Ecological Applications, 19(8), 2009, pp. 2242–2253

Not all ski slopes are created equal: Disturbance intensity affects ecosystem properties

Jennifer W. Burt[1] and Kevin J. Rice

Department of Plant Sciences, University of California, One Shields Avenue, Davis, California 95616 USA

Abstract. In mountain regions around the world, downhill ski areas represent a significant source of anthropogenic disturbance while also providing recreation and revenue. Ski-run creation always results in some level of disturbance, but disturbance intensity varies greatly with construction method. Ski runs may be established either by clearing (cutting and removing tall vegetation) or by clearing and then machine-grading (leveling the soil surface with heavy equipment). To quantify how these different intensities of initial disturbance affect ecosystem properties, we extensively surveyed vegetation, soils, and environmental characteristics on cleared ski runs, graded ski runs, and adjacent reference forests across seven large downhill ski resorts in the northern Sierra Nevada, USA. We found that the greater disturbance intensity associated with grading resulted in greater impacts on all ecosystem properties considered, including plant community composition and diversity, soil characteristics relating to processes of nutrient cycling and retention, and measures of erosion potential. We also found that cleared ski runs retained many ecological similarities to reference forests and might even offer some added benefits by possessing greater plant species and functional diversity than either forests or graded runs. Because grading is more damaging to multiple indicators of ecosystem function, clearing rather than grading should be used to create ski slopes wherever practical.

Key words: ecological restoration; ecosystem services; erosion control; gradient; high-elevation ecosystems; hydrology; intermediate disturbance; Sierra Nevada, California, USA; ski piste; soil function; species diversity; vegetation management.

Introduction

Downhill ski areas dramatically alter the ecology and aesthetics of the landscapes they occupy. Most large downhill ski areas in the United States are on lands managed by the USDA Forest Service, a federal agency charged with encouraging multiple uses while attempting to protect and maximize ecosystem services (Kessler et al. 1992, Briggs 2000, Rivera and de Leon 2004, Zhang 2005). Certainly not all ecosystem uses and services can be maximized simultaneously in one location. However, ski areas are managed almost exclusively for recreation, when they might also be managed to minimize negative impacts on compatible ecological services, such as water storage, nutrient cycling, and maintenance of biodiversity. Ski slopes are of great conservation concern and restoration interest because they extensively and significantly alter fragile high-elevation ecosystems (Tsuyuzaki 1994, Tenenbaum 2001, Clifford 2002, Rivera and de Leon 2004). Ski areas also provide unique opportunities as large-scale natural experiments in that downhill ski runs are large, replicated disturbances amid relatively undisturbed landscapes. Ski areas thus facilitate experimental examination of the effects of large-scale disturbances of different intensities on multiple aspects of plant community structure and ecosystem properties.

Ski slopes are "not all created equal" principally because there are two basic approaches to ski-run construction that correspond to distinctly different initial disturbance intensities. "Cleared" ski runs are created by cutting and removing tall woody vegetation as needed to create open skiing pathways, but leaving the soil and seedbank largely intact. "Graded" ski runs, in contrast, are cleared and then machine-graded or leveled to remove tree stumps, boulders, and slope irregularities. This grading process disturbs and/or removes much of the topsoil and most of the vegetation. These differences in the severity of initial disturbance are likely to differentially alter environmental capacities for ecosystem recovery after ski-run construction.

Although there is much scientific interest in ski-slope ecology and impacts, the preponderance of research on this topic focuses on alpine (above timberline) grasslands and heathlands in Europe (e.g., Mosimann 1985, Bayfield 1996, Urbanska 1997, Urbanska et al. 1998, Urbanska and Fattorini 1998, 2000, Rixen et al. 2003, Gros et al. 2004, Wipf et al. 2005, Barni et al. 2007, Delgado et al. 2007), and with only one exception (Wipf et al. 2005), on machine-graded ski runs. As a result, there is paucity of studies describing ecological impacts of ski slopes in montane or subalpine (below tree line)

Manuscript received 16 April 2008; revised 20 January 2009; accepted 25 February 2009. Corresponding Editor: A. R. Townsend.

[1] E-mail: jenniferwburt@gmail.com

ecosystems. Despite this lack of studies, ski runs are predominately located below tree line in western North America (Price 1985) and are common in upper montane and subalpine zones elsewhere (Ruth-Balaganskaya and Myllynen-Malinen 2000, Tsuyuzaki 2002, Laiolo and Rolando 2005). In Finland, Ruth-Balaganskaya and Myllynen-Malinen (2000) conducted one of the few studies below tree line that explicitly compared conditions on graded ski runs to reference forests; they found that soils on graded ski runs were nutrient depleted relative to undisturbed boreal forests to such an extent that recovery would not occur without active restoration.

Furthermore, of all the studies we reviewed that describe the ecology and impacts of ski slopes, only one considered ungraded ski runs. That study, conducted in alpine grasslands and dwarf heathlands in the Swiss Alps, demonstrated that graded and ungraded ski runs differed greatly in many respects, including vegetation cover and productivity, plant indicator values, and species diversity (Wipf et al. 2005: Table 1). These alpine ecosystems are very different from the conifer forest ecosystems that characterize many ski areas, and we know of no studies comparing cleared ski runs and graded ski runs below timberline.

In the context of vegetation succession, which is initiated or reset by disturbance, the intensity of disturbance influences recovery time (Coffin et al. 1998, Whisenant 1999, Hirst et al. 2003, Nishimura 2006). Disturbance severity fundamentally determines whether a system will undergo primary or secondary succession or follow some intermediate model (Whisenant 1999, Pickett and Cadenasso 2005). Cleared ski runs likely retain a greater biotic legacy (residual soil function and plant propagules) than graded ski runs, because grading can severely disturb or remove the topsoil and seed bank. We might, therefore, expect cleared ski runs to follow a model of secondary succession, and graded ski runs, primary succession (Whisenant 1999). Greater disturbance severity has also been found to lead to less predictable successional trajectories (Turner et al. 1998, Urbanska and Chambers 2002, Hirst et al. 2003).

Disturbance intensity may produce varying effects on patterns of plant community diversity as well as on underlying soil properties. The intermediate-disturbance hypothesis predicts that plant community diversity should be highest at intermediate disturbance levels (Grime 1973, Connell 1978, Huston 1979). This hypothesis has been supported by many studies, but an even greater number have failed to support it (reviewed in Mackey and Currie 2001). Beyond affecting plant community composition, increased disturbance intensity can also influence soil nutrient availability, organic matter, microbial biomass, and soil respiration (McNabb et al. 1997, Whisenant 1999, Claassen and Hogan 2002, DeBusk et al. 2005). Soil structure and hydrological parameters, including depth, compaction, soil aggregation, and water-holding capacity, may also be influenced by soil disturbance (Grismer and Hogan 2005*b*). Impacts to soil physical structure resulting from ski-run creation can result in some of the most problematic and pervasive consequences of anthropogenic disturbance: erosion, nutrient leaching, and sediment runoff. Intensified erosion, leaching, and runoff increase nutrient and sediment loads in nearby waterways, thus reducing water quality (Claassen and Hogan 2002, Grismer and Hogan 2004, Houser et al. 2006). Because water-quality protection in the United States is mandated federally by the Clean Water Act, and because ski areas present potentially large sediment sources (Maholland 2002, Grismer and Hogan 2004), impacts to soil and hydrologic properties on ski slopes often receive most attention from agencies and ski-area managers.

Our study goals were to examine the effects of high- and low-intensity disturbance on multiple ecosystem properties using ski areas as large, replicated, anthropogenic disturbance experiments. In particular, we hoped to provide valuable missing information on the relative impacts of clearing and grading in understudied forested upper montane and subalpine habitats. We hypothesized that greater disturbance intensity would result in greater divergence from reference conditions for four categories of ecosystem properties: (1) plant community composition; (2) patterns of plant community diversity; (3) soil physical characteristics related to hydrologic function and erosion potential; and (4) soil chemical measurements related to soil quality and potential productivity. Within each category we measured several indicators in order to assess the multivariate impact of disturbance intensity on ecosystem properties.

