Using plant functional traits to guide restoration: A case study in California coastal grassland

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Abstract. Restoration ecology can benefit greatly from developments in trait-based ecology that enable improved predictions of how the composition of plant communities will respond to changes in environmental conditions. Plant functional traits can be used to guide the restoration of degraded habitats by closely tailoring treatments to the local species pool. We tested this approach in two heavily invaded coastal California grasslands. We asked whether native plant abundance and plant community trait composition respond to (1) experimental soil fertility reduction in the form of twice-yearly carbon (C) amendments and (2) disturbance in the form of mowing. We measured height, specific leaf area, leaf thickness and leaf density from individuals of 39 species in the control and C addition plots, and supplemented these trait values with database information on growth form, lifespan, nitrogen-fixing ability and seed mass.

Consistent with theoretical predictions, C addition favored short, large-seeded and nitrogen-fixing species, while mowing benefitted short species with high specific leaf area. However, native and exotic species did not differ in any of the measured traits, and neither group benefitted generally from the treatments. Carbon addition led to large intraspecific trait shifts, with individuals in C addition plots having smaller, denser leaves and shorter stature. Species' trait plasticity, however, was not related to the community composition response to C addition.

Our study indicates that trait-based ecology is sufficiently mature to provide useful predictions in the realm of restoration ecology. Trait screening at a site can help predict the success of a particular restoration measure in that community.

Key words: California; carbon addition; exotic; grassland; height; mowing; native; nitrogen; seed mass; specific leaf area.

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Introduction

Attempts to restore degraded communities often have mixed success across different systems, even when similar treatments are applied. This is in part because the plant community contexts for these treatments exert important controls over the restoration outcome (Hendrickson and Lund 2010). For example, in systems where native and exotic species are functionally similar, it may be difficult to design restoration treatments that benefit one group over the other

(Levine and D'Antonio 1999, Corbin and D'Antonio 2010). Further, even if native and exotic species do differ in particular traits, restoration treatments may not benefit all native species equally.

Functional traits and trait-based community ecology theory can provide a basis for predicting the success of a restoration treatment in a particular community (Lavorel and Garnier 2002, Pywell et al. 2003, da Silveira Pontes et al. 2010, Roberts et al. 2010), helping to ensure that treatments are applied only where they will be most beneficial. Some research to date has used functional traits to predict species' success in restoration treatments (Pywell et al. 2003, Roberts et al. 2010), with considerable success. For example, Pywell et al. (2003) have shown that seed germination rates and seedling growth rates are both positively associated with species success in sown restorations. These studies have suggested which species are most likely to successfully establish when creating restored communities and indicate, in a general sense, that the relative competitive and colonizing abilities of species may be predicted from their traits. However, little research has addressed how different restoration schemes, mediated by plant traits, can alter these relative abilities. For example, traits that might be advantageous under high-nutrient conditions, such as high seedling growth rates, may be disadvantageous under restored low-nutrient conditions. Such dependencies are predicted based on trait-environment relationships and can have potentially important consequences for restoration success, but have received little testing in a restoration context.

Nitrogen enrichment of terrestrial habitats via atmospheric N deposition (Galloway et al. 1995, Fenn et al. 2003) and invasion of N-fixing plants (Daehler 1998) is a significant component of anthropogenic global change (Vitousek et al. 1997a). Elevated soil N can facilitate the invasion of non-native species and complicate efforts to restore native biodiversity (Maron and Connors 1996, Vitousek et al. 1997b, Perry et al. 2010). In this study, we focus on two strategies designed to restore habitats where species invasion is associated with elevated N inputs (Perry et al. 2010): carbon (C) addition and the mowing and removal of above-ground biomass. Both of these

techniques have been applied in a variety of systems to control non-native species and to favor native biodiversity (Maron and Jefferies 2001, Van Dyke et al. 2004, Blumenthal 2009, Alpert 2010, Perry et al. 2010). Carbon addition is intended to stimulate bacterial growth, leading to immobilization of N in microbial biomass and a temporary decrease in plant-available N (Baer et al. 2003, Averett et al. 2004, Corbin and D'Antonio 2004). Mowing is meant to remove above-ground biomass, thereby reducing the competitive advantage of early-germinating or highly productive species, while removing mowed clippings exports N from the system (Zobel et al. 1996, Wilson and Clark 2001).

Experimental tests of these methods have produced mixed results. While both treatments have been shown to decrease the exotic-to-native ratio in some ecosystems, in others native species have experienced no benefit or those benefits have been limited to a few species (e.g., Maron and Jefferies 2001, Cione et al. 2002, Van Dyke et al. 2004, Blumenthal 2009). A likely explanation for this is that the simple classification of species into "native" and "exotic" categories may provide relatively little functional information. Direct measurement and description of plant strategies may enable better predictions for species responses to these, and other, restoration treatments (Pywell et al. 2003, Eschen et al. 2006).

One useful system for describing plant strategies is based on three major axes quantifying leaf, growth, and reproductive strategies (Westoby 1998). Plant species are arrayed along the leaf axis according to the speed at which they obtain returns on leaf investments (Chapin 1980, Reich et al. 1997, Westoby et al. 2002, Wright et al. 2004). Species with fast returns exhibit relatively rapid turnover of leaf biomass and tend to produce thin, low density leaves with high specific leaf area (SLA) (Wright and Westoby 2000, Westoby et al. 2002, Wright et al. 2004). The growth axis describes the structural characteristics of a plant, of which height is a key indicator. Tall species invest in structural biomass that improves their access to light, while short species can allocate a larger portion of their biomass towards photosynthetically active tissue, which is advantageous when light is readily available (Falster and Westoby 2003). The reproductive strategy axis can be related to seed mass, as

larger-seeded species typically have a higher probability of germinating and can outcompete smaller-seeded species. However, plants that produce large seeds typically produce smaller numbers of seeds, limiting their ability to colonize available microsites (e.g., Turnbull et al. 1999, Henery and Westoby 2001).

