation pattern, such as topography, are largely overridden. We found multiple references to the relatively minor

effects that variations in slope and aspect have on serpentine vegetation, diversity, and disturbance relative to nearby nonserpentine sites (e.g., McNaughton, 1968; Harrison, 1999; Safford and Harrison, 2001). The serpentine soil factor can likewise overwhelm disturbance as a driver of vegetation community structure. A number of the studies we reviewed found that soil type was more important than disturbance in explaining plant diversity patterns (Coombes and Forst, 1956; Harrison, 1999; Safford and Harrison, 2001; Harrison et al., 2003; Safford, unpublished data). The dearth of scientific studies exploring the effects of natural disturbance on serpentine vegetation is itself probably an effect of the relatively low importance of disturbance to serpentine vegetation in many parts of the world.

How Useful Are Serpentine–Nonserpentine Comparisons for Studying Ecological Patterns and Processes Related to Disturbance?

We believe that serpentine–nonserpentine comparisons provide a powerful model system for studying ecological and evolutionary processes related to disturbance and productivity. Local studies using serpentine and nonserpentine soils can be designed to capture very broad gradients of both productivity and disturbance, perhaps to a greater degree than almost any other natural terrestrial system. In many places, the difficulty comes in finding sites of enough fertility or water availability to complete the high end of the productivity gradient. In California, chaparral productivity in immediate postfire years is often very high, but many nonserpentine grasslands are not particularly productive. Regions with relatively high but not excessive rainfall and warm growing season temperatures (e.g., coastal or montane Mediterranean regions, the humid temperate zone, parts of the tropics and subtropics) may provide the best locations for studies of disturbance effects on diversity, because they are more likely to capture a broad productivity gradient.

Does the unusual plant species composition found on serpentine soils undermine their usefulness for studies related to soil productivity? We would counter that gradients of soil productivity are strong selective forces and evolution will always mold the flora in accordance with the reigning environment. Plants in all truly low-productivity sites are characterized by similar suites of morphologies and life history strategies (Grime, 2001), and serpentine plants fall well within this general suite.

LITERATURE CITED

Abrams, P. A. (1995) Monotonic or unimodal diversity-productivity gradients: What does competition theory predict? *Ecology*, 76, 2019–27.

Alexander, E. B., Coleman, R. G., Keeler-Wolf, T., and Harrison, S. (2007) *Serpentine Geoecology of Western North America*. Oxford University Press, New York.

Arabas, K. B. (2000) Spatial and temporal relationships among fire frequency, vegetation, and soil depth in an eastern North American serpentine barren. *Journal of the Torrey Botanical Society*, 127, 51–65.

Baker, A. J. M., Proctor, J., and Reeves, R. D. (1992) *The Vegetation of Ultramafic Soils*. Intercept, Andover.

Barbour, M. G., Burk, J. H., and Pitts, W. D. (1987) *Terrestrial Plant Ecology*, 2nd ed. Benjamin/Cummings, Menlo Park, NY.

Bond, W. J., and Keeley, J. E. (2005) Fire as a global "herbivore": The ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, 20, 387–94.

Bond, W. J., and van Wilgen, B. W. (1996) *Fire and Plants*. Chapman and Hall, London.

Borhidi, A. (1988) Vegetation dynamics of the savannization process on Cuba. *Vegetatio*, 77, 177–83.

Brooks, R. R. (1987) *Serpentine and Its Vegetation: A Multidisciplinary Approach*. Dioscorides Press, Portland.

CAPO. (2007) Un viaggio nell-Italia delle "pietre Verdi." *Aree protette— flora e vegetazione*. Coordinamento Aree Protette Ofiolitiche, Siena.

Chiarucci, A. (2003) Vegetation ecology and conservation on Tuscan ultramafic soils. *Botanical Review*, 69, 252–68.

Chiarucci, A., Rocchini, D., Leonzio, C., and de Dominicis, V. (2001) A test of vegetation-environment relationship in serpentine soils of Tuscany, Italy. *Ecological Research*, 16, 627–39.

Collins, S. L. (1987) Interaction of disturbances in tallgrass prairie: A field experiment. *Ecology*, 68, 1243–50.

Collins, S. L., and Barber, S. C. (1986) Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio*, 64, 87–94.

Collins, S. L., Knapp, A. K., Briggs, J. M., Blair, J. M., and Steinauer, E. M. (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, 280, 745–47.