Methods

Study region

We extensively surveyed vegetation, soils, and environmental characteristics in large (100-m^2) plots on matched sets of graded ski runs, cleared ski runs, and adjoining reference forests in seven large downhill ski resorts located in and around the Lake Tahoe Basin, in the northern Sierra Nevada of California and Nevada, USA (Fig. 1; 38°30′00″ N, 119°51′00″ W to 39°30′00″ N, 120°6′00″ W). These ski resorts collectively represent broad abiotic gradients and likely capture much of the potential variation among ski areas in the northern Sierra Nevada (Appendix A).

Surveyed ski areas include: Sugarbowl, Northstar-at-Tahoe, Diamond Peak, Mount Rose, Heavenly, Sierra-at-Tahoe, and Kirkwood. Most of these ski areas are fairly large; the largest ski area included in this study boasts 1943 skiable hectares and 95 ski runs, and the average ski-area size is 864 skiable hectares and 66 ski runs. We sampled all ski areas in our study region that met two basic criteria: (1) they had sufficient interspersion of cleared runs with graded runs below the tree line to satisfy the blocked sampling design, and (2) we could

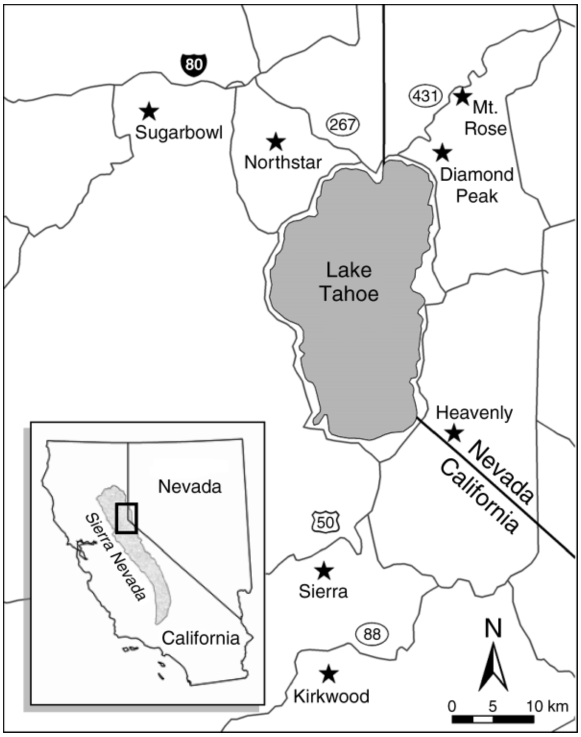

FIG. 1. Study region and locations of the seven ski areas included in this study within the northern Sierra Nevada, California and Nevada, USA.

gain access (either on public lands or private landowner granted access).

Sampled ski slopes were located within mixed-conifer forest ecosystems in the upper montane and subalpine climate zones, between 2100 and 2800 m above sea level. Within these zones, patterns of conifer forest community composition depend on complex climatic gradients, including snowpack depth and duration, elevation, aspect, soil depth and precipitation (Urban et al. 2000, Royce and Barbour 2001, Fites-Kaufman et al. 2007). Forests sampled in this study varied in composition and were dominated or codominated by any of the following species: red fir (*Abies magnifica*), western white pine (*Pinus monticola*), lodgepole pine (*Pinus contorta* ssp. *murrayana*), Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), and (at higher elevations) western hemlock (*Tsuga mertensiana*) and white-bark pine (*Pinus albicaulis*).

Total annual precipitation varies with elevation and location on the precipitation gradient across the Sierra Nevada range. Mean annual precipitation among the ski areas included in this study ranges from 74 cm (at Heavenly) to 164 cm (at Sugarbowl; 1961–1990 averages; Daly and Taylor 1998). Most (70–90%) annual precipitation falls as snow in the winter (November–April), while summers are characterized by very low rainfall, mild temperatures, and low humidity (Barbour et al. 2002, Taylor 2004, Fites-Kaufman et al. 2007).

Soils of the upper montane and subalpine regions of the Sierra Nevada are generally weakly developed (Entisols and Inceptisols) from granitic, volcanic and mixed glacial outwash parent materials; all of these types are represented among our study sites (Schruben et al. 1997, O'Geen et al. 2007, USDA-NRCS 2007). High-elevation soils of the Sierra Nevada tend to be shallow (<1 m depth), sandy, and characterized by high coarse-fragment composition; thus rooting depth is an important limiting factor for vegetation in this region (O'Geen et al. 2007). Because these zones experience xeric summers and cold winter temperatures, rates of organic-matter decomposition are slow. This results in a well-developed litter layer and high organic matter in the upper soil horizon. Disturbance of the litter and upper soil layers can cause subsequent soil erosion (Grismer and Hogan 2004, Fites-Kaufman et al. 2007).

Field methods

We conducted field measurements between 18 July and 6 September 2006, during peak blooming periods and before onset of plant senescence. We used a blocked sampling design within each ski area to account for site variation (e.g., topography and soil type) and to spatially intersperse treatments. In each ski area, four or five replicate blocks were established. Each block consisted of three 5 × 20 m (100-m^2) sampling plots corresponding to three treatment or disturbance levels: (1) a graded ski run, (2) an adjacent cleared ski run, and (3) reference forest between the two ski runs, for a total of 31 replicate blocks (93 plots total) across the study region. To increase sample dispersion and independence of blocks at a site, blocks were always located >150 m apart. The ski-run types were easily distinguishable based on the presence of tree stumps and boulders on cleared runs and the absence of these same features on graded ski runs (as well as the frequent presence of cut-and-fill slopes and manufactured water bars or berms). Our field assessments were all confirmed by communications with ski-area managers and/or Forest Service personnel. We also interviewed ski-area managers to determine approximate ski run ages and dates of ski-run grading to determine whether ski runs within sampling blocks had similar post-disturbance ages.

Each 5 × 20 m sampling plot was oriented upslope. Ski run plots were located in the centers of the ski runs, and reference forest plots in forest patches midway between each pair of sampled ski runs. We subdivided each sampling plot into four 5 × 5 m quadrats for more precise vegetation cover estimates. We visually estimated percent cover of each plant species present, as well as cover of bare ground, litter, rock, and total vegetative cover. Most plants were identified to species in the field. Unknowns were collected, pressed, and brought back for identification and verification in the University of California Davis Herbarium. We characterized plants for analyses into life-form groups (trees, shrubs, subshrubs, perennial herbs, annual herbs, herbaceous legumes, and graminoids) based on descriptions contained in Hickman (1993). Plants listed as biennial/annual were classified as annual. All but one species of graminoids encountered was perennial, so we assigned all graminoids to a single category, and we based assignment to the subshrub category on written descriptions and personal observations. Plant nomenclature presented also follows Hickman (1993). For diversity analyses, we calculated the Shannon-Weiner H' total species diversity index for each plot (which incorporates both richness and evenness, hereinafter referred to as "species diversity"). We also calculated functional richness (defined as the number of the seven life-form groups present in a plot).

We measured relative soil depth (i.e., depth to refusal) by pushing a tile probe into the soil to the maximum depth at 10 locations along each plot perimeter. We assessed soil compaction using a cone penetrometer at 10 locations along each plot perimeter, and the depth at which a compacted soil layer was encountered (requiring $>$1700 kPa force to penetrate) was recorded. Plot averages of relative soil depth and depth to compaction were used in subsequent analyses. We quantified visible soil erosion for each of the four plot quadrats based on the maximum level of visible erosion, using ordinal erosion classes we defined as follows: (1) no visible erosion, (2) only minimal sheet erosion visible (evidence of downslope soil movement and pedestalling, but no flow patterns), (3) advanced sheet erosion (some small intermittent flow patterns visible), and (4) rill erosion (visible interconnected and well-defined flow patterns). We averaged the erosion scores made for each subplot to provide an average plot-erosion score for data analysis. We also recorded aspect, slope, elevation, run width, and evidence of snowmaking and erosion-control seeding.

