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The relationship between native richness and exotic success depends on the index of exotic success and environmental gradients

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**THE RELATIONSHIP BETWEEN NATIVE RICHNESS AND
EXOTIC SUCCESS DEPENDS ON THE INDEX OF EXOTIC
SUCCESS AND ENVIRONMENTAL GRADIENTS**

by

Daniel Slakey

Accepted in Partial Completion
Of the Requirements for the Degree
Master of Science

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MASTER'S THESIS

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Daniel Slakey

October 2010

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A thesis

Presented to

The Faculty of

Western Washington University

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of the Requirement for the Degree

Masters of Science

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ABSTRACT

The theory of resource use pre-emption suggests that diverse communities may be more resistant to invasion than simple communities due to lack of niche space for invaders. Studies examining the relationship of native species richness to exotic success have provided mixed support for this idea. To test this theory, I measured plant diversity and cover across topographic gradients differing in resource availability in a California serpentine grassland, and measured exotic success as either species richness, absolute cover, or dominance of exotic species. I then evaluated models predicting these different measures of exotic success, using either native richness alone or in conjunction with environmental variables as predictors. Species richness was a poor index of exotic success, as it was relatively weakly related to more direct measures of exotic success, exotic cover and dominance, and varied differently along environmental gradients from those two variables. Native richness was a significant negative predictor of exotic success whether environmental variables were included or excluded, although the relationship was stronger when using exotic cover or dominance than exotic richness. My results contrast with observational studies that have found positive relationships between native and exotic richness, in part because

environmental conditions favoring native richness at the site (low Ca:Mg) were opposite to those favoring exotics, and in part because exotics likely out-competed natives in more fertile habitats. Using cover or dominance as an index of exotic success and incorporating underlying environmental gradients provided a more realistic assessment of the factors controlling native and exotic success than simple models correlating native and exotic richness.

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INTRODUCTION

Elton (1958) proposed that diverse communities are relatively resistant to invasion. More recent ecological theory suggests that resistance to invasion in diverse communities is conferred by a lack of available niche space (Levine and D'Antonio 1999, Shea and Chesson 2002) or by a sampling effect, wherein very competitive residents are more likely to occur in diverse assemblages (Crawley and Heard 2001, Shea and Chesson 2002). Tests examining invasibility as a function of biodiversity have used both observational and experimental studies, often with contradictory results. Experimental studies have generally found negative effects of diversity on invasibility (e.g., Levine 2000, Dukes 2002). Observational studies of natural systems, however, have found a variety of relationships (positive, negative, or nonsignificant) between native plant species richness and exotic success at small spatial grains (plot size relative to organism size; $\leq 10\text{m}^2$ plots), and positive relationships at large spatial grains ($\geq 1\text{km}^2$ plots; Fridley et al. 2007). This apparent conflict in results - the "invasion paradox" (Fridley et al. 2007) - hinders both theoretical understanding of invasion dynamics and evaluation of which areas are at particular risk for invasion (Stohlgren et al. 2006, Stohlgren et al. 2008).

Differences in these patterns could result from either the indices used to assess exotic success or from the study conditions. Experimental studies typically use some measure of biomass as an index of invader success (e.g., Dukes 2002, Knops et al. 2002), while observational studies most frequently measure exotic success in terms of exotic species richness (Fridley et al. 2007). However, the latter may not be the most biologically relevant measure to reflect the impact of native community structure on exotic success or vice versa, as exotic richness would over-emphasize the impacts of species that are uncommon (Parker

et al. 1999, Lundholm and Larson 2004). In addition, observational studies typically sample across gradients in environmental variables that influence both native richness and exotic success. In contrast, experimental studies often use environmentally homogeneous plots (Levine and D'Antonio 1999). Covariance of both native richness and exotic success with environmental variables could obscure underlying mechanisms involving community interactions (or the lack thereof; Shea & Chesson 2002, Harrison et al. 2006). I assessed the relationships between native richness, different indicators of exotic success, and natural variation in resource availability in a serpentine grassland to better understand the mechanisms behind the invasion paradox.

Indices of exotic success

The use of different indices of exotic success can change the significance and even the direction of the relationship to native richness (Levine and D'Antonio 1999, Cleland et al. 2004, Lundholm and Larson 2004, Crall et al. 2006), with implications for our understanding of the potential mechanisms behind these ecological relationships. I focus on three commonly used vegetation indices in this paper: species richness, absolute cover, and dominance. Species richness refers to the total number of species in a given site. Absolute cover (hereafter simply called cover) refers to the percent area covered by plants; cover values of greater than 100% are possible, as plants often grow in a canopy several layers deep. Dominance, or relative abundance, measures the cover of a subset of plants (in this case, exotics) as a percentage of the total plant cover. Dominance values cannot exceed 100%. Many studies focus on species richness (the number of species) to measure the success of exotics (e.g., Lonsdale 1999, Stohlgren et al. 2002, 2006, Chytrý et al 2005), and

this is often the only information available at larger spatial grains and extents. However, other indices, such as cover and dominance, may be more appropriate for assessing the effects of community interactions on the intensity of invasions (Rejmánek et al. 2005, Harrison et al. 2006). For example, an area with high cover of a single exotic species would have a very low exotic richness, but still potentially large impacts on native species. Exotic dominance, although less frequently used, accounts for the productivity of a site. In an area of low total cover but high exotic dominance, for example, exotic cover would underestimate exotic success when compared with more productive ecosystems (Lundholm and Larson 2004). Positive correlations among indices of exotic success (usually richness and cover) are common in the literature (Tilman et al. 1996, Stohlgren et al. 2001, Harrison et al. 2006), but non-significant or hump-shaped relationships are common as well (Harrison 1999, Stohlgren et al. 1999, Gough et al. 2000), illustrating that one index does not necessarily substitute for the other.

Scale and environmental gradients affect the native richness-exotic success relationship

Both the spatial grain (plot size relative to organism size) and spatial extent (breadth of area or environmental gradient) of a study can influence the relationship of native richness to exotic success (Stohlgren et al. 2006, Fridley et al. 2007). Fine spatial grains are most relevant to the neighborhood scales at which individuals interact via competition, facilitation, or resource partitioning (Wiens 1989, Kennedy et al. 2002, Rahbek 2004). Coarser spatial grains often include environmental heterogeneity that can itself lead to positive correlations of native and exotic species richness if the degree of environmental heterogeneity varies strongly among plots (Shea and Chesson 2002, Davies et al. 2005). Spatial extent can also

influence observed relationships in vegetation, though effects may be less consistent and are less well-studied than effects of spatial grain. At one extreme, experimental studies on homogeneous plots essentially eliminate environmental variation altogether, allowing biotic interactions to be isolated (e.g., Levine and D'Antonio 1999, Crawley and Heard 2001, Hooper and Dukes 2010). While such studies are carefully controlled, their results have been criticized as not necessarily identifying the mechanisms controlling exotic success in “the real world” (Wardle 2001, Stohlgren et al. 2003). In observational studies, spatial extent can determine which patterns dominate a study’s results (Stohlgren et al. 2006). For example, exotic plant cover did not have a significant relationship to native species richness after consideration of environmental gradients in a survey of serpentine sites across California (Harrison et al. 2006), but exotics are a major threat to rare and endemic plants in serpentine grasslands of the San Francisco Bay Area (USFWS 1998). While observational studies can take environmental variation into account, the relationships between native and exotic vegetation will depend on which environmental variables are the dominant drivers of vegetation patterns across a given spatial extent

Environmental gradients can significantly contribute to native richness-exotic success relationships (negatively or positively) even in cases of relatively narrow spatial extents (Levine 2000). Native and exotic richness often respond similarly to environmental gradients (or heterogeneity therein), which can explain many of the positive native-exotic richness relationships (NERRs) in observational studies (e.g., Levine 2000, Davies et al. 2005). For example, inclusion of environmental variables (e.g., anthropogenic disturbance, latitude, soil chemistry, overstory cover) in statistical models can lead to a loss of significance in the relationship between native richness and exotic success (Taylor et al.

1990, Rejmánek 2003, Harrison et al. 2006, Lilley and Vellend 2009). However, exotic species often become invasive because of certain characteristics that allow them to respond differently to environmental gradients than natives. For example, exotic annual grasses in the deserts of southwestern North America respond positively to frequent, low-intensity fires, to which native plants in that region generally respond negatively (Brooks 2008). Thus, while observational studies typically attribute positive relationships to covariance with environment gradients, it is also possible that these gradients could lead to negative relationships between native richness and exotic success (Lilley and Vellend 2009).

Study System

Understanding the potential mechanisms behind the native richness-exotic success relationship requires knowledge of the likely responses of both natives and exotics to environmental gradients in a given study system. This study was conducted in a serpentine grassland in the San Francisco Bay Area of California. In addition to serving as a useful model system for ecology (Harrison and Rajakaruna in press), serpentine grasslands pose important management concerns. The California Floristic Province is one of the world's biodiversity hotspots (Myers et al. 2000), and within this region, serpentine soils account for >10% of the endemic plants, while only making up <2% of the land area (Kruckeberg 1984, Safford et al. 2005).

Serpentine soils are particularly harsh environments for plant growth, generally showing reduced productivity and a low degree of invasions by exotics (Kruckeberg 1984). Several soil chemical and physical properties account for these patterns, including a low Ca:Mg ratio (Vlams and Jenny 1948), low levels of plant macronutrients (Huenneke et al.

1990), heavy metal toxicity (Crooke and Inkson 1955), molybdenum deficiency (Walker 1948), and shallowness (Brooks 1987, Huenneke et al 1990, Gram et al. 2004). Light grazing can reduce the dominance of exotics in some California serpentines, probably because of the preference of cattle for annual grasses (mostly exotic) over forbs (mostly native; Collins et al. 1998) or net loss of N from grazed systems via animal products (Weiss 1999). Although serpentine ecosystems are relatively resistant to invasions, several recent threats, including N deposition (Weiss 1999), the aggressive spread of serpentine-tolerant exotics (Meimberg et al. 2006), and evolutionary adaptations of invaders to serpentine substrates (Harrison et al. 2001) make them a priority for conservation (USFWS 1998).

Mechanisms behind the biodiversity-invasibility relationship

Unlike experimental studies, which can specifically test for mechanisms behind the biodiversity-invasibility relationship (Levine and D'Antonio 1999), observational studies generally must infer the underlying mechanisms. A variety of mechanisms were likely to influence native and exotic success in this study, many of which were reviewed by Fridley et al. (2007; Fig. 1). Two direct mechanistic relationships between native richness and exotic success could explain negative associations of these two variables. Resource pre-emption by natives could reduce the ability of exotics to colonize an area. This pattern could result from niche complementarity – as more niches are filled with increasing numbers of native species (Levine and D'Antonio 1999, Shea and Chesson 2002) or functional groups (Fargione et al. 2005, Hooper and Dukes 2010), fewer resources remain available for new colonists (Arrow

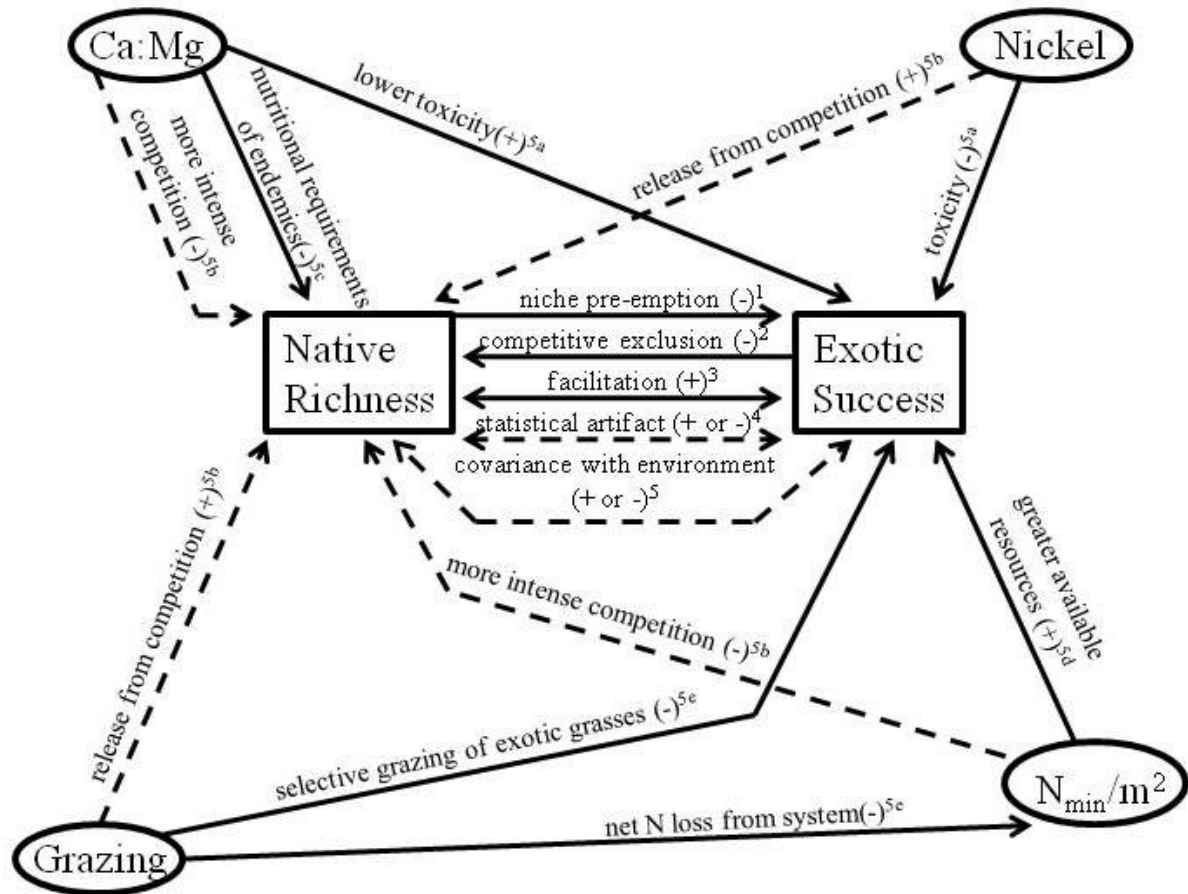


Figure 1. The most likely direct and indirect relationships among native species richness, exotic success, and environmental variables in serpentine grasslands. Direct, causal relationships are depicted with a solid line, while indirect associations are depicted with a dashed line. Numbers in the figure refer to direct (1-3) mechanisms by which native richness and exotic success may influence each other, and indirect (4, 5a-e) mechanisms causing covariance (either positive or negative) with environmental variables, as described in the text. Designations such as + and - refer to directionality in response to increases in the effect variable.

1, Fig. 1). Alternatively, niche pre-emption could result from a sampling effect, wherein competitive natives are more likely to be found in more diverse assemblages (Crawley and Heard 2001, Wardle 2001, Theoharides and Dukes 2007). Conversely, exotics could exclude native species, particularly in cases where aggressive invaders are present (Ortega and Pearson 2005) or in areas with high total cover (Arrow 2, Fig. 1; Cleland et al. 2007, Davies et al. 2007). Positive associations could result from facilitation (Arrow 3, Fig. 1; McPherson et al. 1998). For example, if an N-fixing exotic species colonized an extremely infertile habitat, more native species might be able to inhabit the site.

Several indirect relationships could also explain the association of native richness and exotic success. Statistical artifacts (Arrow 4, Fig. 1) could explain significant associations in very small plots with strong constraints on the number of individuals (negative association), or in large plots with significant variability in species richness between plots (positive association; Fridley et al. 2004, Herben et al. 2004). Covariance with environmental gradients (Arrows 5a-d) is very likely to play an important role (Davies et al. 2005), as natives and exotics can covary in similar (Rejmánek 2003, Davies et al. 2005, Harrison et al. 2006) or opposite ways (Lilley and Vellend 2009) with environmental gradients. The theory of biotic acceptance assumes that native and exotic richness are maximized under the same set of environmental conditions, leading to indirect positive associations (Stohlgren et al. 2006, 2008). In serpentine systems, however, I posit a negative association of native richness and exotic success due to variation in resource availability (dashed arrows, Figure 1), as the literature suggests that some exotics in this system are more competitive than many natives under more resource-rich, less toxic conditions (Huenneke 1990, Weiss 1999, Kolb et al. 2002). Differentiating among these mechanisms will help guide management decisions

aimed at preventing invasions and reducing the further spread of exotics.

Study overview

By carefully choosing vegetation indices, plot size, and spatial extent, and by measuring key environmental variables, I aimed to investigate differences among indices of exotic success and differentiate among mechanisms behind the diversity-invasibility relationship at Coyote Ridge, an area of serpentine grassland near San Jose, CA. I performed an observational study to better understand the relationship of native richness to three indices of exotic success: species richness, absolute cover, and dominance. I also assessed the extent to which covariation with environmental variables might contribute to the observed relationships between natives and exotics across a range of topographic variation in resource availability stratified by slope, aspect, and grazing regime. I used relatively small plots (0.25m^2) so that I might see evidence of biotic interactions, but these plots were still large enough to avoid the potential for confounding statistical artifacts. I also surveyed vegetation in larger plots (250m^2) to avoid missing species (Stohlgren 2007). I had three primary objectives in this study: (1) To quantify the relationship of the three indices of exotic success to each other, using correlations. I predicted that exotic richness would show relatively weak relationships (in terms of the correlation coefficients) to exotic cover and dominance, as species richness and productivity are often maximized under different conditions (Tilman 1987); (2) To determine how the native richness-exotic success relationship would be affected by using different indices of exotic success. I predicted a loss of significance or decrease in explanatory power when using exotic richness as compared to the other two exotic indices, as exotic impacts on natives are often felt in terms of their abundance (Parker

et al. 1999); (3) To evaluate whether covariation with environmental gradients was the primary mechanism driving the relationship between native richness and exotic success. That is, would native richness explain variation in exotic success beyond that explained by environmental variation? Due to the relatively weak biotic interactions seen in many observational studies (Harrison et al. 2006, Davies et al. 2005, Lilley and Vellend 1999), I predicted that it would not.

METHODS

Study Site and Sampling Design

I performed the study on the serpentine grasslands at Coyote Ridge, in Santa Clara County, California (37°15'N, 121°45'W). The region has a Mediterranean-like climate, with hot, dry summers and cool, wet winters. The average long-term (1893-2009) precipitation for nearby San Jose is 374 mm and the average yearly temperature is 16.3°C (Western Regional Climate Center 2009). However, precipitation is highly variable from year to year. I conducted this study in 2008; while the 2007-2008 (July-June) growing season had an average amount of rainfall (372 mm), the previous year was rather dry, with only 226 mm of precipitation (California Department of Water Resources 2009). The grassland is managed under a light spring-grazing regime (one cow and calf per each 4-6 hectares; Weiss 1999). A relatively small portion of the grassland surrounding the Kirby Canyon Sanitary Landfill is fenced off from grazers, providing this study with an ungrazed treatment.