Collins, S. L., and Smith, M. D. (2006) Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prarie. *Ecology*, 87, 2058–67.

Connell, J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, 199, 1302–10.

Coombes, D. E., and Forst, L. C. (1956) The heaths of the Cornish serpentine. *Journal of Ecology*, 44, 226–56.

Crawley, M. J. (1997) *Plant Ecology*, 2nd ed. Blackwell Science, Oxford.

Davies, K. F., Harrison, S., Safford, H. D., and Viers, J. H. (2007) Productivity alters the scale dependence of the diversity-invasibility relationship. *Ecology*, 88, 1940–47.

Dearden, P. (1979) Some factors influencing the composition and location of plant communities on a serpentine bedrock. *Journal of Biogeography*, 6, 93–104.

Dennis, A. (1989) *Effects of Defoliation on Three Native Perennial Grasses in the California Annual Grassland*. PhD diss., University of California, Berkeley.

Denslow, J. S. (1985) Disturbance-mediated coexistence of species. In *The Ecology of Natural Disturbance and Patch Dynamics* (eds. S. T. A. Pickett and P. S. White), pp. 307–24. Academic Press, Orlando.

EBRPD. (2009) *Serpentine Prairie Restoration Plan, Redwood Regional Park*. East Bay Regional Park District, Planning Stewardship Department, Oakland, CA.

Eviner, V. T., and Chapin, F. S. (2003) Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology Evolution and Systematics*, 34, 455–85.

Freestone, A. L., and Inouye, B. D. (2006) Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology*, 87, 2425–32.

Fuhlendorf, S. D., and Engle, D. M. (2004) Application of fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology*, 41, 604–14.

Gelbard, J. L., and Harrison, S. (2003) Roadless habitats as refuges for native plant diversity in California grassland landscapes. *Ecological Applications*, 13, 404–15.

Gough, L. C., and Grace, J. B. (1998) Herbivore effects on plant species density at varying productivity levels. *Ecology*, 79, 1586–94.

Grace, J. B. (1999) The factors controlling species density in herbaceous plant communities: An assessment. *Perspectives in Plant Ecology, Evolution and Systematics*, 2(1), 1–28.

Grace, J. B., Safford, H. D., and Harrison, S. (2007) Large-scale causes of variation in the serpentine vegetation of California. *Plant and Soil*, 293, 121–32.

Grime, J. P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary history. *American Naturalist*, 111, 1169–94.

Grime, J. P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd ed. Wiley, New York.

Grubb, P. J. (1977) The maintenance of species richness in plant communities: The importance of the regeneration niche. *Biological Reviews*, 52, 107–45.

Harrison, S. (1997) How natural habitat patchiness affects the distribution of diversity in California serpentine chaparral. *Ecology*, 78, 1989–906.

Harrison, S. (1999) Native and alien species diversity at the local and regional scales in a grazed California grassland. *Oecologia*, 12, 99–106.

Harrison, S. P., Grace, J., Davies, K. F., Safford, H. D., and Viers, J. H. (2006a) Invasion in a diversity hotspot: Exotic cover and native richness in the California serpentine flora. *Ecology*, 87, 695–703.

Harrison, S. P., Inouye, B., and Safford, H. D. (2003) Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology*, 17, 837–45.

Harrison, S., Rice, K. J., and Maron, J. L. (2001) Habitat patchiness promotes invasions by alien grasses on serpentine soil. *Biological Conservation*, 100, 45–53.

Harrison, S. P., Safford, H. D., Grace, J., Viers, J. H., and Davies, K. F. (2006b) Regional and local species richness in an insular environment: Serpentine plants in California. *Ecological Monographs*, 76, 41–56.

Hobbs, R. J., Gulmon, S. L., Hobbs, V. J., and Mooney, H. A. (1988) Effects of fertiliser addition and subsequent gopher disturbance on a serpentine annual grassland community. *Oecologia*, 75, 291–95.

Hobbs, R. J., and Huenneke, L. (1992) Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology*, 6, 324–37.

Hobbs, R. J., and Mooney, H. A. (1985) Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia*, 67, 342–51.

Hobbs, R. J., and Mooney, H. A. (1991) Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology*, 72, 59–68.

Hobbs, R. J., and Mooney, H. A. (1995) Spatial and temporal variability in California annual grassland: Results from a long-term study. *Journal of Vegetation Science*, 6, 43–57.

Hobbs, R. J., Yates, S., and Mooney, H. A. (2007) Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. *Ecological Monographs*, 77, 545–68.