We collected a soil sample at each plot from the top 0–20 cm of soil after removing the litter layer. The soils were dried, sieved to 2 mm, and analyzed for texture, cation-exchange capacity (CEC), and soil water-holding capacity (WHC at 30.4 kPa) by the University of California Agriculture and Natural Resources Analytical Lab (for methods, see UCANR [2008]). Analyses of total N and total C were conducted by the UC–Davis Stable Isotope Facility, using an elemental analyzer and continuous-flow isotope-ratio mass spectrometer (UCD-SIF 2008).

Statistical analyses

We analyzed the resulting data set using multivariate analysis of variance (MANOVA). We conducted four separate MANOVAs corresponding to variable sets representing four major categories of ecosystem properties: (1) plant community composition by life forms; (2) patterns of plant community diversity; (3) soil physical characteristics; and (4) soil chemical characteristics (see Appendix B for MANOVA details).

The first MANOVA compared patterns of plant community composition by seven basic functional groups or life forms. The dependent variables in this analysis were thus the total cover by trees, shrubs, subshrubs, perennial herbs, herbaceous legumes, annual herbs, and graminoids. The second MANOVA on patterns of plant diversity analyzed total species diversity, total vegetation cover, introduced (nonnative) species richness, introduced species cover, and functional richness (defined as the number of the functional groups present in a plot). The third MANOVA analyzed soil physical properties relating to erosion potential. Dependent variables were soil depth, depth to compaction, cover of litter and bare ground, and average erosion class. The fourth MANOVA analyzed soil chemical characteristics, including total soil N, C:N ratio, CEC, and WHC. Total C was measured (presented in Table 1) but was not included in the MANOVA analysis because it was highly correlated with total N ($r = 0.96$, $P < 0.0001$).

All MANOVAs and protected ANOVAs were hierarchical models with ski area as a fixed factor, block (nested within ski area) as a random factor, and disturbance treatment as a three-level fixed factor comparing graded ski runs, cleared ski runs, and reference forests. Where needed, data were natural log-transformed to meet assumptions of normality and reduce heteroscedasticity. For each MANOVA, we also conducted a priori multivariate contrast tests (JMP 5.0.1a; SAS Institute 2002), and calculated Mahalanobis distances between treatment centroids (SAS 9.1, SAS Institute 2003). The contrast tests indicate significant differences among disturbance levels, while the Mahalanobis distances demonstrate multivariate effect sizes because they represent the degree of separation between disturbance levels.

Pairwise differences between disturbance levels for individual response variables were also of specific interest. We thus conducted follow-up ANOVAs and Tukey hsd tests for each response variable. These univariate analyses also allowed us to investigate the nature of significant interactions between ski area and disturbance level detected in the MANOVAs.

We investigated correlated and potentially confounding factors within our data set to ensure that we could attribute differences between treatments to initial disturbance intensity. We also analyzed environmental variables across treatments and confirmed that the blocked sampling design controlled for most underlying environmental differences except for slope (degrees of incline), which we found to be lower on graded ski runs than on cleared ski runs or reference forests. Aspect, run width, and elevation were not significantly correlated with treatment ($P > 0.10$). The slight difference in slope between treatments appears to be a consequence and not a cause of ski run grading, because even adjacent reference forests had significantly steeper slopes. Moreover, when we included slope as a covariate in each of the MANOVA models, we found it to be nonsignificant in all analyses ($P < 0.50$). As a result, we did not include slope in the final models.

Because approximately half of the graded ski runs sampled had artificial snowmaking (but only one cleared ski run did), it was possible that snowmaking and disturbance intensity effects were potentially confounded. To determine whether the presence of snowmaking might influence our interpretation of disturbance effects, we split our data set in two and reran our MANOVA analyses on the two data subsets: those blocks where graded ski runs experienced snowmaking ($N = 15$ blocks; in one of these the cleared run also had snowmaking), and those blocks without snowmaking ($N = 16$ blocks).

Results

Disturbance intensity (graded vs. cleared vs. reference forest) significantly affected all ecosystem properties examined in this study, including plant community composition, patterns of diversity, soil physical characteristics and erosion potential, and soil chemical characteristics. Multivariate contrast tests indicate that all three disturbance levels significantly differed from one another for all MANOVAs. Effects of disturbance intensity on the four categories of ecosystem properties are discussed in detail, below.

Ski area was also a significant factor in all MANOVAs. The seven ski areas sampled collectively represent a wide range of abiotic conditions and management approaches. The ski area × disturbance treatment interaction term was significant ($P < 0.02$) for three of the four MANOVAs ($P = 0.23$ for soil chemical characteristics). Univariate analyses of these ski area × disturbance treatment interactions reveal that, except for species diversity, significant interactions were generally due to absolute differences in treatment effect size among ski areas, rather than qualitative differences in the effects of disturbance treatment. Thus, except where noted, the significant ski area × disturbance treatment interaction term did not alter our interpretation of overall effects of disturbance intensity.

Plant community composition

Disturbance intensity significantly affected plant life-form composition (Wilks' lambda $= 0.015$, $P < 0.0001$), and the MANOVA canonical centroid plot of treatment effects on plant community composition indicates that graded ski runs, cleared ski runs, and reference forests separate clearly from one another in multivariate space (Fig. 2a). Observed patterns of community composition are suggestive of successional seres following disturbance in that graded ski runs (greatest disturbance intensity) supported greater cover of graminoids and annual herbs, a composition consistent with early successional plant communities (Fig. 2a, Table 1). In contrast, cleared ski runs (intermediate disturbance) were characterized by greater cover by perennial herbs, subshrubs, and shrubs, a composition more typical of mid-successional communities. Reference forests were characterized by greater tree cover, a compositional trait indicative of late successional or climax communities. The tight clustering of graded ski-run plots shows that there was less variance in plant community composition among graded ski runs than among either cleared runs or reference forests (Fig. 2a).

Cleared ski runs are intermediate between and overlap with graded runs and reference forests in the centroid plot. In contrast, graded ski runs and reference forests do not intersect at all, especially along the first canonical axis, which accounted for the most explainable variation between treatments (Fig. 2a). Contrast tests and Mahalanobis distances between disturbance levels support this pattern. Although all disturbance levels were significantly different at the multivariate level, graded ski runs and reference forests were most different from one another, while cleared ski runs and reference forests were the most similar of the three pairings (Table 2).

Patterns of diversity

Patterns of plant community diversity were also significantly affected by disturbance treatment (Wilks' lambda $= 0.072$, $P < 0.0001$). Graded ski runs differed greatly from both cleared ski runs and reference forests based primarily on increased cover and richness of introduced plant species (Fig. 2b, Table 1). While all disturbance levels significantly differed from one another at the multivariate level, Mahalanobis distances emphasize that graded ski runs separate greatly from cleared runs and forests (Table 2). Cleared ski runs and reference forests overlap almost entirely on the canonical centroid plot (Fig. 2b), based on their similarly high total vegetative cover and very low abundance and richness of introduced plants (Table 1). We did not encounter introduced plants in any reference forest plots and only observed introduced plants in three cleared ski-run plots; these each had <4% introduced cover. In contrast, graded ski runs had an average introduced plant cover of 19.6% and an average of 2.5 introduced species per plot (Table 1).