To test my hypotheses, I used a nested sampling design with four replicate hills, two of which were grazed and two of which were ungrazed. Within hills, I stratified study sites based on aspect: 20° north-facing slopes, 20° south-facing slopes, flat hilltops, and swales,

yielding a total of 16 sampling locations. At each location, previous studies had set up a transect ranging in length from 20 to 50m, as some transects were located on slopes that could not accommodate a full 50m transect (Weiss 1999, Gonzalez 2007, S. Weiss and R. Hobbs – unpublished data). Ten equally-spaced 0.25m^2 ($0.5\text{m} \times 0.5\text{m}$) plots alternated sides along each transect. I used the 0.25m^2 spatial scale for all analyses involving environmental variables, but also overlaid a large rectangular plot ($10\text{m} \times 25\text{m} = 250\text{m}^2$) to improve my ability to detect species that were rare or had patchy distributions (Stohlgren 2007). I tested for spatial autocorrelation among nearby plots along a transect by using previously collected vegetation measurements from the plots (Gonzalez 2007). I analyzed the data in ARCGIS 9 (ESRI, Redlands, CA) by creating semivariograms, and found that nearby plots were not more similar in terms of vegetation than distant plots within a transect, allowing use of the individual plots as independent sampling units. I sampled vegetation in all plots at two separate times in the growing season, once in mid-March and once in mid-June, as the dominance of plants in these grasslands changes seasonally (Hobbs and Mooney 1991, Gonzalez 2007). I combined peak cover of each species across dates to give a single estimate of community composition for each plot. During the June sampling I also collected soil samples to analyze for nutrients, toxic minerals, and water content.

Vegetation Measurements

At each 0.25m^2 plot along the transects, I took estimates of species cover using the point quadrat method (Goodall 1952), employing a laser pointer directed through the canopy from above. Each plant that was hit was recorded for that point. I recorded sixteen points for each plot, but each point could have multiple hits, depending on the canopy density. Total

hits for a species were divided by sixteen to get an estimate of proportion of ground area covered. In denser canopies, this proportion could be greater than one. This is roughly equivalent to an estimate of leaf area index, except that all aboveground plant parts (including stems and flowers) were counted. When I missed a species with this method in a plot, I visually estimated its cover using the following categories: 0-0.25%, 0.25-1%, 1-2%, 2-5%, 5-10%, 10-25%. If the laser pointer hit a species that clearly had cover less than 6.25% (1/16 of the plot area), I revised the estimate of that species' cover to a more appropriate estimate of visual cover. I still recorded the hit for estimates of total vegetation cover, however. Within the larger (250 m²) plots, I counted the number of species present, but did not take cover data, so there are only species richness data for these plots.

Soil measurements

I analyzed soils for nutrients known to affect the productivity and invasion potential of serpentine grasslands. Due to time constraints, I sampled soils adjacent to every second 0.25m² plot along each transect in mid-June 2008 (five replicates per transect), at which time the soils are dry and plant and microbial activity are low. I composited two cores (2.5cm diameter x 15 cm deep) taken ~10cm from opposite sides of each plot. For soils shallower than 15cm, I hammered the cores until I reached bedrock or impenetrable clay. The soils were stored in a cooler until I performed the first soil analyses (nitrogen and phosphorous), 2-3 days after coring. Afterwards, the soils were stored in a 4°C cold room until I extracted soil calcium (Ca), magnesium (Mg), potassium (K; ~2 months later) and nickel (Ni; ~6 months later). Once in the lab, soils were sieved to <4mm to remove large rocks and break up large soil aggregates. I used subsamples of the <4mm soil for measurements of soil moisture,

inorganic nitrogen (N), potential net N mineralization (N_{\min}), and available phosphorus (P). Following these procedures, I sieved the tested soils to <2mm, dried and weighed the rocks, and subtracted dry rock weights from dry soil weights.

I used standard methods to determine the bioavailable concentrations of all the measured nutrients. Gravimetric soil moisture was determined by drying samples of field-moist soil at 105°C for 48 hours. I assessed initial ammonium (NH_4^+) and nitrate (NO_3^-) concentration using 2M KCl extractions (15g soil/100ml KCl). I also incubated soils at ~60% water-filled pore space for 28 days, followed by a final KCl extraction, to determine potential net N mineralization (Robertson et al. 1999). I determined available P by placing charged anion exchange resin strips (Bio-Rex AG 1-X8 Anion Exchange Resin, Bio-Rad Laboratories, Richmond, CA) in soil-water mixtures (7g soil/30ml water; Saggari et al. 1990, Hooper and Vitousek 1998). I analyzed the soil extracts for NH_4^+ , NO_3^- , and P on a Smartchem 200 discrete analyzer (Westco Scientific Instruments, Inc., Brookfield, CT). I calculated potential net N mineralization as the difference between the total inorganic N ($\text{NH}_4^+ + \text{NO}_3^-$) in the final extraction and the initial extraction, divided by the number of days of incubation. Gonzalez (2007) previously determined the depth to bedrock for the plots using a 1.25m soil probe at 2 points per plot, and then averaging these values. I calculated available P and net N mineralization per m^2 soil surface (P/m^2 and $\text{N}_{\min}/\text{m}^2$) by taking the soil depth and bulk density ($0.86\text{g}/\text{cm}^3$; determined by Hooper and Vitousek 1998) into account. After grinding oven-dried soil (48 hrs @ 105°C) to a fine powder on a Cyclotec mill (Foss, Eden Prairie, MN), I measured total soil C and N using a Thermo Flash EA112 soil combustion nitrogen/carbon analyzer (CE Elantech, Inc., Lakewood, NJ).

For measurements of soil cations, I sieved soils to <2mm prior to extraction. I

extracted available Ca^{2+} , Mg^{2+} , and K^{+} from the soils with ammonium acetate (NH_4OAc ; Simard 1993). I extracted available nickel (Ni) with DTPA (pH=7.3), using a 5:1 extractant:soil ratio (25g extractant: 5g soil) with a solution of 5mM DTPA, 10mM CaCl_2 , and 0.1M triethanolamine (TEA; Soon and Abboud 1993). This method provides a reliable estimate of bioavailable Ni (Chardot et al. 2007). I measured all cations using a Spectra AA220FS flame atomic absorption spectrometer (Varian, Inc., Palo Alto, CA). For more detailed descriptions of the soil methods, see Appendix 1.

Statistical analyses

Correlations of exotic success to native richness and among indices of exotic success

I tested the relationships of three indices of exotic success to each other as well as to native richness. I ran Spearman Rank correlations because the data did not meet the assumption of bivariate normal distributions. I ran a total of seven correlations: three correlations among the indices of exotic success at the 0.25m^2 plot scale, and four correlations of native richness to the various indices of exotic success (three at the 0.25m^2 plot scale, and only one at the 250m^2 plot scale, because I did not have independent measurements of cover or dominance for the large plots). To make fair comparisons between significance at different plot sizes, I had to account for differences in sample size, since significant results would be much more likely at the small plot size ($n=160$) than at the large plot size ($n=16$). Thus, in addition to standard Spearman Rank correlations on the full dataset, I ran correlations on randomly sampled subsets of the data with a sample size of $n=16$, running 1000 iterations for each correlation. All correlation analyses were done in SPSS (SPSS Inc., Chicago, Illinois).

Evaluating the relationship of environmental variables to vegetation

I evaluated the native richness-exotic success relationship with consideration of environmental gradients by using Akaike's Information Criterion (AIC) to select models that best predicted indices of native and exotic vegetation. This method of analysis requires that the number of possible models be limited, so that models that fit the data well by chance, but do not represent real biological mechanisms, are not selected (Burnham and Anderson 2002). I therefore examined the literature and data previously collected at the study site by Gonzalez (2007) and coworkers to evaluate potential variables to include in predictive models (see literature review in Appendix 1). For the regression analysis, I decided to use grazing (presence or absence), a single macronutrient index (potential net N mineralization, $\mu\text{g N}\cdot\text{day}^{-1}\cdot\text{m}^{-2}$), and two toxicity indices: Ni ($\mu\text{g/g soil}$) and Ca:Mg ($\mu\text{g Ca}:\mu\text{g Mg}$; Table 1).

This choice of variables was strengthened by a principal components analysis of the continuous environmental variables. Major variation amongst almost all of the environmental variables was covered by the first two principal component axes, together explaining ~55% of the variance. Most of the macronutrient indices were strongly weighted on the first axis (Appendix 2: Table S1). The second axis had strong positive weight on Ni per g soil and June soil moisture, and strong negative weight on Ca:Mg. The third and fourth axes were also significant (22% of variance together), but covered variables already subsumed in the other axes: the third axis had strong weight on P per g soil (negative) and soil depth (positive), and the fourth axis had strong positive weight on Mg per gram soil. (Appendix 2: Table S1).

AIC analysis

I developed generalized linear models to predict native and exotic success at the 0.25m² scale. I fit the models with simple linear regression and evaluated them for parsimony and goodness of fit using AIC_c (Akaike's Information Criterion for small sample sizes) because the ratio of the sample size (n=78) to the number of parameters in the global models (K=5) was less than 40 (Burnham and Anderson 2002). Global models and related model sets were developed based on a literature review (see Appendix 1) and analysis of data previously collected at the study site by Gonzalez (2007) and coworkers (Table 1).

I analyzed three groups of model sets: 1) model sets that included both native richness and environmental variables as predictors of exotic success, 2) sets that only analyzed environmental variables as predictors of exotic success, and 3) sets that analyzed environmental variables as predictors of native success. Each group consisted of three model sets: one for each type of vegetation index as a response (richness, cover, and dominance), leading to a total of nine model sets. There were a total of 31 models in each set that included native richness as a predictor, and 16 models in each set that omitted native richness as a predictor. These represented every possible combination of predictors, ranging from one to five, as I was unable to eliminate models from my sets while still maintaining balanced model sets. This produced a fairly large number of models relative to the sample size, but I did not exceed the threshold of having more models than data points (Burnham and Anderson 2002). I calculated the relative importance of the predictor variables as the sum of the Akaike weights of models in which a particular variable was present. Finally, I made a

Table 1. Expected relationships of native richness and selected environmental variable to indices of native and exotic success. The expected relationships were either derived by the results of the cited studies, or from further analysis of the data presented in those studies. See the literature review in Appendix 1 for more details.

Predictor Variable	Units	Expected relationship to vegetation indices	Sources
Native richness	Number of species	Linear (+ or -) relationship to exotic indices	Fridley et al. 2007; Gonzalez 2007
Grazing	Presence/absence	Negative linear relationship to exotic indices Positive linear relationship to native indices	Weiss 1999; Safford and Harrison 2001; Harrison et al. 2006 Collins et al. 1998; Weiss 1999; Safford and Harrison 2001; Harrison et al. 2006
Nitrogen	$\mu\text{g N}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$	Positive linear relationship to exotic richness and cover Positive natural log relationship to exotic dominance Negative linear relationship to native richness and cover Negative natural log relationship to native dominance	Tilman 1987; Gonzalez 2007 Huenneke et al. 1990; Gonzalez 2007 Koide et al. 1988, Tilman 1987 Gonzalez 2007
Ca:Mg	$\mu\text{g Ca}/\mu\text{g Mg}$	Positive natural log relationship to exotic indices Negative natural log relationship to native indices	Walker et al. 1955; Madhok and Walker 1969; Proctor 1971; Main 1974; Harrison et al. 2006 Walker et al. 1955; Main 1974
Nickel	$\mu\text{g Ni/g soil}$	Negative linear relationship to exotic indices Positive linear relationship to native indices	Crooke and Inkson 1955; Soane and Saunder 1959 Crooke and Inkson 1955; Soane and Saunder 1959

multimodel inference, a model including all of the predictors with averaged coefficients weighted by the Akaike weight of individual models (Burnham and Anderson 2002). I assumed a Gaussian error distribution and performed no transformations of the response variables for exotic and native richness and cover. Native indices fit normal distributions based on the Shapiro-Wilks test. Although exotic richness deviated from normality, examination of Q-Q plots indicated a near-normal distribution. Native and exotic dominance were negative arcsine (square root) transformed, because they were constrained by the values of 0 and 1 (Sokal and Rohlf 1969). AIC analyses were carried out in R v. 2.6.1 (R-Project, Vienna, Austria).

ANOVA analysis

To understand how topographic variation and grazing influenced the vegetation and resource variables, I ran Analyses of Variance (ANOVA) on these data at the 0.25m² scale, and on species richness at the large plot (250m²) scale. I used the following model for analyses at the 0.25m² scale, in which grazing regime (G) was crossed with aspect (A), and hill (H) was nested within grazing regime:

$$Y_{ijkl} = \mu + G_i + A_j + G*A_{ij} + H_{(i)k} + H*A_{(i)jk} + \varepsilon$$

At the 250m² scale, I used the following model:

$$Y_{ijk} = \mu + G_i + A_j + G*A_{ij} + H_{(i)k} + \varepsilon$$

Since there was no replication within each H x A combination at this scale, the H

x A interaction is the error term. For environmental variables, I had five replicate plots, and for vegetation variables I had either ten replicate plots (0.25m² scale) or two replicate G x A combinations (250m² scale). I tested the ANOVA assumptions of homogeneity of variance and normal distributions using the Shapiro-Wilks test and Bartlett's test, and checked for heteroscedasticity by plotting residuals vs. estimated values. If the data did not meet the ANOVA assumptions, I attempted to rectify the problems by transforming the data; I note the few cases where I could not homogenize the variance. When I found a main effect or interaction term significant at $\alpha=0.05$, I performed post-hoc pairwise comparisons, using the Scheffé correction for multiple comparisons when agglomerating across treatments. For significant grazing effects, I compared means among aspects within a grazing regime (twelve comparisons) and means of the same aspect across grazing regime (four comparisons), using the Dunn-Šidák correction.

RESULTS

Patterns in dominance of native and exotic vegetation

In the 0.25m² plots there was a total of 84 different vascular plant species, 67 of which were native, fifteen of which were exotic, and two that could not be identified to species, due to the plants' phenology. By surveying the large plots, I added an additional thirteen species – eight natives, two exotics, and three plants that I could not identify to species (Appendix 2: Table S2). No single native species clearly dominated the plots: *Plantago erecta*, the most common native species, had an average cover of 4.6%. When I considered only the 101 plots in which this species was found, its average cover increased to 6.7%. Of the 160 plots I surveyed, only eleven of them contained a native

species with >50% dominance. Species that reached this level of dominance included *Chlorogalum pomeridianum*, *Elymus multisetus*, *Eriogonum nudum*, *Hemizonia congesta* ssp. *luzulifolia*, *Lomatium utriculatum*, *Plantago erecta*, and *Ranunculus californicus*. Exotic plants showed different patterns. The most successful exotic, *Lolium perenne* ssp. *multiflorum*, hereafter called *Lolium*, had an average cover of 30.9%, or 33.0% in the 150 plots where it was found. Its dominance is highlighted by the fact that the next most successful native, *Bromus hordeaceus*, had an average cover of only 4.9%. Thirty-four of the 160 plots had >50% dominance by *Lolium*; no other exotic species reached this level of dominance in even a single plot. Although a single exotic was very dominant in many of the plots, natives were overall more successful than exotics, with an average total relative abundance of 59%. Thus, the success of natives can be attributed to a wide variety of species, while the success of exotics can largely be attributed to *Lolium*.

Correlations among indices of exotic success and with native richness

All three indices of exotic success were positively correlated to each other, but the correlations involving exotic richness were the weakest (Figure 2). Exotic cover and dominance varied greatly at a given value of exotic richness. Exotic dominance was typically high at high exotic richness, but at low exotic richness (≤ 3 spp.), exotic dominance varied from <5% to >90%. Both high and low exotic cover occurred across almost the entire range of exotic richness, but low cover was more likely at low richness. On the other hand, exotic cover and dominance correlated much more tightly, though the relationship leveled off at high values of dominance because of the constraint of 100% exotic dominance (Figure 2).

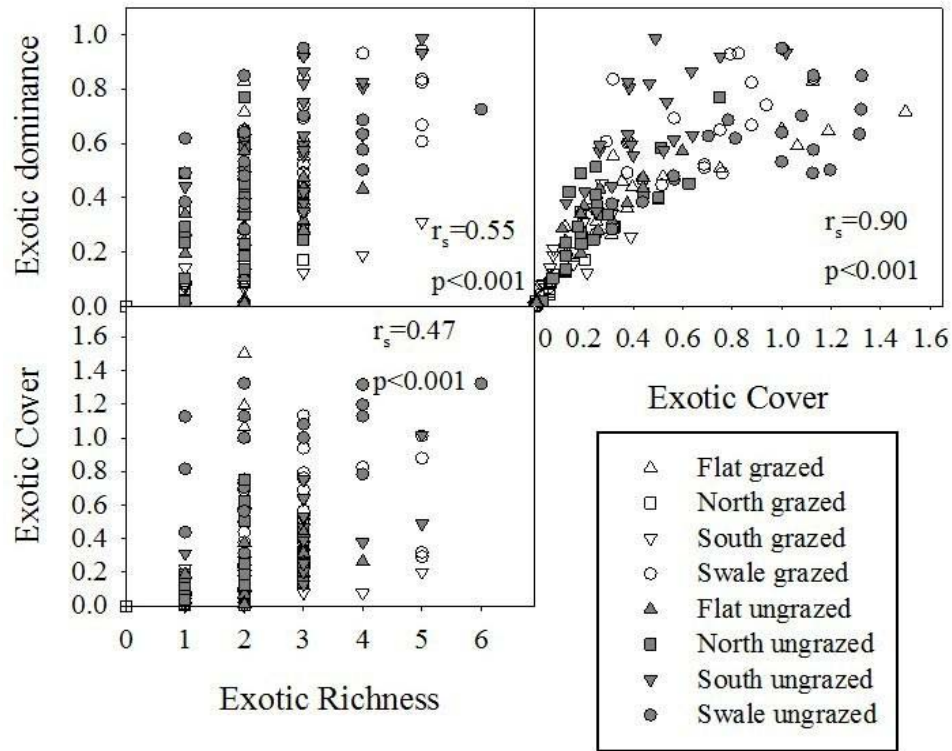


Figure 2. Correlations of the three indices of exotic success with each other at the 0.25m² scale. Here I display the actual data, but give the r_s - and p -values of the Spearman rank correlations.