Huntly, N., and Reichman, O. J. (1994) Effects of subterranean mammalian herbivores on vegetation. *Journal of Mammalogy*, 75, 852–59.

Huntsinger, L., McClaran, M. P., Dennis, A., and Bartolome, J. W. (1996) Defoliation response and growth of *Nassella pulchra* (A. Hitchc.) Barkworth from serpentine and non-serpentine populations. *Madroño*, 43, 46–57.

Huston, M. A. (1994) *Biological Diversity: The Coexistence of Species*. Cambridge University Press, Cambridge.

Kimball, S., and Schiffman, P. M. (2003) Differing effects of cattle grazing on native and alien plants. *Conservation Biology*, 17, 1681–93.

Knox, R. G. (1984) Age structure of forests on Soldiers Delight, a Maryland serpentine area. *Bulletin of the Torrey Botanical Club*, 111, 498–501.

Kruckeberg, A. R. (1984) California serpentines: Flora, vegetation, geology, soils, and management problems. *University of California Publications in Botany*, 87, 1–180.

Kruckeberg, A. R. (2004) *Geology and Plant Life: The Effects of Landforms and Rock Types on Plants*. University of Washington Press, Seattle.

Mackey, R. L., and Currie, D. J. (2000) A re-examination of the expected effects of disturbance on diversity. *Oikos*, 88, 483–93.

Mackey, R. L., and Currie, D. J. (2001) The diversity-disturbance relationship: Is it generally strong and peaked? *Ecology*, 82, 3479–92.

Matos Mederos, J., and Torres Bilbao, A. (2000) Primeros estadíos sucesionales del Cuabal en las serpentinas de Santa Clara. *Revista del Jardín Botánico Nacional*, 21(2), 167–82.

McCallum, D. A. (2006) *Diversity and Conservation of Ultramafic Flora in Swaziland*. PhD diss., University of the Witwatersrand, Johannesburg.

McCoy, S., Jaffré, T., Rigault, F., and Ash, J. E. (1999) Fire and succession in the ultramafic maquis of New Caledonia. *Journal of Biogeography*, 26, 579–94.

McIntyre, S., Lavorel, S., and Tremont, R. M. (1995) Plant life-history attributes: Their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology*, 83, 31–44.

McNaughton, S. J. (1968) Structure and function in California grasslands. *Ecology*, 49, 962–72.

Meimberg, H., Hammond, J. I., Jorgensen, C. M., Park, T. W., Gerlach, J. D., Rice, K. J., and McKay, J. K. (2005) Molecular evidence for an extreme genetic bottleneck during introduction of an invading grass to California. *Biological Invasions*, 8, 1355–66.

Milchunas, D. G., Sala, O. E., and Lauenroth, W. K. (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, 132, 87–106.

Miller, G. L. (1981) Secondary succession following fire on a serpentine barren. *Proceedings of the Pennsylvania Academy of Sciences*, 55, 62–64.

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., Willig, M. R., Dodson, S. I., and Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, 82, 2381–96.

Niederer, C., and Weiss, S. B. (2007) Ecological management of serpentine grassland in the face of nitrogen deposition and invasive grasses. In *Ecological Society of America/Society for Restoration Ecology Joint Meeting, Abstract of presentation*, pp. 59–71. San Jose, CA. Available online at http://eco.confex.com/eco/2007/techprogram/P3812.HTM.

Noy-Meir, I. (1995) Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. *Journal of Vegetation Science*, 6, 701–10.

Oberhuber, W., Pagitz, K., and Nicolussi, K. (1997) Subalpine tree growth in serpentine soil: A dendroecological analysis. *Plant Ecology*, 130, 213–21.

O'Dell, R. E., James, J. J., and Richards, J. H. (2006) Congeneric serpentine and nonserpentine shrubs differ more in leaf Ca:Mg than in tolerance of low N, low P, or heavy metals. *Plant and Soil*, 280, 49–64.

Olff, H., Brown, V. K., and Drent, R. H. (eds.) (1999) *Herbivores: Between Plants and Predators*. Blackwell Science, Oxford.

Olff, H., and Ritchie, M. E. (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, 13, 261–65.

Parker, V. T. (1990) Problems encountered while mimicking nature in vegetation management: An example from fire prone vegetation. In *Proceedings of the Fifteenth Annual Natural Areas Conference. Bulletin No. 471* (eds. R. S. Mitchell, C. J. Sheviak, and D. J. Leopold), pp. 231–34. New York State Museum, New York.