Most of the introduced plant species detected in this study were seeded for erosion control. Nearly all graded ski runs sampled had been seeded for erosion control while there was no evidence that any cleared ski runs had been seeded. Previous seeding efforts were evidenced both by the presence of typical erosion-control species and confirmed by personal communications (J. Burt) with ski-area managers. Typical seeding indicators on our sites included intermediate wheatgrass (*Elytrigia intermedia* ssp. *intermedia*), orchardgrass (*Dactylis glomerata*), smooth brome (*Bromus inermis* ssp. *inermis*), hard fescue (*Festuca trachyphylla*), and birdsfoot trefoil (*Lotus corniculatus*). Because almost all nonnative plants observed during this study are used for erosion control, the higher introduced species cover and richness on graded ski runs can be attributed almost entirely to this active management practice.

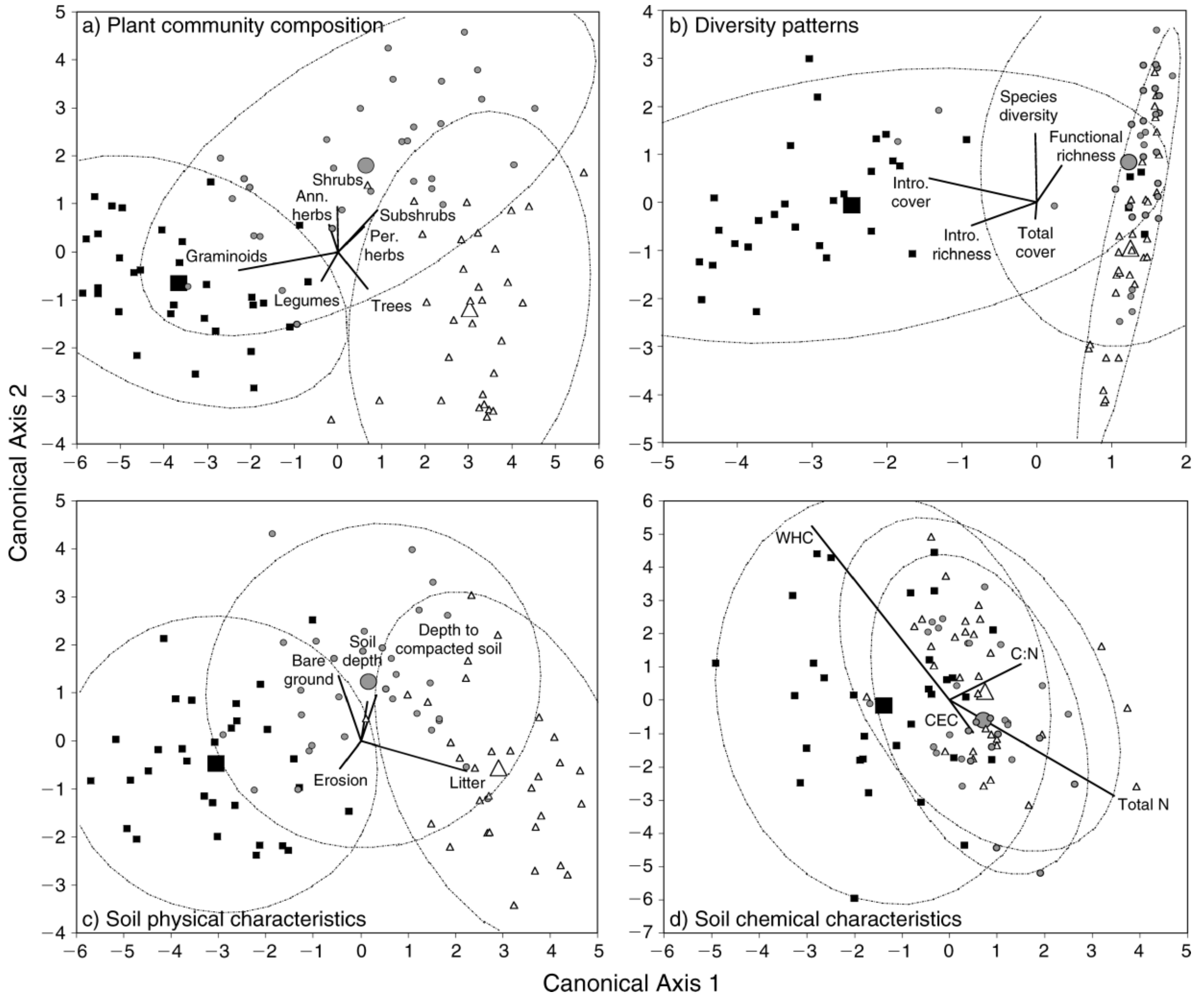

FIG. 2. MANOVA canonical centroid plots illustrate multivariate effects of disturbance treatment on ecosystem properties. Small symbols represent individual sample units: graded ski runs (solid squares), cleared ski runs (gray circles), and reference forests (open triangles). Treatment centroids are indicated with enlarged symbols, and dotted-line ellipses represent 95% confidence intervals for each disturbance level. Canonical Axis 1 accounts for most of the explainable variation in all plots: the proportion of variation accounted for ranged from 82% to 90% for panels (a)–(d). Key to abbreviations: CEC, cation-exchange capacity; Intro richness, richness of introduced plants; WHC, water-holding capacity.

Cleared ski runs did separate somewhat from reference forests because of their increased species diversity (Shannon's H') and functional richness. This apparent difference in the centroid plot was supported by results of univariate analyses that indicated that cleared ski runs possess significantly greater species diversity on average than either graded runs or reference forests, and significantly greater functional richness than forests (Fig. 2b, Table 1). However, the effects of disturbance intensity on species diversity were not entirely consistent across ski areas; although five of the seven ski areas had a hump-shaped effect of disturbance intensity on diversity, two ski areas exhibited different patterns. At the Sugarbowl site, cleared runs and reference forests both had high levels of species diversity, and at the Heavenly site, cleared ski runs had lower diversity than either graded runs or reference forests.

Soil physical characteristics and erosion potential

Disturbance intensity greatly affected soil physical characteristics and erosion potential (Wilks' $\lambda = 0.035$, $P < 0.0001$); the centroid plot indicates that cover by litter was a primary differentiating factor between disturbance levels, with bare ground and visible erosion also contributing to the separation of treatments (Fig. 2c). Univariate pairwise analyses indicated that graded ski runs significantly differed from cleared ski runs and from reference forests for all soil physical characteristics (Table 1). In contrast, cleared ski runs and reference forests had statistically indistinguishable average soil depths and compaction levels, and more similar values for bare ground, litter, and visible erosion class (Table 1). Similarly, comparing Mahalanobis distances between treatment centroids reveals that the multivariate difference between graded ski runs and reference forests was

TABLE 1. Response variable means and pairwise comparisons among disturbance levels associated with ski-run creation, grouped by ecosystem property.