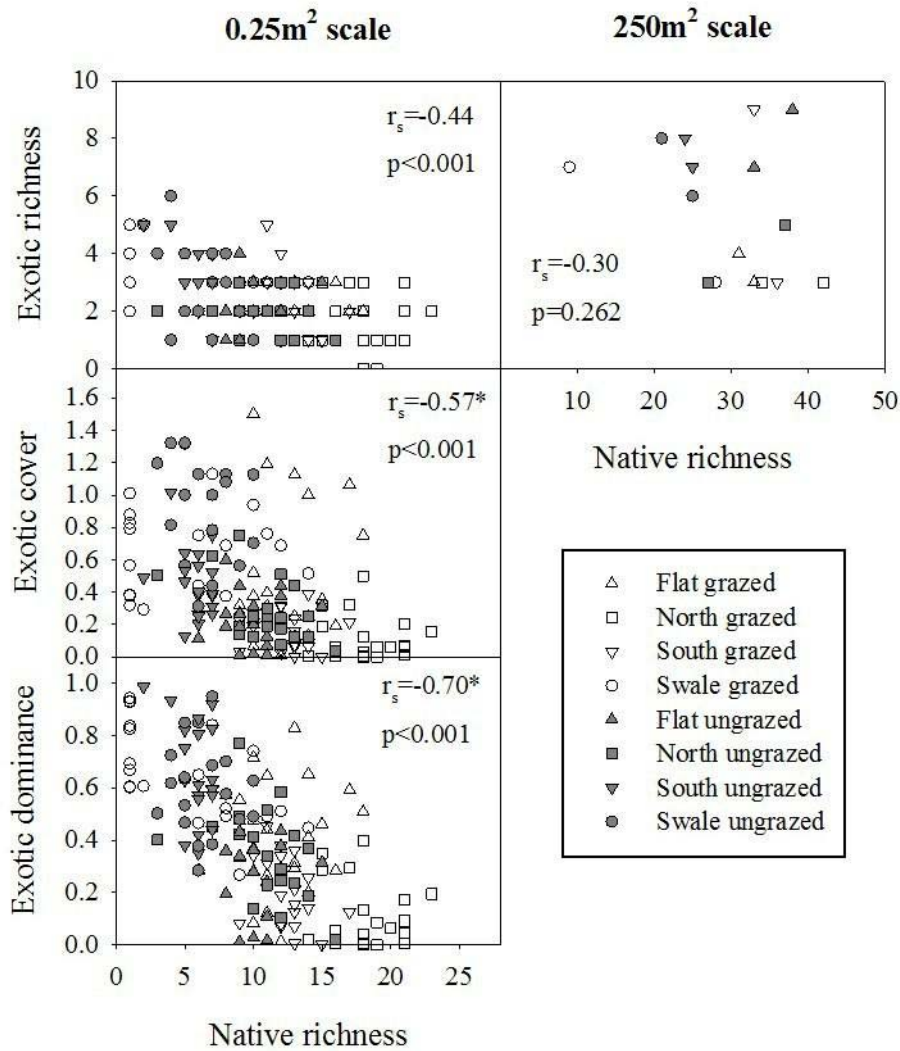


Figure 3. Correlations of native richness to three indices of exotic success at two spatial grains. Here I display the actual data, but give the r_s - and p -values of the Spearman rank correlations. *denotes significance after bootstrapping the data ($n=16$, 1000 iterations) to control for sample size across spatial scales (Appendix 2: Table S3).

The correlations of native richness with the three indices of exotic success produced only negative or non-significant relationships (Figure 3). Exotic dominance had the strongest association with native richness, whereas exotic richness consistently had the weakest. The latter relationship was non-significant at the 250m² scale and with bootstrapping (n=16) at the 0.25m² plot size (Figure 3, Appendix 2: Table S3).

Selection of models for predicting native and exotic success

I compared three separate sets of models to explain community composition: a) exotic success as a function of native richness and environmental variables; b) exotic success as a function of environmental variables only; and c) native success as a function of environmental variables only. Contrary to my predictions, native richness was a consistent and strong negative predictor of exotic success even after including environmental variation in the first set of models (Table 2). The best models for the three indices of exotic success contained both environmental gradients and native richness as predictors, and all explained 41-47 percent of the variance (Table 2). The best models with only environmental gradients explained 30-36% of the variance, and models only including native richness explained 22-28% of the variance (except in the case of exotic dominance, in which native richness alone explained 43% of the variance; Table S4). Environmental variables alone predicted native richness better than exotic richness, but predicted exotic cover better than native cover. They predicted native and exotic dominance equally well, which is understandable, given that these two response variables are inversely related to each other (Table 2). Although native richness was a strong predictor for all estimators of exotic success, the best models ($\Delta AIC_c < 2$) always

Table 2. Best models for predicting native and exotic success based on Akaike's Information Criterion for small sample sizes (AIC_c). Here I present three sets of models: A) models predicting exotic success, using both native richness and environmental variables as predictors, B) models predicting exotic success, with only environmental variables as predictors, and C) models predicting native success, with only environmental variables as predictors. ΔAIC_c values indicate the difference between a selected model and the best model. This table only displays models with very strong support ($\Delta AIC_c \leq 2$; Burnham and Anderson 2002). Akaike weights were calculated by dividing a model's likelihood by the sum of the likelihood of all models, where model likelihood = $EXP(-0.5 * \Delta AIC_c)$. Likelihood gives an estimate of a model's strength in comparison to the best model (the likelihood of which must equal 1). The evidence ratio is the ratio of the Akaike weight of a given model to that of the best model. $N=78$ for all models (two data points were omitted because of missing data). Predictor variables are denoted as follows: I = intercept, R = native richness, G = grazing (0 or 1), N = potential net N mineralization ($\mu\text{g N} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), C = Ca:Mg ($\mu\text{g Ca} : \mu\text{g Mg}$), Ni = nickel ($\mu\text{g/g}$ soil). Dominance data were negative arcsine (square root) transformed. For statistics on all models in each model set, see Appendix 2, Table S4.

Response	Model	ΔAIC_c	Akaike weight	Evidence ratio	Adj. r^2	Predictor coefficients						
						Int.	R	G	N	C	Ni	
A.	Ex. rich.	R+G+C	0.00	0.524	1.00	0.417	6.222	-0.080	0.815		2.003	
		R+G+N+C	1.81	0.212	2.47	0.412	6.403	-0.083	0.825	-0.702	2.059	
	Ex. cov.	R+N+C+Ni	0.00	0.246	1.00	0.469	0.673	-0.033		0.532	0.234	0.010
		R+C+Ni	0.34	0.208	1.18	0.459	0.796	-0.035			0.280	0.010
		R+N+Ni	0.56	0.186	1.33	0.457	0.380	-0.040		0.644		0.009
	Ex. dom.	R+C+Ni	0.00	0.336	1.00	0.472	-0.175	-0.037			0.301	0.004
		R+N+C+Ni	2.00	0.124	2.72	0.467	-0.151	-0.036		0.017	0.281	0.003
	B.	Ex. rich.	G+C	0.00	0.538	1.00	0.346	6.702		0.710		2.767
Ex. cov.			N+C+Ni	0.00	0.552	1.00	0.360	0.856			0.790	0.545
G+N+C+Ni		1.74	0.231	2.39	0.356	0.785		-0.059	0.793	0.491	0.009	

Table 2 (Cont.)

Response	Model	ΔAIC_C	Akaike weight	Evidence ratio	Adj. r^2	Predictor coefficients						
						Int.	R	G	N	C	Ni	
Ex.												
B. dom.*	C+Ni	0.00	0.258	1.00	0.299	0.107				0.689	0.003	
	C	0.78	0.174	1.48	0.281	0.137				0.627		
	N+C	1.04	0.153	1.68	0.289	0.190			0.048	0.572		
	N+C+Ni	1.32	0.145	1.93	0.297	0.149			0.034	0.641	0.003	
	G+C+Ni	1.74	0.108	2.39	0.294	0.043		-0.054		0.639	0.003	
C. Nat. rich.	N+C	0.00	0.209	1.00	0.405	-5.563			-7.164	-10.077		
	C	0.24	0.185	1.13	0.394	-7.522				-10.898		
	G+N+C	0.44	0.167	1.25	0.410	-3.912		1.383	-7.397	-8.670		
	G+C	0.83	0.138	1.51	0.398	-6.009		1.319		-9.582		
	N+C+Ni	1.37	0.105	1.99	0.403	-5.588			-7.891	-9.534	0.022	
	C+Ni	2.00	0.077	2.72	0.389	-7.676				-10.582	0.015	
Nat. cov.	N+C+Ni	0.00	0.548	1.00	0.277	-0.321			0.624	-0.349	0.004	
Nat. dom.*	C+Ni	0.00	0.257	1.00	0.299	-1.678				-0.689	-0.003	
	C	0.77	0.175	1.47	0.281	-1.709				-0.627		
	N+C	1.04	0.153	1.68	0.289	-1.761			-0.048	-0.573		
	N+C+Ni	1.32	0.133	1.94	0.297	-1.720			-0.034	-0.641	-0.003	
	G+C+Ni	1.74	0.108	2.38	0.294	-1.614		0.054		-0.640	-0.003	

*Models for native dominance are generally just the inverse for models of exotic dominance, since native dominance \approx 1 - exotic dominance. There are slight differences in the models, as I could not identify a few species, and these were not included in native or exotic dominance measurements.

included environmental variables as well as native richness.

Multimodel inferences help to summarize the consistency and strength of the various predictor variables across all the models (Table 3). Ca:Mg was the strongest environmental predictor, and had a positive effect on all indices of exotic success, and a negative effect on native success (Table 3, Appendix 2: Table S5). Ca:Mg ratios ranged from 0.11 to 0.35 at the site. Because Ca:Mg was natural log transformed, vegetation changed more rapidly with increasing Ca:Mg at its lower ranges: native richness decreased by four species when increasing Ca:Mg (g Ca: g Mg) from 0.1 to 0.15, but only decreased by 1.5 species as Ca:Mg increased from 0.3 to 0.35. Below the median value of 0.19, six of the fifteen exotic species found in the small plots were absent. These species were relatively uncommon in the plots, and included *Avena fatua*, *Hordeum murinum*, *Lactuca serriola*, *Lactuca virosa*, *Melilotus officinalis*, and *Silene gallica*.

Other environmental variables were strong to moderate predictors of some vegetation indices. Higher N_{\min}/m^2 decreased both native and exotic richness and increased native and exotic cover. For each $0.10\mu\text{g}$ increase in N_{\min}/m^2 , there was an increase of five percentage units of exotic cover and 6.25 percentage units of native cover (N_{\min}/m^2 ranged from 0.002 to $0.56\mu\text{g}\cdot\text{m}^{-2}/\text{day}$). Grazing increased both native and exotic species richness and decreased cover of natives and exotics; these relationships were strong for both exotic richness and native cover. In the regression models, grazing increased exotic richness by 0.4 species, and native richness by 1.3 species (Table 3). Nickel ranged from 11 to 94 μg per g soil, and contrary to expectations, higher nickel increased native and exotic cover and native richness, but with no appreciable effect on exotic richness (Table 3). For each $10\mu\text{g}$ increase in Ni/g soil, there was an increase of ten percentage units of exotic cover and an increase of three

Table 3. Multimodel inferences for three sets of models at the 0.25m² scale: A. indices of exotic success as a response, with native richness and environmental variables as predictors, B. indices of exotic success, with only environmental variables as predictors, and C. indices of native success, with only environmental variables as predictors. Coefficients for these models were derived by summing all coefficients from models that were examined for each response variable, weighted by the model's relative predictive power (Akaike weight) to produce a more robust multi-model prediction. Cells are coded by shading for the relative importance of the predictor variable, where relative importance equals the sum of the Akaike weights of all models in which that predictor is present. Unshaded predictors are unimportant (relative importance <0.5), light grey cells are moderately important (0.5<relative importance<0.75), and dark grey cells are very important (relative importance >0.75). Predictor variables are denoted as follows: R = native richness, N = potential net N mineralization ($\mu\text{g N}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$), G = grazing (0 or 1), C = Ca:Mg ($\mu\text{g Ca}:\mu\text{g Mg}$), Ni = nickel ($\mu\text{g/g}$ soil). For exact values of relative importance for each predictor, see Table S5. Ca:Mg was natural log transformed for all models and N was natural log transformed for dominance indices; all other indices were modeled with linear relationships.

	Response	Intercept	R	G	N	C	Ni
A.	Exotic richness	6.006	-0.077	0.778	-0.623	1.944	0.000
	Exotic cover	0.598	-0.036	-0.037	0.582	0.252	0.010
	Exotic dominance	-0.230	-0.038	-0.019	0.027	0.281	0.003
B.	Exotic richness	6.442		0.439	-0.011	2.482	0.000
	Exotic cover	0.876		-0.005	0.491	0.547	0.009
	Exotic dominance	0.124		-0.004	0.007	0.628	0.001
C.	Native richness	-5.803		1.327	-7.475	-9.755	0.018
	Native cover	-0.278		-0.016	0.625	-0.339	0.005
	Native dominance	-1.696		0.045	-0.041	-0.629	-0.003

percentage units of exotic dominance, as well as an increase of five percentage units of native cover and a decrease of three percentage units of native dominance.

Effects of topography and grazing regime on vegetation and resources

Variation in vegetation and resources across topographic gradients helped to explain some of the patterns in the regression analysis. In particular, swales tended to have both high exotic success and high resource availability. Across aspects, swales generally had higher cover and exotic success than other aspects: they had higher exotic cover and dominance than N-facing slopes and higher total cover than S-facing slopes ($p \leq 0.05$; Table 4). Also, native and total species richness as well as native cover were lower on swales than on N-facing slopes (0.25m² scale; Table 4). For complete ANOVA results on vegetation indices, see Appendix 2: Table S6.

In terms of resource availability, swales had more available nutrients than other aspects, including higher levels of P/m² than all other aspects and higher levels of N_{min}/m² than flats and S-facing aspects (Table 5). Swales were not significantly different from other aspects in terms of N_{min} or P per g soil (both of which were highest in flats and lowest in S-facing slopes), indicating the importance of soil depth (deepest in swales, shallowest in S-facing slopes and flats) in driving nutrient availability and exotic success. However, swales differed in the amounts of other nutrients per gram of soil: they contained more Ca than N-facing slopes, more Mg than S-facing slopes, and more K than all other aspects (Table 5). Soil organic matter, in terms of %C and %N, was higher on swales, flats, and N-facing slopes than on S-facing slopes (Table 5).

As noted above, Ca:Mg was consistently the most important environmental predictor

Table 4. Effects of grazing and aspect on vegetation variables at two spatial scales (means \pm standard errors). N=160 for analyses at the 0.25m² scale; N=16 for analyses at the 250m² scale. Significant aspect effects (irrespective of grazing regime; Scheffé correction) are denoted by superscripted letters (a-c): means that are significantly different from each other do not display the same letters. Bolded means indicate significant grazing effects. None of the mean comparisons for grazing x aspect interactions were significant after Dunn-Šidak correction (adjusted $\alpha=0.0032$, $\pi=0.05$), probably because this approach is conservative (Quinn and Keough 2002). However, I denote trends with borderline significance ($0.0032 < p < 0.05$) where ANOVAs indicated a significant grazing x aspect interaction. Within a grazing regime, means with different subscripted digits (1-3 for grazed; 7-9 for ungrazed) show such trends. Across grazing regimes, italicized means show the trend of being different from the same aspect under the other grazing regime. I denote significant hill effects at the 0.25m² scale; those hills not included in the hill effect column were not significantly different from any other hills. Hills 1 and 2 were grazed, while hills 3 and 4 were ungrazed. I could not test for hill effects at the 250m² scale, and did not run pairwise comparisons when I found significant hill x aspect interactions, due to the lack of biological relevance. I transformed some of the variables to meet the ANOVA assumptions of normal distributions and homogeneity of variance, as denoted in the table. For full results of ANOVAs on vegetation variables see Appendix 2, Table S6. Variables are abbreviated as follows: Nat. = native, Ex. = exotic, Tot. = total (native + exotic + unknown), Rich. = richness, Cov. = cover, Dom. = dominance.

Scale	Variable	Grazed				Ungrazed				Hill Effect
		Flat	North	South	Swale	Flat	North	South	Swale	
0.25m ²	Nat. rich.*	12.6 \pm 2.5 ^{ab}	18.3 \pm 2.4 ^b	12.6 \pm 1.7 ^{ab}	5.1 \pm 4.5 ^a	9.9 \pm 1.9 ^{ab}	11.0 \pm 2.8 ^b	5.9 \pm 1.3 ^{ab}	6.3 \pm 2.0 ^a	3=4<2<1
0.25m ²	Nat. cov. †	0.56 \pm 0.18 ₁₂	0.81 \pm 0.31 ₂	<i>0.58\pm0.31</i> ₁₂	0.35 \pm 0.23 ₁	0.54 \pm 0.15 ₈	0.55 \pm 0.31 ₇₈	<i>0.22\pm0.13</i> ₇	0.60 \pm 0.29 ₈	3<1
0.25m ²	Nat. dom. \pm	0.59 \pm 0.22 ^{ab}	0.89 \pm 0.13 ^b	0.80 \pm 0.13 ^{ab}	0.35 \pm 0.19 ^a	0.71 \pm 0.15 ^{ab}	0.66 \pm 0.18 ^b	0.34 \pm 0.19 ^{ab}	0.40 \pm 0.17 ^a	
0.25m ²	Ex. Rich.*	2.3 \pm 0.4	1.6 \pm 0.9	2.3 \pm 1.1	3.4 \pm 1.1	2.3 \pm 0.7	1.9 \pm 0.7	3.2 \pm 0.9	2.6 \pm 1.3	1<2=4
0.25m ²	Ex. Cov. †	0.50 \pm 0.44 ^{ab}	0.11 \pm 0.14 ^a	0.15 \pm 0.12 ^{ab}	0.64 \pm 0.26 ^b	0.24 \pm 0.16 ^{ab}	0.27 \pm 0.19 ^a	0.45 \pm 0.21 ^{ab}	0.91 \pm 0.33 ^b	2<3=4
0.25m ²	Ex. Dom. \pm	0.41 \pm 0.22 ^{ab}	0.11 \pm 0.13 ^a	0.20 \pm 0.13 ^{ab}	0.65 \pm 0.19 ^b	0.29 \pm 0.15 ^{ab}	0.34 \pm 0.18 ^a	0.66 \pm 0.19 ^{ab}	0.60 \pm 0.17 ^b	
0.25m ²	Tot. rich.	14.9\pm2.6^{ab}	19.9\pm2.6^b	14.9\pm1.8^{ab}	8.5\pm4.0^a	12.1 \pm 2.2 ^{ab}	12.9 \pm 2.8 ^b	9.1 \pm 1.2 ^{ab}	8.8 \pm 2.0 ^a	
0.25m ²	Tot. cov. †	1.07 \pm 0.47 ^{ab}	0.92 \pm 0.32 ^{ab}	0.73 \pm 0.36 ^a	1.00 \pm 0.32 ^b	0.86 \pm 0.32 ^{ab}	0.84 \pm 0.33 ^{ab}	0.69 \pm 0.21 ^a	1.51 \pm 0.43 ^b	2<1
250m ²	Nat. rich.	32.0 \pm 1.4	38.0 \pm 5.7	34.5 \pm 2.1	18.5 \pm 13.4	35.5 \pm 3.5	32.0 \pm 7.1	24.5 \pm 0.7	23.0 \pm 2.8	
250m ²	Ex. Rich.	3.5 \pm 0.7	3.0 \pm 0.0	6.0 \pm 4.2	5.0 \pm 2.8	8.0 \pm 1.4	4.0 \pm 1.4	7.5 \pm 0.7	7.0 \pm 1.4	
250m ²	Tot. rich.	35.5 \pm 0.7	41.0 \pm 5.7	41.0 \pm 2.8	24.5 \pm 10.6	43.5 \pm 4.9	36.5 \pm 9.2	33.0 \pm 1.4	30.0 \pm 1.4	

*could not meet homogeneity of variance assumption: no transformations improved the fit, †sqrt transform; \pm negative arcsine(sqrt) transform.