Petraitis, P. S., Latham, R. E., and Niesenbaum, R. A. (1989) The maintenance of species diversity by disturbance. *Quarterly Review of Biology*, 64, 393–418.

Pickett, S. T. A., and White, P. S. (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando.

Proctor, J., and Woodell, S. R. J. (1971) The plant ecology of serpentine: I. serpentine vegetation of England and Scotland. *Journal of* Ecology, 59, 375–95.

Proulx, M., and Mazumder, A. (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology*, 79, 2581–92.

Reddy, R. A., Balkwill, K., and McLellan, T. (2009) Plant species richness and diversity of the serpentine areas on the Witwatersrand. *Plant Ecology*, 201, 365–81.

Reice, S. R. (1994) Nonequilibrium determinants of biological community structure. *American Scientist*, 82, 424–35.

Ricklefs, R. E., and Schluter, D. (1993) *Species Diversity in Ecological Communities*. University of Chicago Press, Chicago.

Rosiere, R. E., and Vaughn, C. E. (1986) Nutrient content of sheep diets on a serpentine barrens range site. *Journal of Range Management*, 39, 8–13.

Rosenzweig, M. L., and Abramsky, Z. (1993) How are diversity and productivity related? In *Species Diversity in Ecological Communities* (eds. R. E. Ricklefs and D. Schluter), pp. 52–65. University of Chicago Press, Chicago.

Rune, O. (1953) Plant life on serpentines and related rocks in the north of Sweden. *Acta Phytogeografia Suecica*, 31, 1–139.

Safford, H. D. (2008) Fire and ultramafic vegetation in northern California. In *6th International Conference on Serpentine Ecology, Program and Abstracts* (ed. N. Rajakaruna), p. 6. College of the Atlantic, Bar Harbor.

Safford, H. D., and Harrison, S. P. (2001) Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. *Ecological Applications*, 11, 1112–22.

Safford, H. D., and Harrison, S. (2004) Fire effects on plant diversity in serpentine vs. non-serpentine chaparral. *Ecology*, 85, 539–48.

Safford, H. D., and Harrison, S. (2008) The effects of fire on serpentine vegetation and implications for management. In *Proceedings of the 2002 Fire Conference on Managing Fire and Fuels in the Remaining Wildlands and Open Spaces of the Southwestern United States* (ed. M. Narog), PSW-GTR-189, pp. 321–28. USDA Forest Service, PSW Research Station, Albany.

Safford, H. D., Viers, J. H., and Harrison S. P. (2005) Serpentine endemism in the California flora: A database of serpentine affinity. *Madroño*, 52, 222–57.

Spence, D. H. N. (1957) Studies on the vegetation of Shetland: I. The serpentine debris vegetation in Unst. *Journal of Ecology*, 45, 917–45.

Sugihara, N. G., van Wagtendonk, J. W., Shaffer, K. E., Fites-Kaufman, J., and Thode, A. E. (eds.) (2007) *Fire in California's Ecosystems*. University of California Press, Berkeley.

Takaoka, S., and Sasa, K. (1996) Landform effects on fire behavior and post-fire regeneration in the mixed forests of northern Japan. *Ecological Research*, 11, 339–49.

Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

Tolman, D. A. (2007) Soil patterns in three *Darlingtonia* fens in southwestern Oregon. *Natural Areas Journal*, 27, 374–84.

Tyndall, R. W. (1992) Historical considerations of conifer expansion in Maryland serpentine "barrens." *Castanea*, 57, 123–31.

Tyndall, R. W. (1994) Conifer clearing and prescribed burning effects to herbaceous layer vegetation on a Maryland serpentine barrens. *Castanea*, 59, 255–73.

van Wagtendonk, J. W. (2007) Fire as a physical process. In *Fire in California's Ecosystems* (eds. N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode), pp. 38–57. University of California Press, Berkeley.

Vogl, R. J., Armstrong, W. P., White, K. L., and Cole, K. L. (1977) The closed-cone pines and cypress. In *Terrestrial Vegetation of California* (eds. M. G. Barbour and J. Major), pp. 295–358. Wiley, New York.

Weiss, S. (1999) Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grassland for a threatened species. *Conservation Biology*, 13, 1476–86.

Wells, P. V. (1962) Vegetation in relation to geological substratum and fire in the San Luis Obispo quadrangle. *Ecological Monographs*, 32, 79–103.

Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30, 279–338.