	Disturbance level		
Response variable	Graded ski runs	Cleared ski runs	Reference forests
Plant community composition			
Cover graminoids (%)	26.4^{a}	4.5^{b}	0.8^{c}
Cover annual herbs (%)	2.7^{a}	1.0^{b}	0.3^{c}
Cover leguminous herbs (%)	2.2^{a}	0.8^{a}	0.7^{a}
Cover perennial herbs (%)	7.1^{a}	13.9^{b}	6.8^{a}
Cover shrubs (%)	3.4^{a}	26.6^{c}	10.0^{b}
Cover subshrubs (%)	0.1^{a}	2.6^{c}	1.2^{b}
Cover trees (%)	3.7^{a}	5.5^{a}	51.6^{b}
Diversity patterns			
Shannon-Weiner species diversity, H'	1.4^{b}	1.7^{a}	1.1^{c}
Species richness†	13.0^{ab}	15.3^{b}	10.8^{a}
Introduced richness	2.5^{a}	0.1^{b}	0.0^{b}
Functional richness	4.5^{ab}	5.1^{b}	4.0^{a}
Cover introduced plants (%)	19.7^{a}	0.2^{b}	0.0^{b}
Total vegetative cover (%)	43.5^{a}	51.8^{ab}	62.1^{b}
Soil physical characteristics			
Visible-erosion class	2.6^{a}	1.8^{b}	1.2^{c}
Cover bare ground (%)	48.4^{a}	23.2^{b}	6.3^{c}
Cover litter (%)	4.3^{a}	16.3^{b}	57.7^{c}
Depth to compaction (cm)	8.4^{a}	18.8^{b}	17.1^{b}
Soil depth (cm)	13.8^{a}	31.3^{b}	30.2^{b}
Soil chemical characteristics			
Total nitrogen (mg/g soil)	1.4^{a}	2.5^{b}	2.2^{b}
Total carbon (mg/g soil)†	32.8^{a}	63.9^{b}	64.3^{b}
C:N ratio	23.6^{a}	28.2^{b}	31.7^{b}
Soil water-holding capacity (% at 0.3 ATM)	19.0^{a}	20.9^{b}	22.3^{b}
Cation-exchange capacity (meq/100 g)	12.4^{a}	17.0^{b}	17.5^{b}

Notes: Disturbance levels with the same superscript lowercase letter are not significantly different (Tukey hsd pairwise comparisons on transformed data; $\alpha = 0.05$). All response variables (except cover by leguminous herbs) were significantly affected by disturbance treatment (separate ANOVAs), even after a Bonferroni correction for multiple tests ($P < 0.001$).

† Not included in MANOVA analyses because highly redundant with variables already included in the models.

>3 times greater than the difference between cleared runs and forests (Table 2).

Soil chemical characteristics

Ski-run grading resulted in greater changes to soil chemical characteristics and nutrient status (Wilks' lambda = 0.278, $P < 0.0001$). The centroid plot indicates a much greater degree of overlap between treatments than was observed for other ecosystem properties (Fig. 2d). Multivariate contrast tests and Mahalanobis distances between disturbance-level centroids indicate similar patterns as found for other ecosystem properties, however; cleared ski runs and reference forests were much more similar to one another than graded ski runs were to either one (by fivefold; Table 2). Graded ski runs significantly differed from cleared ski runs and from reference forests for all soil chemical response variables at the univariate level, including N, C, C:N ratio, CEC

TABLE 2. Comparison of multivariate effect sizes between disturbance levels for each set of ecosystem properties.

	Graded ski runs vs. reference forests		Graded ski runs vs. cleared ski runs		Cleared ski runs vs. reference forests	
Ecosystem properties	Mahalanobis distance	Contrast F	Mahalanobis distance	Contrast F	Mahalanobis distance	Contrast F
Plant community composition	30.8	85.8***	18.1	46.9***	16.1	27.7***
Diversity patterns	20.2	41.0***	17.7	40.8***	3.0	9.0***
Soil physical characteristics	43.5	99.9***	17.5	37.2***	12.9	30.1***
Soil chemical characteristics	5.6	16.8***	5.8	16.6***	1.1	2.7*

Note: All multivariate contrasts are statistically significant, but greater Mahalanobis distances between treatment centroids and contrast test F statistics indicate greater degree of separation between treatment levels.

* $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$.

(cation-exchange ratio) and WHC (water-holding capacity). Cleared ski runs and forests, in contrast, had statistically indistinguishable values for all response parameters (Table 1).

Soil texture (represented by percentage sand) was strongly negatively correlated with both CEC ($r = -0.72$; $P < 0.0001$) and WHC ($r = -0.85$; $P < 0.0001$) across sites. Although soil texture was statistically unaffected by disturbance level (ANOVA $P > 0.07$ for all soil-texture classes), CEC and WHC were still highly significantly affected by disturbance treatment (Table 1). Disturbance may alter some biotically mediated soil characteristics that we did not measure that affect both CEC and WHC.

Other factors

The follow-up analyses we conducted to detect potential confounding effects of snowmaking indicated that the effects of disturbance intensity were consistent across ski runs with and without snowmaking. Results from MANOVAs on the two separate subsets of data (blocks where graded ski runs had snowmaking and blocks without snowmaking) were similar to results from MANOVAs on the overall data set; differences among disturbance treatments were still significant despite reduced statistical power of the data subsets. Canonical centroid plots revealed similar patterns across treatments to those observed in the complete data set. Snowmaking may indeed have impacts not addressed in this study, but it appears that the effects of disturbance intensity on measured ecosystem properties are consistent, whether or not the graded ski runs had artificial snowmaking.

Based on information provided by ski-area managers, we found that clearing and grading of adjacent ski runs occurred simultaneously for most ski areas, and thus the blocked sampling design accounted reasonably well for post-disturbance age. However, for three of the seven ski areas, we were either unable to determine when runs were graded (Heavenly) or determined that some runs were graded later, anywhere from 8 to 46 years after creation (Mt. Rose and Sierra), potentially confounding initial disturbance intensity and time since disturbance at these ski areas. We reran our analyses with these three ski areas excluded and found the results were robust and remained highly significant for all four groups of ecosystem properties, despite greatly reduced statistical power. We also found responses at these ski areas to be qualitatively similar to the other ski areas. These results suggest that time since disturbance may be less important than the severity of disturbance to the response variables we measured; as a result, we retained all ski areas in the final models.

Discussion

Our results offer compelling evidence that impacts on ecosystem properties increase with the increased severity of disturbance associated with ski-run grading. Graded ski runs (which are machine-leveled to remove slope irregularities) are clearly distinct from both cleared ski runs and reference forests in plant community composition and diversity, soil physical characteristics and erosion potential, and soil fertility and potential productivity. In contrast, cleared ski runs (which are cut over but not machine-graded) retain many similarities with reference forests, including indicators of soil structure, nutrient status, and overlap in plant community composition. We found, unexpectedly, that cleared ski runs are often more similar to reference forests than they are to graded ski runs, as indicated by multivariate Mahalanobis distances, centroid plots, and univariate comparisons (Tables 1 and 2, Fig. 2). The magnitude of differences between disturbance levels on ecosystem properties varies slightly across ski areas and abiotic conditions, but these basic results are consistent and robust with respect to site and management differences.

The measured ecosystem properties were chosen because they are indicators of important aspects of ecosystem function. For example, plant community composition and diversity have been shown to influence productivity, wildlife habitat quality, ecosystem resilience to disturbance, and nutrient cycling, as well as aesthetics (Hooper and Vitousek 1998, Tilman 1999, Diaz and Cabido 2001, Loreau et al. 2001). Greater functional diversity of vegetation has also been shown to benefit water and sediment conservation (Bautista et al. 2007). Similarly, physical soil indicators measured (including depth, compaction, visible erosion, bare ground and litter cover) relate directly to hydrologic function and erosion prevention, via their effects on water-storage capacity and processes affecting sediment retention (Kozlowski 1999, Grismer and Hogan 2004, Bautista et al. 2007). Soil depth and compaction also relate to soil rooting depth and rooting volume, and thus potential vegetation productivity (Kozlowski 1999, Meyer et al. 2007). Finally, soil chemistry and fertility indicators measured also influence multiple ecosystem functions, including capacity to support productive soil biota and vegetation growth, processes of nutrient cycling and retention, buffering capacity, and smaller-scale aspects of water and sediment retention (Whisenant 1999, Claassen and Hogan 2002, Clark et al. 2007, Watt et al. 2008). We think that the impacts we observed to ecosystem properties result in alterations to important ecosystem functions and services, all of which could be managed for in ski areas.