Table 5. Effects of grazing and aspect on environmental variables in the 0.25m² plots (means and standard errors). Means that are significantly different from each other across aspect (irrespective of grazing regime; Scheffé correction) have different superscripted letters. Bold values indicate a significant difference between grazing regimes. There were no significant grazing x aspect interactions. Regarding hill effects, hills 1 and 2 were grazed, while hills 3 and 4 were ungrazed. I transformed some variables to meet the assumption of bivariate normal distributions, as denoted in the table. See Appendix 2, Table S7 for full ANOVA results and the methods section for details on each variable.

Variable	N	Grazed				Ungrazed				Hill Effect
		Flat	North	South	Swale	Flat	North	South	Swale	
N _{min} /g (µg N* soil ⁻¹ *day ⁻¹) *†	78	0.29±0.010 ^b	0.19±0.12 ^{ab}	0.12±0.07 ^a	0.20±0.14 ^{ab}	0.21±0.06 ^b	0.16±0.09 ^{ab}	0.19±0.09 ^a	0.25±0.08 ^{ab}	1<2
N _{min} /m ² (µg N*m ⁻² *day ⁻¹)†±	78	0.04±0.02 ^a	0.08±0.04 ^{ab}	0.02±0.01 ^a	0.14±0.16 ^b	0.03±0.02 ^a	0.05±0.05 ^{ab}	0.06±0.04 ^a	0.25±0.10 ^b	1<4
% N±6	80	0.26±0.05 ^b	0.23±0.21 ^{ab}	0.14±0.03 ^a	0.20±0.06 ^b	0.24±0.04 ^b	0.20±0.04 ^{ab}	0.16±0.04 ^a	0.29±0.06 ^b	
% C±	80	2.59±0.49 ^b	2.31±0.25 ^b	1.54±0.28 ^a	2.07±0.54 ^b	2.41±0.42 ^b	2.17±0.43 ^b	1.70±0.45 ^a	3.22±0.65 ^b	
P(µg/g soil)†±	77	5.23±4.28	1.35±0.51	1.47±0.53	1.85±0.62	1.95±1.00	1.96±0.86	1.99±1.18	2.78±1.16	
P (µg/m ²)†±	77	0.74±0.66 ^a	0.59±0.35 ^a	0.28±0.11 ^a	1.14±0.70 ^b	0.30±0.14 ^a	0.57±0.37 ^a	0.71±0.52 ^a	2.69±1.27 ^b	
K (µg/g soil)±	80	228±92 ^a	100±27 ^a	93±28 ^a	300±133 ^b	149±39 ^a	174±51 ^a	165±81 ^a	336±133 ^b	1<2=3=4
Ca (µg/g soil) ¶	80	676±197 ^{ab}	437±37 ^a	502±141 ^{ab}	910±345 ^b	677±176 ^{ab}	586±244 ^a	629±87 ^{ab}	764±136 ^b	1<2=3=4
Mg (µg/g soil)* Ca:Mg (µg Ca/µg Mg)	80	3476±272^{ab}	3330±252^{ab}	3388±642^a	4112±452^b	3212±286 ^{ab}	2859±594 ^{ab}	2384±259 ^a	3184±333 ^b	3=4<1=2
§**††	80	0.20±0.06	0.13±0.01	0.15±0.04	0.22±0.07	0.21±0.04	0.20±0.03	0.26±0.04	0.24±0.04	1<2=3=4
Ni (µg/g soil) ††	80	57.6±19.2	51.8±7.7	36.5±8.2	50.6±38.8	36.1±8.0	34.2±1.8	26.4±5.1	55.6±4.6	
June soil moisture(%)†, ††	78	10.3±1.5	10.5±1.0	9.0±2.0	9.3±1.4	9.9±1.0	8.4±1.4	7.3±1.2	11.1±1.5	3<2
Soil Depth (cm)*, **	80	18.4±9.7 ^a	54.9±27.5 ^{ab}	22.2±7.5 ^a	80.6±42.5 ^b	18.6±5.6 ^a	33.9±16.7 ^{ab}	38.0±13.5 ^a	113.1±25.1 ^b	

*square root transform, †several samples were likely contaminated (value is more than eight standard deviations greater than the mean for N_{min} and P), so there is a reduced sample size for these variables, ±log10 transform, ¶negative inverse transform, §-arcsine(sqrt) transform, **Could not meet homogeneity of variance assumption; I applied transformations to minimize deviance from this ANOVA assumption, ††there were significant main effects, but the differences among means were too weak to be detected after using the Scheffé correction (Table S7).

of exotic success (Table 3). N-facing slopes generally had the lowest values of Ca:Mg, while swales had the highest values, but this difference was not significant ($p=0.051$; Appendix 2: Table S7). Mg was significantly higher on grazed than ungrazed hills. Although there was no significant effect of grazing on Ca:Mg, Ca, and K, these variables were significantly lower on hill 1 (grazed) than the ungrazed hills (hill main effect, Table 5). The differences in concentrations of these minerals across grazing regime may have been responsible for the strong effect of grazing on exotic richness in the regression analysis (Table 3), despite the lack of a difference in exotic richness between grazed and ungrazed plots in the ANOVA (Table 4). Nickel was also an important predictor of some vegetation indices in the regression analysis. While nickel did not vary significantly with aspect, grazed hill 1 showed the trend of being higher in nickel than all other hills (significant hill effect, but post-hoc tests were not significant after Scheffé correction; Table 5, Appendix 2: Table S7).

DISCUSSION

Overview

In this study I examined the native richness-exotic success relationship in a California serpentine grassland. For the three initial objectives in this study, the following main points emerge. First, all three indices of exotic success were significantly positively correlated with each other, but those involving exotic richness were weakest. Second, all the native richness-exotic success relationships were significant and negative at the 0.25m^2 scale. Again, however, the correlation of native and exotic richness was relatively weak compared to correlations of native richness with exotic cover and dominance. Third, native richness was still one of the most important predictors of exotic success, even after including

environmental variables. This indicates that covariance with the environmental gradients that I tested was not the sole driving factor behind the native richness-exotic success relationship. Together, these results suggest that exotic richness is a relatively poor indicator of the degree of invasion and the potential impacts to the native community. The weak relationships involving exotic richness suggest that many studies that employ this index as their only metric of exotic vegetation (e.g., Lonsdale 1999, Sax 2002, Stohlgren et al. 2002, Davies et al. 2005) could be missing key biological relationships important for management. The persistent negative relationships that I observed between native richness and exotic success contrast with some recent studies that have found positive NERRs at fine spatial grains and extents (Sax 2002, Keeley et al. 2003, Stachowicz and Byrnes 2006) and are consistent with a few potential mechanisms, the most likely of which is the negative impact of exotics on native richness (Parker et al. 1999, Cleland et al. 2004, Ortega and Pearson 2005).

Choosing an appropriate index of exotic success

Not all indices of exotic success reflect the same underlying biotic processes or impacts. Exotic species richness was relatively weakly correlated with exotic dominance and absolute cover. Similar to other studies (Levine and D'Antonio 1999, Larson et al. 2001, Lundholm and Larson 2004, Crall et al. 2006), I also found that the choice of index of exotic success could potentially alter the observed native richness-exotic success relationship, due to its relatively weak relationship to native richness. Overall, greater resource availability in swales led to greater exotic cover, greater exotic dominance, and lower native richness, but not necessarily greater exotic richness. Most observational studies that have examined the

native richness-exotic success relationship have used species richness as their index of exotic success (e.g., Lonsdale 1999, Stohlgren et al. 2001, Sax 2002, Davies et al. 2005, Fridley et al. 2007). This is understandable, as cover data may be impractical to assess at larger scales. Nonetheless, exotic richness may be an inappropriate measure of exotic success when competition between natives and exotics is the question of interest.

Although the various indices of exotic success are often positively correlated (Mittelbach et al. 2001, Harrison et al. 2006), they may reflect different aspects of the invasion process and therefore may be associated with different mechanisms. Exotic species richness can reflect the successful establishment by new individuals, or the ability of already-established exotic species to co-exist at low abundances; exotic cover and dominance generally reflect the proliferation of exotics once established. The invasion resistance afforded by high native diversity may curb this proliferation, but not entirely prevent the establishment of individuals of multiple exotic species (Levine 2000, Cleland et al. 2004). Differences in relationships between native richness and various exotic vegetation indices may also be driven by differential responses of the vegetation indices to environmental gradients (Gough et al. 2000, Huston 2004, Ortega and Pearson 2005, Crall et al. 2006; see below). In this study, exotic cover and dominance had similar responses to both grazing and N_{\min}/m^2 , reflecting a growth strategy of greater resource use in response to greater resource availability. Exotic richness responded in an opposite manner to these variables, as would be expected from the common finding of negative relationships between fertility and species richness (Tilman 1987). These differences likely explained the weaker relationships involving exotic richness (see below).

The relationship of environmental gradients to vegetation indices

Natives and exotics covaried along many of the same environmental gradients, sometimes in similar ways, and sometimes in opposite ways. Of these gradients, Ca:Mg was the most consistent predictor of both native and exotic success: higher Ca:Mg coincided with increases in all measures of exotic success and with decreases in all measures of native success (Table 3). Low Ca:Mg ratios can be an important component of the toxicity of California serpentines, and contribute to patterns of exotic success at local (Vlamis and Jenny 1948, Harrison 1999, Gram et al. 2004, O'Dell and Claassen 2006) and statewide scales (Harrison et al. 2006). This study, conducted at a relatively small spatial grain and extent, found similar results.

The opposite responses of natives and exotics to Ca:Mg contributed to the negative relationship between native richness and exotic success and points to competitive exclusion of natives by exotics as a mechanism behind the observed relationships. Native species found on serpentine often respond positively (in terms of biomass) to increased Ca:Mg in the absence of competition (Walker et al. 1955, Main 1974), suggesting that the lower native cover and dominance in high Ca:Mg plots likely resulted from increased competition with exotics. Strict serpentine endemics, which often respond to decreasing Ca:Mg with increased growth (Madhok and Walker 1969, Main 1981), made up a relatively small portion of the native flora in this study (<10% of the native species; based on Safford et al. 2005).

Grazing had similar effects on both native and exotic vegetation indices. Grazing increased both native and exotic richness and decreased both native and exotic cover, but favored native over exotic dominance (Table 3). These results are consistent with the idea

that cows selectively graze annual grasses, which are mostly exotic, allowing for forbs, which are mostly native, to dominate grazed plots (Collins et al. 1998, Gelbard and Harrison 2003). The overall increase in species richness with the light spring grazing regime (Table 4) is consistent with the intermediate disturbance hypothesis, which proposes that species richness will be maximized under moderate levels of disturbance, with intermediate time spans between disturbance events (Collins et al. 1995).

Although effects of grazing followed expected patterns, it was a relatively weak predictor of exotic cover, exotic dominance, and all indices of native success (Table 3; in contrast to Huston 1979, Olf and Ritchie 1998, Harrison 1999, Weiss 1999). Patterns of environmental variation across hills, particularly for Ca:Mg and nitrogen availability, may explain this result: some portion of the grazing effect may have been attributed statistically to variation in resources across grazing regimes. Both of the grazed hills had higher Mg than the ungrazed hills (Table 5), and while there was not a significant effect of grazing on many environmental gradients, Hill 1 (grazed) was particularly infertile when compared to the ungrazed hills. Hill 1 had the lowest levels of N_{\min}/g soil, N_{\min}/m^2 , Ca, Ca:Mg, and K. These differences coincided with high native richness, high native cover, and low exotic richness on Hill 1 (Table 4). The extent of topographic variation at Coyote Ridge in both resource availability and species composition warrants further investigation.

N_{\min}/m^2 had the opposite effect of grazing on all of the vegetation indices: it decreased both native and exotic richness, increased native and exotic cover, and favored exotic over native dominance (Table 3). It had strong predictive power for both native and exotic cover, native richness, and dominance of exotics (particularly *Lolium*) in more

nutrient-rich sites, consistent with the literature on serpentine nutrient limitation (Turitzin 1982, Hobbs et al. 1988, Koide et al. 1988, Huenneke et al. 1990, Harrison 1999, Weiss 1999, Going et al. 2009). The relationship between N_{\min}/m^2 and cover was driven primarily by the swales, which had the deepest soils, the highest N_{\min}/m^2 (and P/m^2), the highest exotic cover, and the lowest native richness and dominance. In turn, the effects of swales on nutrient availability were likely driven primarily by soil depth, as patterns of N mineralization and P per g soil did not match observed patterns in native or exotic vegetation. For example, N_{\min} and P per g soil were highest on flats and lowest on south-facing slopes, but these aspects were similar in terms of most vegetation indices. Other studies have also found strong effects of soil depth on the extent of exotic invasion (Huenneke et al. 1990, Gram et al. 2004, Gonzalez 2007).

Soil nickel exhibited patterns different from those that I expected: rather than repelling exotics and reducing cover through its toxicity (Soane and Saunder 1959, Kruckeberg 1984), it was a strong positive predictor of both native and exotic cover as well as exotic dominance (Table 3). Only a few plots (<10%) reached concentrations that slightly reduced growth of corn plants in other experiments (75-85 $\mu\text{g Ni/g soil}$; L'Huillier and Edighoffer 1996), explaining the lack of nickel toxicity. Because nickel is not a limiting nutrient on serpentine, the higher cover associated with higher nickel in this study likely resulted from covariance with other environmental variables. Nickel loaded opposite to Ca:Mg in the PCA (Appendix 2: Table S1), suggesting that any toxic (negative) effects of higher Ni concentrations in the regression analysis would have been taken up by the positive effect of higher Ca:Mg on exotics. Positive effects of Ni may have resulted from a weak

correlation with total C and N (Appendix 2: Table S1), both of which were low on S-facing slopes and particularly high in ungrazed swales (Table 5). These patterns of covariance among different environmental variables highlight the need for caution when interpreting the results of observational studies.

A persistently significant and negative native richness-exotic success relationship

Native richness was a strong negative predictor of all three indices of exotic success even in models that included most of the recognized environmental drivers of invasion success in serpentine soils. In other studies, inclusion of environmental gradients in models predicting native-exotic relationships has resulted in shifts from positive to negative relationships (Rejmánek 2003, Taylor and Irwin 2004), shifts from significant to nonsignificant relationships (Harrison et al. 2006, Lilley and Vellend 2009), or no change in the significance or direction of the relationship (Stohlgren et al. 1999, Gilbert and Lechowicz 2005). There are several possible explanations for the persistent negative relationship that I observed between native richness and exotic success: 1) native richness had an inhibitory effect on the success of exotic species, 2) exotics had a negative effect on the richness of native species, 3) I failed to include some important environmental predictors in the model sets, 4) native richness was favored over the environmental predictors because it offered a more parsimonious solution than multiple environmental variables, and 5) the negative native richness-exotic success relationship was produced by neutral processes, wherein constraints on the total number of individuals resulted in negative correlations. I address each of these possibilities below.

Higher diversity may enhance resistance of the native community to invasion through resource preemption (Stohlgren et al. 1999, Levine 2000, Knops et al. 2002, Fridley et al. 2007). Previous experiments at this site have demonstrated the potential for functional complementarity among native species to increase productivity (Hooper and Dukes 2004), decrease nutrient availability (Hooper and Vitousek 1997), and decrease invader success (Hooper and Dukes 2010). I could not directly test for such biotic resistance in this observational study, however, and evidence for this mechanism playing a role in my results is equivocal. On one hand, plots lacking native species from at least one complementary functional group (early- and late-season annuals, or early annuals and perennials; Hooper and Dukes 2004; Hooper and Dukes 2010), generally had higher exotic dominance than plots with at least two complementary groups (data not shown). About 20% of the plots lacked complementary functional groups, mostly in swales. Effects of biotic resistance could be spatially variable, however, and may be more important where native communities approach the productivity of the more aggressive exotics in swales (e.g., on N-facing slopes), as high native cover can reduce exotic success (Going et al. 2009). On the other hand, constructed community studies typically report an asymptotic relationship between resident diversity and invasibility, with effects of resident diversity on invasion success leveling off around ten to twelve species (Naeem et al. 2000, Hector et al. 2001, Dukes 2002). Average native richness in my plots ranged from five to eighteen species across aspects (swales and grazed north slopes, respectively), up to a maximum of twenty-three species in a single plot. Thus, if biotic resistance from the native community were an important mechanism behind the negative correlations, it probably did not have increased inhibitory effects on exotic success

above intermediate values of native richness.