As predicted, graded ski runs appear to be "set back" in succession relative to cleared ski runs. The more severe disturbance associated with grading reduced soil quality and may have removed or destroyed much of the existing seed bank and any underground plant storage organs. Graded ski runs in this study were characterized by plant communities more typical of early-successional seres, including annual herbs (which are nearly absent in cleared runs or forests), graminoid species, and herbaceous legumes. In part, this early-successional structure may reflect the seeding of exotic grasses and legumes on graded runs. Notably, these results are consistent despite differences in post-disturbance ski run "ages" across ski areas. Ongoing vegetation maintenance on both types of ski runs may contribute to this lack of recovery. For example, brush cutting (of shrubs and sapling trees) is generally conducted every 3–5 years on both types of ski runs (J. Burt, *unpublished data*).

Although greater disturbance intensity negatively affected certain ecosystem properties, we found intermediate disturbance on average resulted in greater species and functional-group diversity. In contrast to many observational studies on the effects of intermediate disturbance, replication of ski-run types within sites allowed us to experimentally tease out categorical effects of disturbance intensity (although seeding of nonnative species in graded runs may also have had an influence on diversity). In our study, plots within moderately disturbed, cleared ski runs exhibited the greatest species diversity and functional richness. While graded ski runs were more likely to be dominated by early successional species, and reference forests often had nearly closed canopies with reduced understory, cleared ski runs were more representative of an intermediate successional state, with all functional groups well represented and a greater diversity of perennial herbs, subshrubs, and shrubs. Cleared ski runs also exhibited greater variation among plots in terms of composition by functional groups than did graded ski runs or forests (Fig. 2a). These results support the long-standing hypothesis in community ecology that an intermediate-disturbance regime (in terms of either frequency or intensity) will have the highest species diversity (Grime 1973, Connell 1978, Huston 1979).

Evidence for higher diversity on intermediately disturbed cleared ski runs was consistent across five of the seven ski areas, but two ski areas did not fit this pattern. At the Sugarbowl site, reference forests exhibited the highest species diversity. Interestingly, forests sampled there were highly fragmented and appeared to be experiencing windthrow effects, and had very open canopy conditions compared to forests sampled elsewhere. Thus, this site may be an "exception that proves the rule" because these forests may also be experiencing intermediate disturbance. The second exception was at the Heavenly site, where cleared ski runs had the lowest species diversity of any treatment. Low diversity on the cleared ski runs at this site is likely due to dominance of the low-growing shrub, pinemat manzanita (*Arctostaphylos nevadensis*). This species comprised 37–65% ground cover of all cleared ski-run plots at this site, while it was much less prevalent in graded ski runs or in forests. Other ericaceous shrubs have elsewhere been observed to create dense "recalcitrant understory layers" that hinder forest succession (Royo and Carson 2006:1346).

We found that graded ski runs were generally seeded for erosion control (with mostly nonnative grasses and legumes), while cleared runs were not seeded. Within graded ski runs, native cover and introduced cover were significantly negatively correlated ($r = -0.54$, $P = 0.002$), and introduced cover and native richness were marginally negatively correlated ($r = -0.33$, $P = 0.069$), suggesting that seeding with nonnatives for erosion control has adverse effects on the local abundance and diversity of native plants. Revegetation efforts ideally should promote increased native plant cover and litter and reduced bare ground and erosion, thus hastening recovery. However, revegetated graded runs still had significantly more bare ground, less litter cover, and greater visible erosion than cleared runs, even after the passage of many years.

Grading ski runs significantly degrades a number of soil and hydrologic properties. Despite active seeding, graded ski runs exhibited more exposed bare ground and visible erosion than did cleared ski runs, and importantly had greatly increased erosion potential compared to cleared ski runs. The increased soil compaction and reduced soil depth that we measured on graded ski runs can reduce infiltration rates and water-storage capacity of the soil profile that, in turn, increase overland flows and erosion (Kozlowski 1999, Grismer and Hogan 2005*a*, *b*). Soil traits that limit plant growth, including nutrient levels, cation-exchange capacity (CEC), and water-holding capacity (WHC) were also significantly reduced by the greater initial disturbance associated with grading. Although cleared ski runs did exhibit somewhat lower litter cover, greater bare ground, and more visible erosion than did forests, their soils were indistinguishable in terms of other soil and hydrologic properties, including depth, compaction, nutrient status, CEC, and WHC.

The impacts on soil and hydrologic properties observed in graded ski runs may be especially long-lasting in high-elevation ecosystems where soil development is slow. Our results demonstrate that grading ski runs is detrimental to all measured indicators of soil structure and hydrologic function, compared to clearing ski runs, which left these indicators mostly unchanged from reference forest conditions. The impacts of soil disturbance on hydrologic function are very much recognized in the Lake Tahoe Basin, where runoff from degraded upland habitats has been responsible for much loss of lake clarity (Naslas et al. 1994, Claassen and Hogan 2002).

Cleared ski runs may even offer some ecological benefits in a surrounding matrix of dense forests. Because they represent diverse mid-successional communities, cleared ski runs could potentially provide important wildlife habitat and contribute to greater regional diversity through increased habitat heterogeneity. One study of bird communities in forested ski areas indicates that graded ski runs have negative edge effects on bird diversity, whereas pasturelands promote diversity (Laiolo and Rolando 2005). Cleared ski runs were not considered in that study, but the pasturelands may have been more like the cleared ski runs observed in our study region in that they created less abrupt vegetation transitions and were characterized by diverse grass and shrub communities (Laiolo and Rolando 2005). Other studies of wildlife use of powerline rights-of-way and ski slopes demonstrate that compositional and structural diversity of vegetation leads to increased (open-habitat) wildlife use and mitigates dispersal barriers (Goldingay and Whelan 1997, Goosem and Marsh 1997, Russell et al. 2005, Rolando et al. 2007). While abrupt vegetation changes may often be detrimental to wildlife (such as those presented by the edges of graded ski runs), vegetated ecotones along the edges of cleared ski runs can possibly benefit wildlife if managed appropriately; at minimum they may not present such imposing barriers to wildlife dispersal as graded ski runs.

As mentioned previously, most published literature on the impacts of ski-slope creation focuses entirely on graded ski runs, primarily in alpine habitats, with no comparison with ungraded ski runs. These studies found similar impacts of ski-run grading in alpine habitats as we encountered in habitats below timberline: graded ski runs differ from reference habitats in terms of plant community diversity, cover, composition, and structure (Bayfield 1996, Urbanska 1997, Urbanska et al. 1998, Rixen et al. 2003, Wipf et al. 2005, Barni et al. 2007); erosion rates (Mosimann 1985); and soil characteristics (Gros et al. 2004, Barni et al. 2007, Delgado et al. 2007). Other studies have found differences between alpine graded ski runs and reference habitats in terms of winter ground temperatures (Rixen et al. 2003, 2004) and seed-rain diversity and abundance (Urbanska et al. 1998, Urbanska and Fattorini 1998). Below tree line, Ruth-Balaganskaya and Myllynen-Malinen (2000) determined graded ski-run soils were severely depleted in nutrients relative to reference forest conditions, as we also encountered in our study system. Without intervention, many graded ski runs fail to recover and remain barren of vegetation for many decades after creation (Mosimann 1985, Bayfield 1996, Urbanska and Fattorini 2000, Urbanska and Chambers 2002, Wipf et al. 2005); where time since grading was explicitly analyzed, no mitigating effects of time on plant community recovery could be detected over a 4–30 year age span (Wipf et al. 2005).

We have encountered a marked tendency in the literature and even among local agencies to consider all ski runs equal. In contrast, our research indicates that cleared ski runs present a viable, ecologically preferable alternative to graded ski runs. A similar conclusion was drawn by the only published study we encountered that explicitly compared graded and ungraded ski runs, conducted in European alpine grasslands and dwarf healthlands (Wipf et al. 2005). This begs the question as to why ski runs are graded. Informal surveys of ski area managers indicate that grading ski runs reduces topographical irregularities (depressions, hummocks, and boulders); graded ski runs thus require less snowfall to open for use than do cleared ski runs. Managers estimate that approximately 0.5 m additional snowfall is required on average to open cleared ski runs. Consequently, graded ski runs can open earlier in the season with a concomitant increase in revenue. We monitored the internet-posted status of a set of paired cleared and graded ski runs in the early part of the 2006–2007 season and observed that, indeed, graded ski runs did open about a week earlier on average. However, managers also indicated that graded ski runs generally require more total summertime maintenance effort, due to erosion-control seeding and water-bar repairs (even though they require less effort for ongoing vegetation clearing).