While much of the literature has focused on the ability of native richness to repel invasions, the patterns I observed could also have resulted from the displacement of native species by exotics (Levine et al. 2003, Cleland et al. 2004). Areas with an aggressive invader (Ortega and Pearson 2005) and areas with high total cover (Cleland et al. 2004, Davies et al. 2007) tend to produce negative relationships between native richness and exotic success that are attributed to this mechanism. This site fits into both of these categories, as the exotic annual grass *Lolium*, which is known to displace native species (Kolb et al. 2002), dominated high productivity plots in swales and was fairly abundant on other aspects, except for grazed N-facing slopes. Also, ~80% of the plots had over 60% total cover. In a previous study, plots above this cover value were more likely to show negative NERRs, presumably due to competitive exclusion of natives (Davies et al. 2007). Similar displacement of native species by *Lolium* occurred in experimental plots where colonization by harvester ants dramatically increased nutrient availability (D. Hooper, J. Dukes, S. Teas, unpublished data). Theory also suggests that an invader's impact on the native community will be a function of that invader's abundance (Parker et al. 1999), consistent with the strong negative relationships I observed between native richness and exotic cover and dominance. Finally, the negative relationship of native cover and dominance to Ca:Mg suggests that natives are being excluded by exotics at higher Ca:Mg values, as described above (Walker et al. 1955, Main 1974, Safford et al. 2005). Of all the potential mechanisms leading to the consistent negative relationships between native richness and exotic success in this study, competitive exclusion of natives by exotics had the strongest support.

I may not have included all of the most important environmental variables that play a role in exotic success and covary with native richness. However, I chose the variables with the strongest literature support for analysis in this study, given the importance of minimizing the number of models in an AIC analysis (Burnham and Anderson 2002) and the fact that most omitted variables covaried with variables I did evaluate (Appendix 2: Table S1). Additional variables – either not measured or not included in the regression analysis – may not have improved the fit of our models. Variation in soil moisture across environmental gradients, for example, could play a role in the success of exotics, as several dominant exotic grasses performed much better in years of high rainfall than in drought years (Hobbs and Mooney 1991, Hobbs et al. 2007). The plots used in this study varied significantly in terms of April moisture content in previous years – with flats being the wettest and south-facing slopes the driest (Gonzalez 2007), but this pattern did not correspond with invasion success in this study (Table 5). Some California serpentines are limited in their productivity by low molybdenum availability (Walker 1948, 2001), but previous studies at this site found no effect of micronutrients (including Mo) on exotic success (Huenneke et al. 1990), so I did not measure this variable. Gopher disturbance can significantly affect the species composition of vegetation in serpentine grasslands in the year following disturbance (Hobbs and Mooney 1991), but I only observed large gopher disturbances (>6.25% cover) in eight of the 160 plots. Soil P (Huenneke et al. 1990, Going et al. 2009) and K (Harrison et al. 2006) may also play a role in the success of exotics. However, these soils were more likely N-limited (Koide et al. 1988, Huenneke et al. 1990, Going et al. 2009), and both P and K were strongly correlated with N_{\min}/m^2 , which was included in the analysis (Appendix 2: Table S1). This

evidence suggests that the native richness-exotic success relationship I observed after accounting for environmental variation could not be fully explained by other environmental gradients.

Evidence also helps rule out the two experimental artifacts (regression parsimony and small plot size) that could have explained my results. I performed a second AIC analysis by reducing the collective penalties for environmental variables to that of a single variable. This was done because of the possibility that native richness simply served as a more parsimonious proxy for the environmental gradients and was therefore favored in the selection process. However, native richness still remained the best single predictor in this re-analysis (data not shown), indicating that native richness explained additional variation beyond the environmental gradients. Neutral processes were also unlikely. Statistical inevitability leads to negative correlations at very small spatial grains (10-100 individuals per plot; Fridley et al. 2004, Herben et al. 2004). Although my plot size was small, one would expect an average of 500-600 individual plants in a 0.25m² plot on a California serpentine grassland (Gulmon et al. 1983).

CONCLUSIONS

While many studies focusing on the relationship of native richness to exotic success typically only measure exotic richness (e.g., Lonsdale 1999, Stohlgren et al. 2002, 2006, Chytrý et al 2005), three lines of evidence support the use of alternative indices: 1) exotic cover and dominance may be more responsive to native richness (Levine 2000), and, conversely, they better approximate the impacts of exotics on native richness than does

exotic richness (Cleland et al. 2004, Lundholm and Larson 2004, Ortega and Pearson 2005); 2) exotic richness was not strongly correlated to the other indices that better reflect the impacts of exotics (Figs. 1 and 2); and 3) exotic richness varied along environmental gradients differently from exotic cover and dominance (Table 3). This evidence suggests that the native-exotic richness relationship is not a good metric for testing mechanisms related to biotic resistance for species invasions.

Differential responses to soil fertility likely contributed to the negative relationships between native richness and exotic success in this study, but biotic interactions were also an important factor (Fig. 1). Biotic resistance may have played some role in these results, particularly as complementary functional groups were added, or in sites with high native productivity and richness (e.g., N-facing slopes). However, displacement of natives by the exotic *Lolium* offers an equally compelling explanation for my results. All native indices responded negatively to increased fertility (Ca:Mg), suggesting that competitive exclusion of natives took place at the study site. The high total cover of aggressive invaders in swales is consistent with this explanation (Cleland et al. 2004, Ortega and Pearson 2005, Davies et al. 2007).

Similar to the index of exotic success, a study's spatial extent can dramatically impact its results. A large spatial extent can be useful for large-scale management considerations, but different geographic or qualitative subsets of data can produce different relationships, indicative of different local patterns (Stohlgren et al. 2006, Davies et al. 2007). In contrast to a non-significant relationship between native richness and exotic cover at the scale of all California serpentine soils (Harrison et al. 2006), I found significant negative relationships

between native richness and exotic success. This may have resulted from the scale of the topographic gradients in this study coinciding with impacts of dominant invaders, or as a result of the relatively high fertility of San Francisco Bay Area serpentines (Weiss 1999).

My results bring attention to the warnings posed by several recent studies, which assert that biodiversity hotspots are at particular risk for invasion (Stohlgren et al. 1999, 2001, 2003, 2006, 2008). These studies, which show support for the hypothesis of biotic acceptance, tend to focus on native-exotic richness relationships at relatively large spatial grains and extents. Such relationships are positive with very little exception, likely due to covariation with environmental gradients or heterogeneity (Davies et al. 2005), or statistical artifacts (Fridley et al. 2004, Herben et al. 2004). While many areas of high biodiversity are home to rare, threatened, and endemic species that warrant targeted conservation efforts (Myers et al. 2000), my study suggests that these areas do not inherently face greater threat of exotic invasions. Case-by-case evaluation by finer-scale studies, such as this one, should help land managers focus their efforts of invasive species prevention, control, and eradication on those areas most vulnerable to invasion. This is an important task in a world where anthropogenic activities continually cause new biological invasions and the resources to manage them are finite.

LITERATURE CITED

- Brooks, M. L. 2008. Plant invasions and fire regimes. Wildland fire in ecosystems—fire and nonnative invasive plants. USDA Forest Service General Technical Report RMRS-GTR-42-6. Rocky Mountain Research Station, Fort Collins, Colorado, USA. 33-45.
- Brooks, R. R. 1987. Serpentine and its vegetation: a multidisciplinary approach. Dioscorides Press, Portland, Oregon, USA.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: an information-theoretic approach. Springer, New York, New York, USA.
- California Department of Water Resources. 2009. California Irrigation Management Information System. Sacramento, California, USA. URL <http://www.cimis.water.ca.gov/> (date last accessed: December 2009).
- Chardot, V., G. Echevarria, M. Gury, S. Massoura, and J. L. Morel. 2007. Nickel bioavailability in an ultramafic toposequence in the Vosges Mountains (France). *Plant and Soil* **293**:7-21.
- Chytrý, M., P. Pyšek, L. Tichý, I. Knollová, J. Danihelka. 2005. Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia* **77**: 339-354.
- Cleland, E. E., M. D. Smith, S. J. Andelman, C. Bowles, K. M. Carney, M. C. Horner-Devine, J. M. Drake, S. M. Emery, J. M. Gramling, and D. B. Vandermaast. 2004. Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity. *Ecology Letters* **7**:947-957.
- Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental Analysis of Intermediate Disturbance and Initial Floristic Composition: Decoupling Cause and Effect. *Ecology* **76**:486-492.
- Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* **280**:745-747.
- Crall, A. W., G. J. Newman, T. J. Stohlgren, C. S. Jarnevich, P. Evangelista, and D. Guenther. 2006. Evaluating dominance as a component of non-native species invasions. *Diversity & Distributions* **12**:195-204.
- Crawley, B. and E. Heard. 2001. Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* **2**:140-148.
- Crooke, W. M. and R. H. E. Inkson. 1955. The relationship between nickel toxicity and major nutrient supply. *Plant and Soil* **6**:1-15.

- Davies, K. F., P. Chesson, S. Harrison, B. D. Inouye, B. A. Melbourne, and K. J. Rice. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* **86**:1602-1610.
- Davies, K. F., S. Harrison, H. D. Safford, and J. H. Viers. 2007. Productivity alters the scale dependence of the diversity-invasibility relationship. *Ecology* **88**:1940-1947.
- Dukes, J. S. 2002. Species composition and diversity affect grassland susceptibility and response to invasion. *Ecological Applications* **12**:602-617.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. John Wiley and Sons, Inc., New York, New York, USA.
- Fargione, J. E. and D. Tilman. 2005. Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters* **8**:604-611.
- Fridley, J. D., R. L. Brown, and J. F. Bruno. 2004. Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology* **85**:3215-3222.
- Fridley, J. D., J. J. Stachowicz, S. Naeem, D. F. Sax, E. W. Seabloom, M. D. Smith, T. J. Stohlgren, D. Tilman, and B. V. Holle. 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* **88**:3-17.
- Gabbrielli, R. and T. Pandolfini. 1984. Effect of Mg^{2+} and Ca^{2+} on the response to nickel toxicity in a serpentine endemic and nickel-accumulating species. *Physiologia Plantarum* **62**:540-544.
- Gelbard, J. L. and S. Harrison. 2003. Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. *Ecological Applications* **13**:404-415.
- Gilbert, B. and M. J. Lechowicz. 2005. Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. *Ecology* **86**:1848-1855.
- Going, B., J. Hillerislambers, and J. Levine. 2009. Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. *Oecologia* **159**:839-847.
- Gonzalez, L. M. 2007. *Plant species and functional diversity across gradients of resource availability and grazing in a California grassland*. Western Washington University, Bellingham, Washington, USA.
- Goodall, D. W. 1952. Some considerations in the use of point quadrats for the analysis of vegetation. *Australian journal of scientific research. Series B* **5**:1-41.
- Goodwin, B. J., A. J. McAllister, and L. Fahrig. 1999. Predicting invasiveness of plant species based on biological information. *Conservation Biology* **13**:422-426.
- Gough, L., C. W. Osenberg, K. L. Gross, and S. L. Collins. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos*

- 89**:428-439.
- Gram, W. K., E. T. Borer, K. L. Cottingham, E. W. Seabloom, V. L. Boucher, L. Goldwasser, F. Micheli, B. E. Kendall, and R. S. Burton. 2004. Distribution of plants in a California serpentine grassland: are rocky hummocks spatial refuges for native species? *Plant Ecology* **172**:159-171.
- Gulmon, S. L., N. R. Chiariello, H. A. Mooney, and C. C. Chu. 1983. Phenology and resource use in three co-occurring grassland annuals. *Oecologia* **58**:33-42.
- Harrison, S. 1999. Native and alien species diversity at the local and regional scales in a grazed California grassland. *Oecologia* **121**:99-106.
- Harrison, S., J. B. Grace, K. E. Davies, H. D. Safford, and J. H. Viers. 2006. Invasion in a diversity hotspot: exotic cover and native richness in the Californian serpentine flora. *Ecology* **87**:695-703.
- Harrison, S. & Rajakaruna, N. 2011. *Serpentine: The evolution and ecology of a model system*. University of California Press, Berkeley, CA.
- Harrison, S., K. Rice, and J. Maron. 2001. Habitat patchiness promotes invasion by alien grasses on serpentine soil. *Biological Conservation* **100**:45-53.
- Hector, A., K. Dobson, A. Minns, E. Bazeley-White, and J. Hartleylawton. 2001. Community diversity and invasion resistance: An experimental test in a grassland ecosystem and a review of comparable studies. *Ecological Research* **16**:819-831.
- Herben, T., B. Mandák, K. Bímová, and Z. Münzbergová. 2004. Invasibility and species richness of a community: a neutral model and a survey of published data. *Ecology* **85**:3223-3233.
- Hickman, J. C. 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley, California, USA.
- Hobbs, R. J. and H. A. Mooney. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* **72**:59-68.
- Hobbs, R. J., S. L. Gulmon, V. J. Hobbs, and H. A. Mooney. 1988. Effects of fertilizer addition and subsequent gopher disturbance on a serpentine annual grassland community. *Oecologia* **75**:291-295.
- Hobbs, R. J., S. Yates, and H. A. Mooney. 2007. Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. *Ecological Monographs* **77**:545-568.
- Hooper, D. U. and J. S. Dukes. 2010. Functional composition controls invasion success in a California serpentine grassland. *Journal of Ecology* **98**: 764-777.
- Hooper, D. U. and J. S. Dukes. 2004. Overyielding among plant functional groups in a long-

- term experiment. *Ecology Letters* **7**:95-105.
- Hooper, D. U. and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* **68**:121-149.
- Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* **71**:478-491.
- Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist* **113**:81-101.
- Huston, M. A. 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. *Diversity and Distributions* **10**:167-178.
- Inorganic Ventures. 2003. *Reliable Measurements: a guidebook for trace analysts*. Christiansburg, Virginia, USA.
- Johnston, W. R. and J. Proctor. 1981. Growth of serpentine and non-serpentine races of *Festuca rubra* in solutions simulating the chemical conditions in a toxic serpentine soil. *The Journal of Ecology* **69**:855-869.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* **13**:1355-1374.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* **417**:636-638.
- Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, and E. Siemann. 2002. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* **2**:286-293.
- Koide, R. T., L. F. Huenneke, S. P. Hamburg, and H. A. Mooney. 1988. Effects of applications of fungicide, phosphorus and nitrogen on the structure and productivity of an annual serpentine plant community. *Functional Ecology* **2**:335-344.
- Kolb, A., P. Alpert, D. Enters, and C. Holzapfel. 2002. Patterns of invasion within a grassland community. *Journal of Ecology* **90**:871-881.
- Kruckeberg, A. R. 1984. *California serpentes: flora, vegetation, geology, soils, and management problems*. University of California Press, Berkeley, California, USA.
- L'Huillier, L. and S. Edighoffer. 1996. Extractability of nickel and its concentration in cultivated plants in Ni rich ultramafic soils of New Caledonia. *Plant and Soil* **186**:255-264.

- Larson, D. L., P. J. Anderson, and W. Newton. 2001. Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecological Applications* **11**:128-141.
- Levine, J. M. 2000. Species Diversity and Biological Invasions: Relating Local Process to Community Pattern. *Science* **288**:852-854.
- Levine, J. M. and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**:15-26.
- Levine, J. M., M. Vila, C. Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**:775-781.
- Lilley, P. L. and M. Vellend. 2009. Negative native–exotic diversity relationship in oak savannas explained by human influence and climate. *Oikos* **118**:1373-1382.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522-1536.
- Lundholm, J. T. and D. W. Larson. 2004. Dominance As An Overlooked Measure of Invader Success. *Biological Invasions* **6**:505-510.
- Madhok, O. P. and R. B. Walker. 1969. Magnesium Nutrition of Two Species of Sunflower. *Plant Physiology* **44**:1016-1022.
- Main, J. L. 1974. Differential responses to magnesium and calcium by native populations of *Agropyron spicatum*. *American Journal of Botany* **61**:931-937.
- Main, J. L. 1981. Magnesium and calcium nutrition of a serpentine endemic grass. *American Midland Naturalist* **105**: 196-199.
- Mardia, K. V., J. T. Kent, and J. M. Bibby. 1979. *Multivariate Analysis*. Academic Press, London, England.
- McPherson, G. R., H. A. Wright, D. B. Wester. 1988. Patterns of shrub invasion in semiarid Texas grasslands. *American Midland Naturalist* **120**:391-397.
- Meimberg, H., J. Hammond, C. Jorgensen, T. Park, J. Gerlach, K. Rice, and J. McKay. 2006. Molecular Evidence for an Extreme Genetic Bottleneck During Introduction of an Invading Grass to California. *Biological Invasions* **8**:1355-1366.
- Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? *Ecology* **82**:2381-2396.
- Myers, N., R. A., Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**:853-858.

- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**:97-108.
- O'Dell, R. E. and V. P. Claassen. 2006. Relative performance of native and exotic grass species in response to amendment of drastically disturbed serpentine substrates. *Journal of Applied Ecology* **43**:898-908.
- Olf, H. and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* **13**:261-265.
- Ortega, Y. K. and D. E. Pearson. 2005. Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecological Applications* **15**:651-661.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, and J. E. Byers. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**:3-19.
- Proctor, J. 1971. The plant ecology of serpentine: III. The influence of a high magnesium/calcium ratio and high nickel and chromium levels in some British and Swedish serpentine soils. *The Journal of Ecology* **59**:827-842.
- Quinn, G. P. and M. J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, Massachusetts, USA.
- Rahbek, C. 2004. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8**:224-239.
- Rejmánek, M. 2003. The rich get richer – responses. *Frontiers in Ecology and the Environment* **1**:123.
- Rejmánek, M., D. M. Richardson, and P. Pyšek. 2005. Plant invasions and invasibility of plant communities. Pages 332–355 *in* E. van der Maarel, editor. *Vegetation ecology*. Blackwell Publishing, Malden, Massachusetts, USA.
- Robertson, G. P., D. Wedin, P. M. Groffman, J. M. Blair, E. A. Holland, K. J. Nadelhoffer, and D. Harris. 1999. Soil carbon and nitrogen availability. Pages 258-271 *in* G. P. Robertson, D. C. Coleman, C. S. Bledsoe, and P. Sollins, editors. *Standard soil methods for long-term ecological research*. Oxford University Press, New York, New York, USA.
- Safford, H. D. and S. P. Harrison. 2001. Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. *Ecological Applications* **11**:1112-1122.
- Safford, H. D., J. H. Viers, and S. P. Harrison. 2005. Serpentine endemism in the California flora: a database of serpentine affinity. *Madroño* **52**:222-257.

- Saggar, S., M. J. Hedley, and R. E. White. 1990. A simplified resin membrane technique for extracting phosphorus from soils. *Nutrient Cycling in Agroecosystems* **24**:173-180.
- Sax, D. F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions* **8**:193-210.
- Shea, K. and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* **17**:170-176.
- Simard, R. R. 1993. Ammonium acetate-extractable elements. Pages 39-42 *in* M. R. Carter, editor. *Soil sampling and methods of analysis*. Lewis Publishers, Boca Raton, Florida, USA.
- Soane, B. D. and D. H. Saunder. 1959. Nickel and chromium toxicity of serpentine soils in Southern Rhodesia. *Soil Science* **88**:322-330.
- Sokal, R. R. and F. J. Rohlf. 1969. *Biometry. The principles and practice of statistics in biological research*. WH Freeman & Co, New York, New York, USA.
- Soon, Y. K. and S. Abboud. 1993. Cadmium, chromium, lead and nickel. Pages 101-108 *in* M. R. Carter, editor. *Soil sampling and methods of analysis*. Lewis Publishers, Boca Raton, Florida, USA.
- Stachowicz, J. J. and J. E. Byrnes. 2006. Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. *Marine Ecology Progress Series* **311**:251-262.
- Stohlgren, T. J. 2007. *Measuring plant diversity: lessons from the field*. Oxford University Press, New York, New York, USA.
- Stohlgren, T. J., D. T. Barnett, C. S. Jarnevich, C. Flather, J. Kartesz, and F. S. Usda. 2008. The myth of plant species saturation. *Ecology Letters* **11**:313-322.
- Stohlgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment* **1**:11-14.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**:25-46.
- Stohlgren, T. J., G. W. Chong, L. D. Schell, K. A. Rimar, Y. Otsuki, M. Lee, M. A. Kalkhan, and C. A. Villa. 2002. Assessing Vulnerability to Invasion by Nonnative Plant Species at Multiple Spatial Scales. *Environmental Management* **29**:566-577.
- Stohlgren, T. J., C. Jarnevich, G. W. Chong, and P. H. Evangelista. 2006. Scale and plant invasions: a theory of biotic acceptance. *Preslia* **78**:405-426.
- Stohlgren, T. J., Y. Otsuki, C. A. Villa, M. Lee, and J. Belnap. 2001. Patterns of plant

- invasions: a case example in native species hotspots and rare habitats. *Biological Invasions* **3**:37-50.
- Taylor, B. W. and R. E. Irwin. 2004. Linking economic activities to the distribution of exotic plants. *Proceedings of the National Academy of Sciences of the United States of America* **101**:17725-17730.
- Taylor, D. R., L. W. Aarssen, and C. Loehle. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* **58**:239-250.
- Theoharides, K. A. and J. S. Dukes. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist* **176**:256-273.
- Tilman, D. 1987. Secondary Succession and the Pattern of Plant Dominance Along Experimental Nitrogen Gradients. *Ecological Monographs* **57**:189-214.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**:718-720.
- Turitzin, S. N. 1982. Nutrient limitations to plant growth in a California serpentine grassland. *American Midland Naturalist* **107**:95-99.
- United States Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS). 2009. Plants Database. URL <http://plant.usda.gov> (date last accessed: November 2009).
- United States Fish and Wildlife Service (USFWS). 1998. Recovery plan for serpentine soil species of the San Francisco Bay Area. USFWS, Portland, Oregon, USA.
- Varian. 1989. Analytical methods: flame atomic absorption spectrometry. Varian, Palo Alto, CA.
- Vlamin, J. and H. Jenny. 1948. Calcium Deficiency in Serpentine Soils as Revealed by Adsorbent Technique. *Science* **107**:549.
- Walker, R. B. 1948. Molybdenum Deficiency in Serpentine Barren Soils. *Science* **108**:473-475.
- Walker, R. B. 2001. Low molybdenum status of serpentine soils of western North America. *South African Journal of Science* **97**:565-568.
- Walker, R. B., H. M. Walker, and P. R. Ashworth. 1955. Calcium-magnesium nutrition with special reference to serpentine soils. *Plant physiology* **30**:214-221.
- Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility: evidence of a biological mechanism or a consequence of sampling effect? *Oikos*

95:161-170.

Weiss, S. B. 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology* **13**:1476-1486.

Western Regional Climate Center. 2009. Western Regional Climate Center. Reno, NV. URL <http://www.wrcc.dri.edu> (date last accessed: November 2009).

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385-397.

APPENDIX 1: DETAILED METHODS

Soil extractions

I assessed initial ammonium and nitrate concentrations using KCl extractions and used a laboratory assay to determine potential N mineralization (Robertson et al. 1999). I added ~10g dry weight equivalent of <4mm soil for each sample to 100 ml 2M KCl, shook samples manually, let stand overnight in a 4°C coldroom, then shook on a rotary shaker for 1 hour before filtering through Whatman No. 1 filter paper. I then incubated samples of the same amount of soil in loosely-capped specimen cups for 28 days at 25°C in the dark. During this time, I monitored soil moisture once every 3 days, and added water as necessary to maintain ~60% water-filled pore space. At the end of the 28 days, I again extracted the soils using the same procedure as above.

To determine available phosphorous, I charged anion exchange resin strips (Bio-Rex AG 1-X8 Anion Exchange Resin, Bio-Rad Laboratories, Richmond, CA) in 0.5M NaCl for 24 hours and then rinsed them in nanopure water for several day-long rinses (Saggar et al. 1990). I then placed ~7g dry weight equivalent of soil in a centrifuge tube containing 30mL of nanopure water and one resin strip, and shook these tubes overnight (14-16 hours). The strips were then removed and washed with nanopure water. I removed the phosphorous from the strips by shaking them for 4-6 hours in 25mL of 0.5 M HCl. After extracting both N and P, I sieved the soil samples to <2mm, dried the rocks, weighed them, and subtracted the rock weights from the soils.

I extracted Ca^{2+} , Mg^{2+} , and K^{+} from the soils with ammonium acetate (NH_4Oac ; Simard 1993). I added 3g of <2mm soil and 30mL of 1M NH_4Oac to specimen cups and shook them for 15 minutes on a reciprocal shaker. Extracts were filtered through Whatman

No. 2 paper and stored in low-density polyethylene (LDPE) containers to reduce adsorption of the ions to the container (Inorganic Ventures 2003). I extracted available nickel (Ni) with DTPA (pH=7.3), using a 5:1 extractant:soil ratio (25g extractant: 5g soil) with a solution of 5mM DTPA, 10mM CaCl₂, and 0.1M triethanolamine (TEA; Soon and Abboud 1993). I shook samples on a rotary shaker for 2 hours, then filtered extracts through Whatman No. 42 paper.

To suppress ionization of the targeted minerals and bring the solutions into an appropriate range for the instruments, I diluted samples for Ca and Mg analysis 1:40 with a solution of 5,000 ppm K (as KCl), and we diluted samples for K analysis 1:10 with a solution of 1,000 ppm cesium (as cesium chloride; Varian 1989). I then analyzed the extracts of Ca, Mg, and K by atomic absorption spectrometry with a nitrous-oxide acetylene flame; I used an air-acetylene flame for the Ni extracts (Varian 1989).

Literature review on the relationship of environmental gradients to exotic success in serpentine soils

Grazing

Personal observation of the study site and several small-scale studies on serpentine suggested that grazing has an overall negative effect on the richness, cover, and dominance of exotic plants, and a positive effect on the richness, cover, and dominance of native plants (Weiss 1999, Safford and Harrison 2001). An increase in the abundance of native forbs due to a release from competition with exotic grasses may account for this relationship (Collins et al. 1998). However, in a statewide study of serpentine soils, animal disturbance and grazing by livestock were positive predictors of both exotic cover and native richness (Harrison et al.

2006). I coded grazing as 0 (ungrazed) or 1 (grazed) in the models. Although I collected data on several variables related to grazing intensity (footprints and cow dung), I did not include these in the analysis. There was concern that footprints might be much more prominent in deeper, wetter soils, thus causing aspect to unduly influence the grazing results. Cow dung was distributed in a very patchy manner, occurring in only ~25% of the grazed plots, so I also did not include this grazing indicator.

Plant macronutrients (N, P, K)

At the statewide scale, N and P were not significant predictors of exotic cover or native richness (Harrison et al. 2006), but studies with smaller spatial extents have suggested otherwise. Nutrient-addition experiments indicate that plant growth on many California serpentine is limited by N and P (Turitzin 1982). Reduced overall species richness (Koide et al. 1988) and increased dominance by exotics (Huenneke et al. 1990) follows fertilization with these nutrients. Thus, I expected a positive correlation between these nutrients and exotic success. However, serpentine areas with shallower soils can have higher native dominance than neighboring areas with deeper soils, despite having comparable levels of N and P per gram soil (Huenneke et al. 1990, Gram et al. 2004, Gonzalez 2007). Therefore, I used nutrient availability per m², instead of per gram soil, to better reflect the nature of the relationship to vegetation. The majority of nutrient addition studies on California serpentine grasslands have found that N is more limiting than P in these systems (Turitzin 1982, Huenneke et al. 1990, Going et al. 2009). I only found two studies that examined K in relation to the California serpentine flora: Harrison et al. (2006) found K to be a positive predictor of native herb richness, while Turitzin (1982) found no effect on plant growth after

K fertilization. Because of the lack of consistent support for P and K as predictors of exotic success, as well as my finding that N, P, and K ordinate together in principles components analysis (Appendix 2: Table S1), I included N mineralization per m^2 as the only macronutrient.

I attempted to predict the type of relationship between N and exotic success. Studies on non-serpentine soils have shown positive linear relationships between N availability and productivity and negative linear relationships between N availability and species richness (Tilman 1987). I also examined data previously collected at the site (Gonzalez 2007), and found that $N_{\text{min}}/\text{m}^2$ had a positive linear relationship to exotic cover, a positive natural log relationship to exotic dominance, and no significant relationship to exotic richness. I therefore expected either a non-significant or linear relationship of $N_{\text{min}}/\text{m}^2$ to exotic richness and cover, and a natural log relationship to exotic dominance (Table 1).

Soil calcium and magnesium

The Ca:Mg ratio of serpentine soil can be a strong predictor of vegetative cover, due to Mg toxicity and the lack of available Ca to ameliorate it (Johnston and Proctor 1981). At the statewide scale, Ca:Mg was a positive quadratic predictor of exotic cover (Harrison et al. 2006) and a negative predictor of the proportion of total species that were native (Harrison 1999). However, experimental studies have shown contradictory results: some have found that Ca ameliorates Mg toxicity (Vlamis and Jenny 1948, O'Dell and Claassen 2006), while others have found no effect of Ca addition on vegetation (Turitzin 1982, Going et al. 2009).

Several greenhouse experiments measured the productivity of serpentine and non-serpentine species under different Ca:Mg ratios (Walker et al. 1955, Madhok and Walker

1969, Proctor 1971, Main 1974). For data from studies conducted in my expected range of Ca:Mg ratios (0 to 0.8), a positive natural log relationship was the best fit for relative growth rates (percentage of the most productive treatment in the study) of non-serpentine plants in each study. In the absence of competition, many plants found on serpentine (but not serpentine endemics) do not show reductions in productivity at high Ca:Mg ratios (up to at least 6.4; Walker et al. 1955, Main 1974), suggesting that any negative relationship between native cover or dominance and Ca:Mg may be due to displacement by exotics. Because I do not have more specific data on the relationships between the three targeted vegetation indices and Ca:Mg, I estimated all the relationships to follow a natural log pattern.

Soil Nickel

Relatively high levels of Ni are characteristic of some serpentine soils and are thought to be responsible for reduced vegetative growth on some serpentines (Crooke and Inkson 1955, Walker et al. 1955, Soane and Saunder 1959, Kruckeberg 1984), but toxicity associated with this element is not well-understood. Some soils may be very high in Ni but have low levels of plant available Ni (Soane and Saunder 1959), so I performed a 5mM DTPA soil Ni extraction, which gives a reliable estimate of bioavailable Ni (Chardot et al. 2007). Complex interactions between Ni, Ca, and Mg further complicate the issue of nickel toxicity (Gabbrielli and Pandolfini 1984), so I included nickel in a linear relationship to the response variables to simplify the model set.

APPENDIX 2: SUPPLEMENTARY TABLES

Table S1. Principle components analysis of environmental variables. For details about the variables, see Methods section. The variable loadings in bold are those loading strongly onto that axis ($\geq 70\%$ of the highest loading for a given axis; Mardia et al. 1979). Together, the first four axes (the only ones significant, with eigenvalues >1) explained 77.5% of the variance.

Variable	Principal Components			
	1	2	3	4
% of variance	38.4	17.2	12.4	9.52
Eigenvalue	4.99	2.23	1.61	1.24
N _{min} ($\mu\text{g} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$)	0.600	-0.041	-0.332	0.058
N _{min} ($\mu\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$)	0.741	-0.309	0.396	-0.143
P ($\mu\text{g/g soil}$)	0.450	0.146	-0.584	-0.030
P ($\mu\text{g/m}^2$)	0.813	-0.101	0.228	-0.384
Ni ($\mu\text{g/g soil}$)	0.230	0.765	0.164	0.004
Ca ($\mu\text{g/g soil}$)	0.636	-0.461	-0.092	0.570
Mg ($\mu\text{g/g soil}$)	0.317	0.187	0.383	0.819
K ($\mu\text{g/g soil}$)	0.789	-0.178	-0.029	-0.019
Ca:Mg ($\mu\text{g Ca}/\mu\text{g Mg}$)	0.507	-0.644	-0.412	0.020
% N	0.752	0.495	-0.279	-0.032
% C	0.779	0.436	-0.242	-0.094
June soil moisture (%)	0.460	0.560	0.232	0.054
Soil Depth (cm)	0.628	-0.278	0.643	-0.237

Table S2. Species found at the study site. Nomenclature follows Hickman (1993), except in cases where plant names have since changed. I updated these species names by using the USDA Plants Database (USDA 2009). *Denotes plant was only found in 250 m² plots.

Name	Family	Native?
<i>Achillea millefolium</i> L.	Asteraceae	Native
<i>Agoseris heterophylla</i> (Nutt.) Greene	Asteraceae	Native
<i>Allium serra</i> McNeal & Ownbey	Liliaceae	Native
<i>Amsinckia menziesii</i> (Lehm.) A. Nelson J.F. Macbr.	Boraginaceae	Native
<i>Aphanes arvensis</i> L.	Rosaceae	Native
<i>Astragalus gambellianus</i> Sheldon	Fabaceae	Native
<i>Avena barbata</i> Pott ex Link	Poaceae	Exotic
<i>Avena fatua</i> L.	Poaceae	Exotic
<i>Bombycilaena californica</i> (Fisch. & C.A. Mey.) Holub var. <i>californica</i>	Asteraceae	Native
<i>Bromus diandrus</i> Roth	Poaceae	Exotic
<i>Bromus hordeaceus</i> L.	Poaceae	Exotic
<i>Bromus madritensis</i> L. ssp. <i>Rubens</i> (L.) Duvin	Poaceae	Exotic
<i>Calandrinia ciliata</i> (Ruiz & Pav.) DC.	Portulacaceae	Native
<i>Calochortus venustus</i> Douglas ex Benth.	Liliaceae	Native
<i>Calystegia subacaulis</i> Hook. & Arn.	Convolvulaceae	Native
<i>Capsella bursa-pastoris</i> (L.) Medik.*	Brassicaceae	Exotic
<i>Castilleja densiflora</i> (Benth.) T.I. Chuang & Heckard	Orobanchaceae	Native
<i>Chlorogallum pomeridianum</i> (DC.) Kunth	Liliaceae	Native
<i>Cirsium fontinale</i> (Greene) Jeps. Var. <i>campylon</i> (H.K. Sharsmith) Pilz ex Keil & C. Turner*	Asteraceae	Native
<i>Claytonia exigua</i> Torr. & A. Gray	Portulacaceae	Native
<i>Claytonia perfoliata</i> Donn ex Willd.	Portulacaceae	Native
<i>Crassula connata</i> (Ruiz & Pav.) A. Berger	Crassulaceae	Native
<i>Cryptantha flaccida</i> (Douglas ex Lehm.) Greene	Boraginaceae	Native
<i>Cuscuta denticulata</i> Engelm.	Cuscutaceae	Native
<i>Daucus pusillus</i> Michx.*	Apiaceae	Native
<i>Delphinium hesperium</i> A. Gray	Ranunculaceae	Native
<i>Delphinium variegatum</i> Torr. & A. Gray	Ranunculaceae	Native
<i>Dichelostemma capitum</i> (Benth.) Alph. Wood	Liliaceae	Native
<i>Dodecatheon hendersonii</i> A. Gray	Primulaceae	Native
<i>Dudleya setchellii</i> (Jeps.) Britton & Rose	Crassulaceae	Native
<i>Elymus glaucus</i> Buckley	Poaceae	Native
<i>Elymus multisetus</i> M.E. Jones	Poaceae	Native
<i>Epilobium brachycarpum</i> C. Presl.	Onagraceae	Native
<i>Epilobium minutum</i> Lindl. Ex Lehm.	Onagraceae	Native
<i>Eriogonum saxatile</i> S. Watson	Polygonaceae	Native
<i>Eriogonum nudum</i> Douglas ex Benth.	Polygonaceae	Native
<i>Eriophyllum confertiflorum</i> (DC.) A. Gray	Asteraceae	Native
<i>Erodium cicutarium</i> (L.) L'Hér. ex Aiton	Geraniaceae	Exotic
<i>Eschscholzia californica</i> Cham.	Papaveraceae	Native
<i>Euphorbia spathulata</i> Lam.	Euphorbiaceae	Native
<i>Galium aparine</i> L.*	Rubiaceae	Native
<i>Gilia achilleifolia</i> Benth.	Polemoniaceae	Native
<i>Gilia tricolor</i> Benth.*	Polemoniaceae	Native
<i>Hemizonia congesta</i> DC. ssp. <i>luzulifolia</i> (DC.) Bab. & H.M. Hall	Asteraceae	Native
<i>Hesperivax sparsiflora</i> (A. Gray) Greene	Asteraceae	Native
<i>Hordeum brachyantherum</i> Nevski	Poaceae	Native
<i>Hordeum marinum</i> Huds.	Poaceae	Exotic
<i>Hordeum murinum</i> L.	Poaceae	Exotic