In conclusion, we found that the severe disturbance intensity associated with ski-run grading resulted in increased impacts on most ecosystem properties considered and reduced similarity to reference forests. Because all ski runs are disturbed, open habitats, one might expect ski runs to share more similarities than they do differences. However, we found that cleared ski runs were actually more similar to reference forests than they were to graded ski runs. We found it particularly striking that, despite the wide range of variation in biotic, abiotic, and management conditions represented by our large sample of sites, the effects of ski-run creation methods on ecosystem properties were consistent and repeatable. The results of this study have management implications beyond ski areas to many anthropogenic disturbances, including powerline rights-of-way, firebreaks, temporary access roads, logging areas, and even restoration sites. If maintaining functionally diverse plant communities, soil structure and productivity, and hydrologic function are important goals for ski-area management, then ski runs should be cleared rather than graded whenever possible.

Acknowledgments

We are tremendously grateful to Andrew Burt for providing invaluable field assistance throughout this study. We also extend our gratitude to Kate Mawdsley, Belinda Lo, and Susan Cartwright for their aid during field surveys. We thank many ski area managers, consultants, and Forest Service personnel who were particularly helpful in providing site access and background information on ski run creation and management, including: Mike Bandelin, Paul Borcherding, Andrew Bray, Jack Coughlin, Michael Hogan, John Loomis, Bob Moore, Drew Morris, Marilyn Muse-Meyer, Dave Myers, Sue Norman, Norm Saylor, Cliff Wilson, and Richard Wrenn. Vic Claassen provided generous advice and equipment for soil preparations. Neil Willits superbly advised us on statistical analyses. This manuscript was improved by helpful comments from Michael Barbour, Kari Veblen, George Williamson, Truman Young, and two anonymous reviewers. Funding for this project (to J. Burt) was provided by an NSF Graduate Research Fellowship, the UC–Davis Department of Plant Sciences, the NSF Biological Invasions IGERT program at UC–Davis (NSF-DGE number 0114432), and a UC–Davis Jastro-Shields research fellowship.

Literature Cited

Barbour, M., E. Kelley, P. Maloney, D. Rizzo, E. Royce, and J. Fites-Kaufmann. 2002. Present and past old-growth forests of the Lake Tahoe Basin, Sierra Nevada, US. Journal of Vegetation Science 13:461–472.

Barni, E., M. Freppaz, and C. Siniscalco. 2007. Interactions between vegetation, roots, and soil stability in restored high-altitude ski runs in the Alps. Arctic, Antarctics, and Alpine Research 39:25–33.

Bautista, S., A. G. Mayor, J. Bourakhouadar, and J. Bellot. 2007. Plant spatial pattern predicts hillslope semiarid runoff and erosion in a Mediterranean landscape. Ecosystems 10: 987–998.

Bayfield, N. G. 1996. Long-term changes in colonization of bulldozed ski pistes at Cairn Gorm, Scotland. Journal of Applied Ecology 33:1359–1365.

Briggs, J. 2000. Ski resorts and national forests: rethinking forest service management practices for recreational use. Boston College Environmental Affairs Law Review 28:79–118.

Claassen, V. P., and M. P. Hogan. 2002. Soil nitrogen pools associated with revegetation of disturbed sites in the Lake Tahoe area. Restoration Ecology 10:195–203.

Clark, C. M., E. E. Cleland, S. L. Collins, J. E. Fargione, L. Gough, K. L. Gross, S. C. Pennings, K. N. Suding, and J. B. Grace. 2007. Environmental and plant community determinants of species loss following nitrogen enrichment. Ecology Letters 10:596–607.

Clifford, H. 2002. Downhill slide: why the corporate ski industry is bad for skiing, ski towns, and the environment. Sierra Club Books, San Francisco, California, USA.

Coffin, D. P., W. A. Laycock, and W. K. Lauenroth. 1998. Disturbance intensity and above- and belowground herbivory effects on long-term (14 y) recovery of a semiarid grassland. Plant Ecology 139:221–233.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs—high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199:1302–1310.

Daly, C., and G. Taylor. 1998. California average monthly or annual precipitation, 1961–90 [geospatial database]. Water Climate Center of the Natural Resources Conservation Service (NRCS), Portland, Oregon, USA.

DeBusk, W. F., B. L. Skulnick, J. P. Prenger, and K. R. Reddy. 2005. Response of soil organic carbon dynamics to disturbance from military training. Journal of Soil and Water Conservation 60:163–171.

Delgado, R., M. Sanchez-Maranon, J. M. Martin-Garcia, V. Aranda, F. Serrano-Bernardo, and J. L. Rosua. 2007. Impact of ski pistes on soil properties: a case study from a mountainous area in the Mediterranean region. Soil Use and Management 23:269–277.

Diaz, S., and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16:646–655.

Fites-Kaufman, J. A., P. Rundel, N. Stephenson, and D. A. Weixelman. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. Pages 456–501 *in* M. G. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. Terrestrial vegetation of California. University of California Press, Berkeley, California, USA.

Goldingay, R. L., and R. J. Whelan. 1997. Powerline easements: Do they promote edge effects in eucalypt forest for small mammals? Wildlife Research 24:737–744.

Goosem, M., and H. Marsh. 1997. Fragmentation of a small-mammal community by a powerline corridor through tropical rainforest. Wildlife Research 24:613–629.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344–347.

Grismer, M. E., and M. P. Hogan. 2004. Simulated rainfall evaluation of revegetation/mulch erosion control in the Lake Tahoe basin—1: Method assessment. Land Degradation and Development 15:573–588.

Grismer, M. E., and M. P. Hogan. 2005*a*. Simulated rainfall evaluation of revegetation/mulch erosion control in the Lake Tahoe basin—2: Bare soil assessment. Land Degradation and Development 16:397–404.

Grismer, M. E., and M. P. Hogan. 2005*b*. Simulated rainfall evaluation of revegetation/mulch erosion control in the Lake Tahoe basin—3: Soil treatment effects. Land Degradation and Development 16:489–501.

Gros, R., L. J. Monrozier, F. Bartoli, J. L. Chotte, and P. Faivre. 2004. Relationships between soil physico-chemical properties and microbial activity along a restoration chronosequence of alpine grasslands following ski run construction. Applied Soil Ecology 27:7–22.

Hickman, J. C. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, California, USA.

Hirst, R. A., R. F. Pywell, R. H. Marrs, and P. D. Putwain. 2003. The resistance of a chalk grassland to disturbance. Journal of Applied Ecology 40:368–379.

Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. Ecological Monographs 68:121–149.

Houser, J. N., P. J. Mulholland, and K. O. Maloney. 2006. Upland disturbance affects headwater stream nutrients and suspended sediments during baseflow and stormflow. Journal of Environmental Quality 35:352–365.

Huston, M. 1979. General hypothesis of species diversity. American Naturalist 113:81–101.

Kessler, W. B., H. Salwasser, C. W. Cartwright, and J. A. Caplan. 1992. New perspectives for sustainable natural-resources management. Ecological Applications 2:221–225.

Kozlowski, T. T. 1999. Soil compaction and growth of woody plants. Scandinavian Journal of Forest Research 14:596–619.

Laiolo, P., and A. Rolando. 2005. Forest bird diversity and ski-runs: a case of negative edge effect. Animal Conservation 8: 9–16.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294:804–808.