<i>Koeleria macrantha</i> (Ledeb.) Schult.	Poaceae	Native
<i>Lactuca saligna</i> L.	Asteraceae	Exotic
<i>Lactuca serriola</i> L.	Asteraceae	Exotic
<i>Lactuca virosa</i> L.	Asteraceae	Exotic
<i>Lasthenia californica</i> DC. Ex Lindl.	Asteraceae	Native
<i>Layia platyglossa</i> (Fisch. & C.A. Mey.) A. Gray	Asteraceae	Native
<i>Lepidium nitidum</i> Nutt.	Brassicaceae	Native
<i>Leptosiphon ambiguus</i> (Rattan) J.M. Porter & L.A. Johnson	Polemoniaceae	Native
<i>Leptosiphon liniflorus</i> (Benth.) J.M. Porter & L.A. Johnson	Polemoniaceae	Native
<i>Lessingia micradenia</i> Greene	Asteraceae	Native
<i>Lolium perenne</i> L. ssp. <i>multiflorum</i> (Lam.) Husnot	Poaceae	Exotic
<i>Lomatium dasycarpum</i> (Torr. & A. Gray) J.M. Coult. & Rose	Apiaceae	Native
<i>Lomatium utriculatum</i> (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose	Apiaceae	Native
<i>Lotus wrangelianus</i> Fisch. & C.A. Mey	Fabaceae	Native
<i>Lupinus succulentus</i> Douglas ex K. Koch*	Fabaceae	Native
<i>Madia elegans</i> D. Don ex Lindl.	Asteraceae	Native
<i>Malacothrix glabrata</i> (A. Gray ex D.C. Eaton) A. Gray*	Asteraceae	Native
<i>Medicago polymorpha</i> L.	Fabaceae	Exotic
<i>Melica torreyana</i> Scribn.	Poaceae	Native
<i>Melilotus officinalis</i> (L.) Lam.	Fabaceae	Exotic
<i>Microseris douglasii</i> (DC.) Sch. Bip.	Asteraceae	Native
<i>Microseris lindleyi</i> (DC.) A. Gray	Asteraceae	Native
<i>Microsteris gracilis</i> (Hook.) Greene var. <i>gracilis</i>	Polemoniaceae	Native
<i>Monolopia</i> sp. (<i>gracilens</i> or <i>major</i>)	Asteraceae	Native
<i>Muilla maritima</i> (Torr.) S. Watson	Liliaceae	Native
<i>Nassella pulchra</i> (Hitche.) Barkworth	Poaceae	Native
<i>Pellaea andromedifolia</i> (Kaulf.) Fée	Pteridaceae	Native
<i>Phacelia imbricata</i> Greene*	Hydrophyllaceae	Native
<i>Phacelia distans</i> Benth.	Hydrophyllaceae	Native
<i>Plantago erecta</i> Morris	Plantaginaceae	Native
<i>Platystemon californicus</i> Benth.	Papaveraceae	Native
<i>Poa secunda</i> J. Presl	Poaceae	Native
<i>Ranunculus californicus</i> Benth.	Ranunculaceae	Native
<i>Sanicula bipinnatifida</i> Douglas ex Hook.	Apiaceae	Native
<i>Sanicula tracyi</i> Shan & Constance*	Apiaceae	Native
<i>Silene gallica</i> L.	Caryophyllaceae	Exotic
<i>Sisyrinchium bellum</i> S. Watson	Iridaceae	Native
<i>Streptanthus albidus</i> Greene	Brassicaceae	Native
<i>Trifolium albopurpurem</i> Tott. & A. Gray	Fabaceae	Native
<i>Trifolium gracilentum</i> Torr. & A. Gray	Fabaceae	Native
<i>Trifolium willdenovii</i> Spreng.	Fabaceae	Native
<i>Triteleia laxa</i> Benth.	Liliaceae	Native
Unknown forb A		Unknown
Unknown forb B*		Unknown
Unknown forb C		Unknown
Unknown Asteraceae*	Asteraceae	Unknown
<i>Vicia</i> sp.*	Fabaceae	Unknown
<i>Vulpia microstachys</i> (Nutt.) Munro	Poaceae	Native
<i>Vulpia myuros</i> (L.) C.C. Gmel.*	Poaceae	Exotic

Table S3. Results of the bootstrapped Spearman rank correlations between native richness and indices of exotic success. For all analyses $n=16$, with 1000 iterations. Here I give the bootstrap-estimated correlation coefficients, r_{est} . 95% confidence intervals were calculated using the percentile method. I considered correlations nonsignificant if the 95% confidence intervals for the correlation coefficient spanned both positive and negative values. Significant correlations are in bold.

Scale	Index A	Index B	r_{est}	95% Confidence interval	
				Lower	Upper
0.25m ²	Native richness	Exotic richness	-0.421	-0.808	0.095
0.25m ²	Native richness	Exotic cover	-0.537	-0.846	-0.138
0.25m ²	Native richness	Exotic dominance	-0.661	-0.891	-0.294
250m ²	Native richness	Exotic richness	-0.287	-0.764	0.27

Table S4. Results of AIC analyses for every model used to predict indices of native and exotic success. Models above the bold line have very strong support ($\Delta AIC_C \leq 2$; Burnham and Anderson 2002). Dominance indices were negative arcsine(square root) transformed because they were constrained by 0 and 1. Models are notated as follows: I = intercept, R = native richness, N = N mineralization = $\mu\text{g N}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, G = grazing (presence or absence), C = Ca:Mg ($\mu\text{g Ca}:\mu\text{g Mg}$), Ni = nickel ($\mu\text{g/g}$ soil).

A) Exotic richness as response, native richness included as a predictor

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Predictor Coefficients					
					Interc.	Native richness	Graze	N_{min}/m^2	Ca:Mg	Nickel
R+G+C	0.00	0.524	1.00	0.417	6.222	-0.080	0.815		2.003	
R+G+N+C	1.81	0.212	2.47	0.412	6.403	-0.083	0.825	-0.702	2.059	
R+G+C+Ni	2.29	0.167	3.14	0.409	6.220	-0.080	0.814		2.004	0.000
R+G+N+C+Ni	4.14	0.066	7.91	0.404	2.386	-0.035	0.269	-0.418	0.793	0.001
G+C	7.72	0.011	47.38	0.346	6.702		0.710		2.767	
R+C	9.51	0.005	116.0	0.331	5.379	-0.067			1.323	
G+C+Ni	9.92	0.004	142.6	0.338	6.715		0.715		2.757	-0.001
G+N+C	9.93	0.004	143.3	0.338	6.727		0.711	-0.089	2.778	
R+C+Ni	11.47	0.002	309.5	0.324	5.344	-0.068			1.372	0.003
R+N+C	11.55	0.002	322.1	0.324	5.492	-0.069		-0.467	1.355	
G+N+C+Ni	12.21	0.001	447.1	0.329	6.733		0.715	-0.067	2.766	-0.001
R+N+C+Ni	13.48	0.001	843.6	0.318	5.479	-0.071		-0.590	1.422	-0.003
C	13.73	0.001	959.1	0.284	5.887				2.059	
R+G	14.84	0.000	1666	0.284	3.697	-0.135	0.399			
R	15.56	0.000	2395	0.276	3.705	-0.116				
C+Ni	15.80	0.000	2692	0.275	5.869				2.096	0.002
N+C	15.90	0.000	2830	0.274	5.880	0.000	0.000	-0.006	2.065	0.000
R+G+Ni	16.82	0.000	4492	0.276	3.795	-0.133	0.424			-0.003

A) Exotic richness as response, native richness included as a predictor (cont.)

Predictor Coefficients

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Interc.	Native richness	Graze	N_{min}/m^2	Ca:Mg	Nickel
R+G+N	17.06	0.000	5064	0.274	3.684	-0.134	0.399	0.086		
R+Ni	17.72	0.000	7032	0.257	3.726	-0.116				-0.001
R+N	17.73	0.000	7067	0.257	3.695	-0.012		0.066		
N+C+Ni	18.02	0.000	8185	0.265	5.876	0.000		-0.029	2.100	0.002
R+G+N+Ni	19.08	0.000	>10000	0.267	3.773	-0.132	0.426	0.174		-0.003
R+N+Ni	19.94	0.000	>10000	0.247	3.715	-0.115		0.086		-0.001
N	38.10	0.000	>10000	0.021	2.316	0.000		2.033		0.000
N+Ni	38.40	0.000	>10000	0.031	2.698			2.111		-0.009
Ni	39.17	0.000	>10000	0.007	2.853					-0.008
G+N	39.94	0.000	>10000	0.012	2.398		-0.144	1.915		
G	40.08	0.000	>10000	-0.004	2.590		-0.205	0.000		
G+N+Ni	40.59	0.000	>10000	0.019	2.707		-0.042	2.074		-0.008
G+Ni	41.11	0.000	>10000	-0.003	2.871		-0.122			-0.007

B) Exotic cover as response, native richness included as a predictor

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Predictor Coefficients					
					Interc.	Native richness	Graze	N_{min}/m^2	Ca:Mg	Nickel
R+N+C+Ni	0.00	0.246	1.00	0.469	0.673	-0.033		0.532	0.234	0.010
R+C+Ni	0.34	0.208	1.18	0.459	0.796	-0.035			0.280	0.010
R+N+Ni	0.56	0.186	1.33	0.457	0.380	-0.040		0.644		0.009
R+G+N+Ni	2.09	0.087	2.84	0.455	0.374	-0.038	-0.060	0.631		0.009
R+Ni	2.16	0.084	2.95	0.437	0.466	-0.045				0.009
R+G+N+C+Ni	2.29	0.078	3.14	0.462	0.653	-0.032	-0.018	0.535	0.220	0.010
R+G+C+Ni	2.59	0.068	3.65	0.451	0.781	-0.035	-0.013		0.269	0.010
R+G+Ni	3.51	0.043	5.78	0.436	0.456	-0.042	-0.066			0.010
N+C+Ni	13.36	0.000	797.4	0.36	0.856			0.790	0.545	0.009
G+N+C+Ni	15.11	0.000	1907	0.356	0.785		-0.059	0.793	0.491	0.009
C+Ni	15.96	0.000	2929	0.328	1.065				0.650	0.010
G+C+Ni	17.72	0.000	7033	0.323	0.997		-0.057		0.598	0.010
R+N	22.91	0.000	>10000	0.266	0.647	-0.030		0.898		
G+N+Ni	23.16	0.000	>10000	0.274	0.071		-0.193	1.172		0.008
R+N+C	25.04	0.000	>10000	0.257	0.710	-0.028		0.879	0.048	
R+G+N	25.04	0.000	>10000	0.257	0.646	-0.031	0.023	0.899		
R	26.22	0.000	>10000	0.223	0.786	-0.036				
R+G+N+C	27.11	0.000	>10000	0.249	0.754	-0.029	0.040	0.867	0.082	
N+C	27.12	0.000	>10000	0.181	1.312	0.000	0.000	0.138	0.298	0.000
N+Ni	27.51	0.000	>10000	0.221	0.030			1.346		0.006
R+C	27.94	0.000	>10000	0.217	0.923	-0.032			0.108	
R+G	28.32	0.000	>10000	0.213	0.786	-0.037	0.021			

B) Exotic cover as response, native richness included as a predictor (cont.)

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Predictor Coefficients					
					Interc.	Native richness	Graze	N_{min}/m^2	Ca:Mg	Nickel
R+G+C	29.82	0.000	>10000	0.21	-0.032		0.053		0.152	
G+Ni	31.06	0.000	>10000	0.185	0.164		-0.238			0.008
G+N+C	33.61	0.000	>10000	0.17	0.866		0.000	1.079	0.330	
N	34.86	0.000	>10000	0.132	0.295			1.400		
G+N	35.32	0.000	>10000	0.139	0.352		-0.101	1.317		
C	36.28	0.000	>10000	0.116	1.161				0.453	
Ni	37.84	0.000	>10000	0.098	0.129					0.006
G+C	38.43	0.000	>10000	0.104	1.172		0.010		0.463	
G	43.84	0.000	>10000	0.026	0.484		-0.143			

C) Exotic dominance as response, native richness included as a predictor

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Predictor Coefficients					
					Interc.	Native richness	Graze	N_{min}/m^2	Ca:Mg	Nickel
R+C+Ni	0.00	0.336	1.00	0.472	-0.175	-0.037			0.301	0.004
R+N+C+Ni	2.00	0.124	2.72	0.467	-0.151	-0.036		0.017	0.281	0.003
R+G+C+Ni	2.27	0.108	3.11	0.465	-0.184	-0.037	-0.008		0.294	0.004
R+C	3.23	0.067	5.02	0.441	-0.130	-0.036			0.239	
R+Ni	3.45	0.060	5.60	0.44	-0.529	-0.047				0.003
R+N+C	4.11	0.043	7.79	0.443	-0.085	-0.035		0.036	0.207	
R+G+N+C+Ni	4.32	0.039	8.66	0.459	-0.160	-0.036	-0.008	0.017	0.275	0.003
R+N+Ni	4.35	0.038	8.80	0.442	-0.430	-0.045		0.035		0.002
R+N	4.48	0.036	9.39	0.432	-0.322	-0.042		0.046		
R	4.62	0.033	10.05	0.43	-0.433	-0.044				
R+G+Ni	4.63	0.033	10.11	0.44	-0.540	-0.044	-0.065			0.003
R+G+C	5.40	0.023	14.88	0.434	-0.114	-0.036	0.015		0.252	
R+G+N+Ni	5.81	0.018	18.31	0.44	-0.448	-0.043	-0.058	0.032		0.003
R+G+N+C	6.36	0.014	24.05	0.436	-0.073	-0.035	0.012	0.035	0.218	
R+G	6.45	0.013	25.10	0.418	-0.432	-0.043	-0.037			
R+G+N	6.45	0.013	25.13	0.426	-0.323	-0.040	-0.032	0.046		
C+Ni	20.95	0.000	>10000	0.299	0.107				0.689	0.003
C	21.73	0.000	>10000	0.281	0.137				0.627	
N+C	21.99	0.000	>10000	0.289	0.190			0.048	0.572	
N+C+Ni	22.27	0.000	>10000	0.297	0.149			0.034	0.641	0.003
G+C+Ni	22.69	0.000	>10000	0.294	0.043		-0.054		0.639	0.003
G+C	23.73	0.000	>10000	0.273	0.101		-0.032		0.595	

C) Exotic dominance as response, native richness included as a predictor (cont.)

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Predictor Coefficients					
					Interc.	Native richness	Graze	N_{min}/m^2	Ca:Mg	Nickel
G+N+C	24.01	0.000	>10000	0.282	0.151		-0.035	0.049	0.537	
G+N+C+Ni	24.09	0.000	>10000	0.292	0.086		-0.053	0.034	0.593	0.003
G+N	35.32	0.000	>10000	0.157	-0.539		-0.199	0.088		
G+N+Ni	37.39	0.000	>10000	0.147	-0.576		-0.209	0.085		0.001
G	38.84	0.000	>10000	0.105	-0.783		-0.228			
G+Ni	40.27	0.000	>10000	0.102	-0.849		-0.248			0.002
N	40.94	0.000	>10000	0.081	-0.586			0.105		
N+Ni	42.79	0.000	>10000	0.072	-0.528			0.109		-0.001
Ni	48.49	0.000	>10000	-0.013	-0.885					0.000

D) Exotic richness as response, native richness omitted.

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Predictor Coefficients				
					Interc.	Graze	N_{min}/m^2	Ca:Mg	Nickel
G+C	0.00	0.538	1.00	0.346	6.702	0.710		2.767	
G+C+Ni	2.20	0.179	3.01	0.338	6.715	0.715		2.757	-0.001
G+N+C	2.21	0.178	3.02	0.338	6.727	0.711	-0.089	2.778	
G+N+C+Ni	4.49	0.057	9.44	0.329	6.733	0.715	-0.067	2.766	-0.001
C	6.02	0.027	20.24	0.284	5.887			2.059	
C+Ni	8.08	0.009	56.83	0.275	5.869			2.096	0.002
N+C	8.18	0.009	59.74	0.274	5.880		-0.006	2.065	
N+C+Ni	10.30	0.003	172.7	0.265	5.876		-0.029	2.100	0.002
N	30.39	0.000	>10000	0.021	2.316			2.033	
N+Ni	30.68	0.000	>10000	0.031	2.698			2.111	-0.009
Ni	31.46	0.000	>10000	0.007	2.853				-0.008
G+N	32.22	0.000	>10000	0.012	2.398	-0.144	1.915		
G	32.37	0.000	>10000	-0.004	2.590	-0.205			
G+N+Ni	32.87	0.000	>10000	0.019	2.707	-0.042	2.074		-0.008
G+Ni	33.39	0.000	>10000	-0.003	2.871	-0.122			-0.007

E) Exotic cover as response, native richness omitted.

Model	ΔAIC_C	akaike weight	evidence ratio	r^2_{adj}	Predictor Coefficients				
					Interc.	Graze	N_{min}/m^2	Ca:Mg	Nickel
N+C+Ni	0.00	0.552	1.00	0.36	0.856		0.790	0.545	0.009
G+N+C+Ni	1.74	0.231	2.39	0.356	0.785	-0.059	0.793	0.491	0.009
C+Ni	2.60	0.150	3.67	0.328	1.065			0.650	0.010
G+C+Ni	4.35	0.063	8.82	0.323	0.997	-0.057		0.598	0.010
G+N+Ni	9.79	0.004	133.89	0.274	0.071	-0.193	1.172		0.008
N+C	13.76	0.001	971.4	0.181	1.312		0.138	0.298	
N+Ni	14.14	0.000	1178	0.221	0.030		1.346		0.006
G+Ni	17.69	0.000	6951	0.185	0.164	-0.238			0.008
G+N+C	20.25	0.000	>10000	0.17	0.866	0.000	1.079	0.330	
N	21.50	0.000	>10000	0.132	0.295		1.400		
G+N	21.95	0.000	>10000	0.139	0.352	-0.101	1.317		
C	22.92	0.000	>10000	0.116	1.161			0.453	
Ni	24.48	0.000	>10000	0.098	0.129				0.006
G+C	25.07	0.000	>10000	0.104	1.172	0.010		0.463	
G	30.48	0.000	>10000	0.026	0.484	-0.143			

F) Exotic dominance as response, native richness omitted.

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Predictor Coefficients				
					Interc.	Graze	N_{min}/m^2	Ca:Mg	Nickel
C+Ni	0.00	0.258	1.00	0.299	0.107			0.689	0.003
C	0.78	0.174	1.48	0.281	0.137			0.627	
N+C	1.04	0.153	1.68	0.289	0.190		0.048	0.572	
N+C+Ni	1.32	0.133	1.93	0.297	0.149		0.034	0.641	0.003
G+C+Ni	1.74	0.108	2.39	0.294	0.043	-0.054		0.639	0.003
G+C	2.78	0.064	4.02	0.273	0.101	-0.032		0.595	
G+N+C	3.06	0.056	4.63	0.282	0.151	-0.035	0.049	0.537	
G+N+C+Ni	3.14	0.054	4.80	0.292	0.086	-0.053	0.034	0.593	0.003
G+N	14.37	0.000	1318	0.157	-0.539	-0.199	0.088		
G+N+Ni	16.44	0.000	3714	0.147	-0.576	-0.209	0.085		0.001
G	17.89	0.000	7681	0.105	-0.783	-0.228			
G+Ni	19.32	0.000	>10000	0.102	-0.849	-0.248			0.002
N	19.99	0.000	>10000	0.081	-0.586		0.105		
N+Ni	21.84	0.000	>10000	0.072	-0.528		0.109		-0.001
Ni	27.54	0.000	>10000	-0.013	-0.885				0.000

G) Native richness as response.

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Predictor Coefficients				
					Interc.	Graze	N_{min}/m^2	Ca:Mg	Nickel
N+C	0.00	0.209	1.00	0.405	-5.563		-7.164	-10.077	
C	0.24	0.185	1.13	0.394	-7.522			-10.898	
G+N+C	0.44	0.167	1.25	0.41	-3.912	1.383	-7.397	-8.670	
G+C	0.83	0.138	1.51	0.398	-6.009	1.319		-9.582	
N+C+Ni	1.37	0.105	1.99	0.403	-5.588		-7.891	-9.534	0.022
C+Ni	2.00	0.077	2.72	0.389	-7.676			-10.582	0.015
G+N+C+Ni	2.19	0.070	2.99	0.406	-4.071	1.267	-7.958	-8.355	0.018
G+C+Ni	2.86	0.050	4.19	0.392	-6.202	1.245		-9.432	0.011
G+N+Ni	16.89	0.000	4660	0.272	8.090	3.554	-14.424		0.041
G+N	17.11	0.000	5193	0.259	9.600	4.049	-13.649		
G	22.38	0.000	>10000	0.195	8.230	4.487			
G+Ni	23.10	0.000	>10000	0.199	6.950	4.108			0.033
N+Ni	26.36	0.000	>10000	0.165	8.841		-17.608		0.071
N	30.83	0.000	>10000	0.103	11.905		-16.980		
Ni	35.21	0.000	>10000	0.051	7.548				0.066

H) Native cover as response.

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Predictor Coefficients				
					Interc.	Graze	N_{min}/m^2	Ca:Mg	Nickel
N+C+Ni	0.00	0.548	1.00	0.277	-0.321		0.624	-0.349	0.004
G+N+C+Ni	2.17	0.185	2.96	0.268	-0.347	-0.022	0.626	-0.370	0.005
C+Ni	2.57	0.152	3.61	0.241	-0.156			-0.266	0.005
G+C+Ni	4.70	0.052	10.47	0.232	-0.180	-0.020		-0.285	0.005
N+C	6.63	0.020	27.58	0.201	-0.316		0.771	-0.459	
Ni	7.56	0.013	43.85	0.179	0.006				0.006
G+Ni	8.42	0.008	67.52	0.182	0.218	0.066			0.006
N+Ni	8.81	0.007	82.03	0.178	0.208		0.268		0.006
G+N+C	8.84	0.007	83.23	0.19	-0.306	0.008	0.769		
G+N+Ni	9.21	0.005	100.1	0.186	0.191	0.079	0.340		0.006
C	11.10	0.002	257.1	0.141	-0.105			-0.370	
G+C	13.22	0.001	741.8	0.13	-0.088	0.015		-0.036	
G	19.28	0.000	>10000	0.046	0.440	0.132			
G+N	19.33	0.000	>10000	0.059	0.395	0.146	0.445		
N	22.92	0.000	>10000	0.001	0.479		0.324		

I) Native dominance as response.

Model	ΔAIC_C	Akaike weight	Evidence ratio	r^2_{adj}	Predictor Coefficients				
					Interc.	Graze	N_{min}/m^2	Ca:Mg	Nickel
C+Ni	0.00	0.257	1.00	0.299	-1.678			-0.689	-0.003
C	0.77	0.175	1.47	0.281	-1.709			-0.627	
N+C	1.04	0.153	1.68	0.289	-1.761		-0.048	-0.573	
N+C+Ni	1.32	0.135	1.94	0.297	-1.720		-0.034	-0.641	-0.003
G+C+Ni	1.74	0.108	2.38	0.294	-1.614	0.054		-0.640	-0.003
G+C	2.77	0.064	3.99	0.273	-1.672	0.032		-0.595	
G+N+C	3.06	0.056	4.61	0.282	-1.722	0.035	-0.049	-0.537	
G+N+C+Ni	3.14	0.054	4.80	0.292	-1.658	0.053	-0.034	-0.593	-0.003
G+N	14.37	0.000	1317	0.157	-1.032	0.200	-0.088		
G+N+Ni	16.44	0.000	3714	0.147	-0.995	0.209	-0.085		-0.001
G	17.88	0.000	7641	0.105	-0.788	0.229			
G+Ni	19.31	0.000	>10000	0.102	-0.723	0.248			-0.002
N	20.00	0.000	>10000	0.08	-0.985		-0.105		
N+Ni	21.85	0.000	>10000	0.072	-1.043		-0.109		0.001
Ni	27.55	0.000	>10000	-0.013	-0.687				0.000

Table S5. Relative importance of predictor variables for the three sets of models described in Tables 2 and S4 and as coded by shading in Table 3. The relative importance is calculated by summing the Akaike weights of all models in which a given variable is present. A relative importance above 0.5 means that the inclusion of a predictor variable, on average, improves the fit of the model.

Response	Native Richness	Grazing	N_{\min}/m^2	Ca:Mg	Nickel
Exotic richness	0.979	0.990	0.286	0.999	0.241
Exotic cover	0.999	0.275	0.598	0.601	1.000
Exotic dominance	1.000	0.262	0.326	0.754	0.757
Exotic richness		0.786	0.378	1.000	0.205
Exotic cover		0.297	0.787	0.995	0.999
Exotic dominance		0.282	0.396	1.000	0.553
Native richness		0.424	0.550	1.000	0.301
Native cover		0.259	0.772	0.967	0.971
Native dominance		0.282	0.396	1.000	0.552

Table S6. Complete ANOVA results for the vegetation variables at three spatial scales. Significant effects ($p < 0.05$) are in bold. I tested the homogeneity of variance assumption by performing Bartlett's test, as well as by plotting the residuals vs. the estimates of the variable. When Bartlett's test was non-significant and the plotted residuals did not appear heteroscedastic, I assumed that the assumption of homogeneity of variance was met. If not, I applied transformations until these conditions were met. *Denotes that the homogeneity of variance assumption could not be met. $\sqrt{}$ = square root transform, \pm = negative arcsine square root transform. At the 250m² plot size, I was unable to test for Hill and Hill*Aspect effects, as there was no replication of individual aspects within a hill. Sub-table A gives the ANOVA model for the 0.25m² plot size, while Sub-table B gives the ANOVA design for the 250m² plot size. The only random factors are those including Hill or Plot; all others are fixed factors.

A) ANOVA model for 0.25m² scale

Source	Range	Mean Squares (MS)	df	F
Grazing (G _i)	1-2	$\sigma^2_P + 40\sigma^2_H + 80\theta_G$	1	MSG/MSH
Aspect (A _j)	1-4	$\sigma^2_P + 10\sigma^2_{HA} + 40\theta_A$	3	MSA/MSHA
Grazing*Aspect (G*A _{ij})		$\sigma^2_P + 10\sigma^2_{HA} + 20\theta_{GA}$	3	MSG/MSHA
Hill(Grazing) (H _{(i)k})	1-2	$\sigma^2_P + 40\sigma^2_H$	2	MSH/MSP
Hill(Gr)*Aspect (H _(ijk))		$\sigma^2_P + 10\sigma^2_{HA}$	6	MSHA/MSP
Plot (P _(ijkl))	1-10	σ^2_P	144	
Total			159	

B) ANOVA model for 250m² scale

Source	Range	Mean Squares (MS)	df	F
Grazing (G _i)	1-2	$4\sigma^2_H + 8\theta_G$	1	MSG/MSH
Aspect (A _j)	1-4	$5\sigma^2_{HA} + 4\theta_A$	3	MSA/MSHA
Grazing*Aspect (G*A _{ij})		$5\sigma^2_{HA} + 2\theta_{GA}$	3	MSG/MSHA
Hill(Grazing) (H _{(i)k})	1-2	$4\sigma^2_H$	2	
Hill(Gr)*Aspect (H _(ijk))		$5\sigma^2_{HA}$	6	
Total			15	

C) Native richness (0.25m²)*

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	608.4	1	17.278	0.053
Aspect	1693.125	3	10.537	0.008
Aspect x Grazing	462.25	3	2.877	0.125
Hill(Grazing)	70.425	2	8.412	<0.001
Aspect x Hill(Grazing)	321.375	6	12.795	<0.001
Error	602.8	144		

D) Native cover (0.25m²)†

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.206	1	1.186	0.39
Aspect	1.026	3	3.64	0.083
Aspect x Grazing	1.335	3	4.737	0.05
Hill(Grazing)	0.347	2	6.933	0.001
Aspect x Hill(Grazing)	0.564	6	3.757	0.002
Error	3.602	144		

E) Native dominance
(0.25m²)±

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	1.14	1	15.147	0.06
Aspect	4.766	3	6.739	0.024
Aspect x Grazing	3.112	3	4.4	0.058
Hill(Grazing)	0.15	2	2.01	0.138
Aspect x Hill(Grazing)	1.414	6	6.298	<0.001
Error	5.39	144		

E) Exotic richness (0.25m²)*

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.4	1	0.059	0.831
Aspect	37.475	3	4.17	0.065
Aspect x Grazing	15	3	1.669	0.271
Hill(Grazing)	13.525	2	9.896	<0.001
Aspect x Hill(Grazing)	17.975	6	4.384	<0.001
Error	98.4	144		

F) Exotic cover (0.25m²)†

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.621	1	5.769	0.138
Aspect	5.009	3	8.863	0.013
Aspect x Grazing	1.425	3	2.522	0.154
Hill(Grazing)	0.215	2	3.224	0.043
Aspect x Hill(Grazing)	1.13	6	5.639	<0.001
Error	4.811	144		

G) Exotic dominance
(0.25m²)±

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	1.138	1	15.11	0.06
Aspect	4.767	3	6.735	0.024
Aspect x Grazing	3.109	3	4.393	0.059
Hill(Grazing)	0.151	2	2.013	0.137
Aspect x Hill(Grazing)	1.416	6	6.304	<0.001
Error	5.389	144		

H) Total richness (0.25m²)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	570.025	1	42.779	0.023
Aspect	1248.275	3	10.773	0.008
Aspect x Grazing	320.475	3	2.766	0.134
Hill(Grazing)	26.65	2	2.699	0.071
Aspect x Hill(Grazing)	231.75	6	7.825	<0.001
Error	710.8	144		

I) Total cover (0.25m²)†

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.006	1	0.042	0.857
Aspect	1.558	3	7.817	0.017
Aspect x Grazing	0.722	3	3.622	0.084
Hill(Grazing)	0.296	2	5.613	0.004
Aspect x Hill(Grazing)	0.398	6	2.516	0.024
Error	3.801	144		

J) Native richness (250m²)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	16	1	0.719	0.486
Aspect	498.5	3	4.061	0.068
Aspect x Grazing	152.5	3	1.242	0.374
Hill(Grazing)	44.5	2		
Error	245.5	6		

K) Exotic richness (250m²)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	20.25	1	1.906	0.301
Aspect	23.5	3	4	0.07
Aspect x Grazing	7.25	3	1.234	0.377
Hill(Grazing)	21.25	2		
Error	11.75	6		

L) Total richness (250m²)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.25	1	0.015	0.915
Aspect	387.25	3	3.338	0.097
Aspect x Grazing	178.25	3	1.537	0.299
Hill(Grazing)	34	2		
Error	232	6		

Table S7. Complete ANOVA results for the environmental variables. Transformations are denoted alongside each variable. Significant effects ($p < 0.05$) are in bold. For a thorough description of how each variable was measured, see Methods. See Table S6 for the methods of checking the homogeneity of variance assumption. *Denotes that the homogeneity of variance assumption could not be met, but in some cases I transformed the data to minimize deviance from this assumption. Sub-table A gives the ANOVA design. Some models contain fewer degrees of freedom due to missing datapoints. The only random factors are those including Hill or Plot; all others are fixed factors.

A) ANOVA Model

Source	Range	Mean Squares (MS)	df	F
Grazing (G_i)	1-2	$\sigma^2_P + 20\sigma^2_H + 40\theta_G$	1	MSG/MSH
Aspect (A_j)	1-4	$\sigma^2_P + 5\sigma^2_{HA} + 20\theta_A$	3	MSA/MSHA
Grazing*Aspect (G^*A_{ij})		$\sigma^2_P + 5\sigma^2_{HA} + 10\theta_{GA}$	3	MSG _A /MSHA
Hill(Grazing) ($H_{(i)k}$)	1-2	$\sigma^2_P + 20\sigma^2_H$	2	MSH/MSP
Hill(Gr)*Aspect ($H_{(i)jk}$)		$\sigma^2_P + 5\sigma^2_{HA}$	6	MSHA/MSP
Plot ($P_{(ijk)l}$)	1-5	σ^2_P	64	
Total			79	

B) Nmin/g (sqrt)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.004	1	0.056	0.835
Aspect	0.169	3	8.051	0.016
Aspect x Grazing	0.089	3	4.242	0.063
Hill(Grazing)	0.138	2	7.974	0.001
Aspect x Hill(Grazing)	0.04	6	0.768	0.598
Error	0.538	62		

C) Nmin/m² (log10)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.27	1	1.031	0.417
Aspect	5.705	3	11.524	0.007
Aspect x Grazing	1.849	3	3.736	0.08
Hill(Grazing)	0.524	2	3.807	0.028
Aspect x Hill(Grazing)	0.992	6	2.404	0.037
Error	4.265	62		

D) Percent N (log10)*

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.017	1	2.587	0.249
Aspect	0.615	3	9.155	0.012
Aspect x Grazing	0.151	3	2.254	0.183
Hill(Grazing)	0.013	2	1.053	0.355
Aspect x Hill(Grazing)	0.134	6	3.519	0.005
Error	0.407	64		

E) Percent C(log10)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.038	1	0.2877	0.232
Aspect	0.512	3	8.618	0.014
Aspect x Grazing	0.176	3	2.961	0.12
Hill(Grazing)	0.026	2	2.236	0.115
Aspect x Hill(Grazing)	0.119	6	2.961	0.12
Error	0.377	64		

F) P/g(log10)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.002	1	0.06	0.829
Aspect	0.905	3	2.269	0.181
Aspect x Grazing	0.939	3	2.354	0.171
Hill(Grazing)	0.057	2	0.657	0.522
Aspect x Hill(Grazing)	0.799	6	3.052	0.011
Error	2.661	61		

G) P/g(log10, outliers removed)

Source	Sum of squares	df	F-ratio	p-value
Grazing	0.059	1	1.454	0.351
Aspect	0.368	3	3.694	0.081
Aspect x Grazing	0.21	3	2.11	0.2
Hill(Grazing)	0.081	2	0.976	0.383
Aspect x Hill(Grazing)	0.2	6	0.805	0.57
Error	2.395	58		

H) P/m² (log10)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.104	1	1.655	0.327
Aspect	4.887	3	13.463	0.004
Aspect x Grazing	1.532	3	4.221	0.063
Hill(Grazing)	0.125	2	0.848	0.433
Aspect x Hill(Grazing)	0.724	6	1.634	0.153
Error	4.506	61		

I) P/m² (log10, outliers removed)

Source	Sum of squares	df	F-ratio	p-value
Grazing	0.104	1	1.655	0.327
Aspect	4.887	3	13.463	0.004
Aspect x Grazing	1.532	3	4.221	0.063
Hill(Grazing)	0.125	2	0.848	0.433
Aspect x Hill(Grazing)	0.724	6	1.634	0.153
Error	4.506	61		

J) K/g (log10)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	13260.435	1	0.326	0.626
Aspect	456432.496	3	21.134	0.001
Aspect x Grazing	77226.395	3	3.576	0.086
Hill(Grazing)	81433.287	2	6.896	0.002
Aspect x Hill(Grazing)	43193.647	6	1.219	0.308
Error	377898.309	64		

K) Ca/g (negative inverse)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0	1	0.488	0.557
Aspect	0	3	9.77	0.01
Aspect x Grazing	0	3	1.84	0.232
Hill(Grazing)	0	2	27.248	<0.001
Aspect x Hill(Grazing)	0	6	3.18	0.009
Error	0	64		

L) Mg/g (sqrt)

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	695.412	1	20.25	0.046
Aspect	520.858	3	5.587	0.036
Aspect x Grazing	146.791	3	1.575	0.291
Hill(Grazing)	68.683	2	3.41	0.039
Aspect x Hill(Grazing)	186.452	6	3.086	0.01
Error	644.534	64		

M) Ca:Mg (-arcsine(sqrt))*

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0.103	1	3.277	0.212
Aspect	0.065	3	4.857	0.048
Aspect x Grazing	0.052	3	3.875	0.074
Hill(Grazing)	0.063	2	17.851	<0.001
Aspect x Hill(Grazing)	0.027	6	2.537	0.029
Error	0.112	64		

N) Ni/g

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	2432.511	1	0.622	0.513
Aspect	4963.438	3	1.045	0.438
Aspect x Grazing	2053.676	3	0.432	0.738
Hill(Grazing)	7822.959	2	142.734	<0.001
Aspect x Hill(Grazing)	9502.115	6	57.79	<0.001
Error	1753.86	64		

O) June Soil moisture

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	0	1	0.769	0.473
Aspect	0.006	3	5.747	0.034
Aspect x Grazing	0.004	3	4.274	0.062
Hill(Grazing)	0.001	2	3.871	0.026
Aspect x Hill(Grazing)	0.002	6	1.963	0.085
Error	0.01	62		

P) Soil Depth (sqrt)*

ANOVA	Sum of squares	df	F-ratio	p-value
Grazing	4.602	1	3.266	0.212
Aspect	323.667	3	8.778	0.013
Aspect x Grazing	35.445	3	0.961	0.469
Hill(Grazing)	2.818	2	1.18	0.314
Aspect x Hill(Grazing)	73.746	6	10.295	<0.001
Error	76.406	64		