Mackey, R. L., and D. J. Currie. 2001. The diversity–disturbance relationship: is it generally strong and peaked? Ecology 82:3479–3492.

Maholland, B. L. 2002. Geomorphic assessment of natural and anthropogenic sediment sources in an eastern Sierra Nevada watershed. Thesis. University of Nevada, Reno, Nevada, USA.

McNabb, K. L., M. S. Miller, B. G. Lockaby, B. J. Stokes, R. G. Clawson, J. A. Stanturf, and J. N. M. Silva. 1997. Selection harvests in Amazonian rainforests: long-term impacts on soil properties. Forest Ecology and Management 93:153–160.

Meyer, M. D., M. P. North, A. N. Gray, and H. S. J. Zald. 2007. Influence of soil thickness on stand characteristics in a Sierra Nevada mixed-conifer forest. Plant and Soil 294:113–123.

Mosimann, T. 1985. Geo-ecological impacts of ski piste construction in the Swiss Alps. Applied Geography 5:29–37.

Naslas, G. D., W. W. Miller, G. F. Gifford, and G. C. J. Fernandez. 1994. Effects of soil type, plot condition, and slope on runoff and interrill erosion of two soils in the Lake Tahoe basin. Water Resources Bulletin 30:319–328.

Nishimura, T. B. 2006. Successional replacement mediated by frequency and severity of wind and snow disturbances in a *Picea–Abies* forest. Journal of Vegetation Science 17:57–64.

O'Geen, A. T., R. A. Dahlgren, and D. Sanches-Mata. 2007. California soils and examples of ultramafic vegetation. Pages 456–501 *in* M. G. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. Terrestrial vegetation of California. University of California Press, Berkeley, California, USA.

Pickett, S. T. A., and M. L. Cadenasso. 2005. Vegetation dynamics. Pages 172–198 *in* E. van der Maarel, editor.

Vegetation ecology. Blackwell Publishing, Malden, Massachusetts, USA.

Price, M. F. 1985. Impacts of recreational activities on alpine vegetation in western North America. Mountain Research and Development 5:263–277.

Rivera, J., and P. de Leon. 2004. Is greener whiter? Voluntary environmental performance of western ski areas. Policy Studies Journal 32:417–437.

Rixen, C., W. Haeberli, and V. Stoeckli. 2004. Ground temperatures under ski pistes with artificial and natural snow. Arctic, Antarctics, and Alpine Research 36:419–427.

Rixen, C., V. Stoeckli, and W. Ammann. 2003. Does artificial snow production affect soil and vegetation of ski pistes? A review. Perspectives in Plant Ecology, Evolution and Systematics 5:219–230.

Rolando, A., E. Caprio, E. Rinaldi, and I. Ellena. 2007. The impact of high-altitude ski-runs on alpine grassland bird communities. Journal of Applied Ecology 44:210–219.

Royce, E. B., and M. G. Barbour. 2001. Mediterranean climate effects. I. Conifer water use across a Sierra Nevada ecotone. American Journal of Botany 88:911–918.

Royo, A. A., and W. P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Canadian Journal of Forest Research 36:1345–1362.

Russell, K. N., H. Ikerd, and S. Droege. 2005. The potential conservation value of unmowed powerline strips for native bees. Biological Conservation 124:133–148.

Ruth-Balaganskaya, E., and K. Myllynen-Malinen. 2000. Soil nutrient status and revegetation practices of downhill skiing areas in Finnish Lapland—a case study of Mt. Yllas. Landscape and Urban Planning 50:259–268.

SAS Institute. 2002. JMP 5.0.1a. Statistical computer software. SAS Institute, Cary, North Carolina, USA.

SAS Institute. 2003. SAS 9.1 for Windows. Statistical computer software. SAS Institute, Cary, North Carolina, USA.

Schruben, P. G., R. E. Arndt, and W. J. Bawiec. 1997. Geology of the conterminous United States at 1:2,500,000 scale: a digital representation of the 1974 P. B. King and H. M. Beikman map. Digital data series DDS-11, Series 2. U.S. Geological Survey, Denver, Colorado, USA.

Taylor, A. H. 2004. Identifying forest reference conditions on early cut-over lands, Lake Tahoe basin, USA. Ecological Applications 14:1903–1920.

Tenenbaum, D. J. 2001. Land use. The slippery slope of ski expansion. Environmental Health Perspectives 109:A112.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80: 1455–1474.

Tsuyuzaki, S. 1994. Environmental deterioration resulting from ski-resort construction in Japan. Environmental Conservation 21:121–125.

Tsuyuzaki, S. 2002. Vegetation development patterns on ski slopes in lowland Hokkaido, northern Japan. Biological Conservation 108:239–246.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. Ecosystems 1:511–523.

UCANR [University of California Agriculture and Natural Resources Analytical Lab]. 2008. Soil analysis methods. UCANR, Davis, California, USA. ⟨http://groups.ucanr.org/danranlab/Soil_Analysis_2/⟩

UCDSIF [University of California–Davis, Stable Isotope Facility]. 2008. Soil analysis methods. UC Davis Stable Isotope Facility, Davis, California, USA. ⟨http://stableisotopefacility.ucdavis.edu/⟩

Urban, D. L., C. Miller, P. N. Halpin, and N. L. Stephenson. 2000. Forest gradient response in Sierran landscapes: the physical template. Landscape Ecology 15:603–620.

Urbanska, K. M. 1997. Restoration ecology research above the timber line: colonization of safety islands on a machine-graded alpine ski run. Biodiversity and Conservation 6:1655–1670.

Urbanska, K. M., and J. C. Chambers. 2002. High-elevation ecosystems. Pages 376–400 *in* M. R. Perrow and A. J. Davy, editors. Handbook of ecological restoration. Volume II. Restoration in practice. Cambridge University Press, New York, New York, USA.

Urbanska, K. M., S. Erdt, and M. Fattorini. 1998. Seed rain in natural grassland and adjacent ski run in the Swiss Alps: a preliminary report. Restoration Ecology 6:159–165.

Urbanska, K. M., and M. Fattorini. 1998. Seed bank studies in the Swiss Alps. I. Un-restored ski run and the adjacent intact grassland at high elevation. Botanica Helvetica 108:93–104.

Urbanska, K. M., and M. Fattorini. 2000. Seed rain in high-altitude restoration plots in Switzerland. Restoration Ecology 8:74–79.

USDA NRCS [United States Department of Agriculture, Natural Resources Conservation Service]. 2007. Soil survey geographic (SSURGO) databases for El Dorado National Forest Area, Tahoe National Forest Area, Tahoe Basin Area, Washoe County Area, and Douglas County Area, California and Nevada, USA. ⟨http://soildatamart.nrcs.usda.gov/⟩

Watt, M. S., M. R. Davis, P. W. Clinton, G. Coker, C. Ross, J. Dando, R. L. Parfitt, and R. Simcock. 2008. Identification of key soil indicators influencing plantation productivity and sustainability across a national trial series in New Zealand. Forest Ecology and Management 256:180–190.

Whisenant, S. G. 1999. Repairing damaged wildlands: a process-oriented, landscape-scale approach. Cambridge University Press, New York, New York, USA.

Wipf, S., C. Rixen, M. Fischer, B. Schmid, and V. Stoeckli. 2005. Effects of ski piste preparation on alpine vegetation. Journal of Applied Ecology 42:306–316.

Zhang, Y. Q. 2005. Multiple-use forestry vs. forestland-use specialization revisited. Forest Policy and Economics 7:143–156.

APPENDIX A

Environmental characteristics of reference forest plots in the seven surveyed ski areas (*Ecological Archives* A019-094-A1).

APPENDIX B

MANOVA statistics for four analyses corresponding to aspects of ecosystem function (*Ecological Archives* A019-094-A2).