We used these three strategy axes to make specific predictions regarding how plant community composition should respond to C addition and mowing. Because C addition reduces N availability, plants that maximize their long-term return on each unit of N obtained should benefit (Poorter and De Jong 1999). This should favor species with slow returns on investments (low SLA, high leaf density, Craine et al. 2001). The ability to fix N is also likely to become particularly valuable under C addition, so N-fixing species are likely to increase in abundance (Table 1). As soil resources become more limiting, competition for light should become less important (Tilman 1984, Knops and Reinhart 2000). Under these conditions, large height and high leaf area, both traits related to light capture ability, should be less advantageous (Knops and Reinhart 2000). Finally, large seed masses contribute to improved seedling success, particularly in nutrient-poor environments (Milberg et al. 1998). With reduced soil N availability, the additional resources provided by a large seed should become more useful (Lee and Fenner 1989, Table 1).

In contrast, mowing and biomass removal in a restoration context should be expected to favor species that display rapid returns on leaf investments, with high SLA and low leaf density (Craine et al. 2001, Cruz et al. 2010). This is because long-term investments in leaves become less advantageous when those leaves are periodically destroyed by mowing. Mowing, like grazing, should also favor annual over perennial species (Hayes and Holl 2003a, Diaz et al. 2007). Short-statured species, which may avoid the mowing treatment altogether, should also benefit (Table 1, Louault et al. 2005, DiTomaso et al. 2007, da Silveira Pontes et al. 2010). Thus, though mowing treatments may be intended to benefit late-germinating species over early-germinating species in many cases, there are other modes by which the treatment can affect species differentially.

A final way that we might predict changes in community composition with restoration treatments is in terms of the flexibility of species' traits in the face of environmental variation. Highly plastic species might be better able to take advantage of a wide range of conditions (Funk 2008, Berg and Ellers 2010, da Silveira Pontes et al. 2010). For example, though a species might have low SLA under ambient conditions, it could respond to mowing by producing leaves with a higher SLA, thereby achieving a more appropriate phenotype for the local environmental conditions. Such a species might obtain higher than expected abundances in mowed plots by virtue of its plastic responses. Though such responses are theoretically well-grounded and potentially important, they have rarely been investigated empirically (Berg and Ellers 2010, da Silveira Pontes et al. 2010).

We tested these predictions in two coastal California grasslands. Exotic species, particularly exotic annual grasses, often enjoy competitive advantages over native California grassland species, and are widespread and abundant (for review see Corbin et al. 2007). Among the mechanisms that have been proposed to explain this competitive dominance are the exotics species' rapid germination and growth that allow them to co-opt light and soil resources (Jackson and Roy 1986, Dyer and Rice 1999, Abraham et al. 2009). Exotic species may also benefit from increases in N availability from nitrogen deposition (Weiss 1999, Fenn et al. 2003) and the invasion of nitrogen-fixing shrubs (Maron and Connors 1996, Haubensak et al. 2004). Both C addition and mowing have been applied in these systems, but without consistent benefits to native species (Alpert and Maron 2000, Maron and Jefferies 2001, Hayes and Holl 2003b, Corbin and D'Antonio 2004). We propose that the success or failure of these measures may depend on the presence or absence of significant functional differences between native and exotic species groups that could drive differential responses to these treatments.

We ask (1) whether community composition, summarized using plant functional traits and trait plasticity, responds as predicted to C addition and mowing and (2) whether native species possess suites of traits that allow them to benefit from C addition and mowing. Together,

Table 1. Functional significance of each trait used in the study, with predicted and measured responses for mowing and carbon addition treatments.

Trait	Functional significance	References	Predicted response		Measured response	
			Mowing	Carbon	Mowing	Carbon
Height	Light capture ability	Knops and Reinhart 2000, Westoby et al. 2002, Louault et al. 2005, Diaz et al. 2007	−	−	−	−
Leaf area	Resource allocation to light capture	Knops and Reinhart 2000, Bragg and Westoby 2002	0	−	NS	+/−
SLA	Speed of return on investment, leaf longevity	Poorter and De Jong 1999, Knops and Reinhart 2000, Westoby et al. 2002	+	−	+	NS
Leaf thickness	A component of SLA, resistance to herbivory	Witkowski and Lamont 1991, Craine et al. 2001, Westoby et al. 2002	−	+	NS	+/−
Density	A component of SLA, tissue nutrient concentrations	Witkowski and Lamont 1991, Craine et al. 2001, Westoby et al. 2002	−	+	−	NS
Seed mass	Seedling advantages, colonization trade-off	Lee and Fenner 1989, Milberg et al. 1998, Turnbull et al. 1999, Henery and Westoby 2001	0	+	NS	+
Lifespan (Annual)	Generation times, population response times	Diaz et al. 2007	+	0	+	NS
Growth form (Grass)	Variation in suites of other traits	Craine et al. 2001	0	0	NS	NS
N fixing	Advantage in low-N environments	Eschen et al. 2006	0	+	NS	+

Notes: SLA stands for specific leaf area, and NS indicates a non-significant treatment effect. For categorical traits (lifespan and growth form) hypotheses and treatment effect directions are given for the named trait state (e.g., Annual). Cases where a community mean trait value were expected or observed to increase are indicated with a "+", expected or observed decreases with a "−" and no prediction with a "0". Where measured treatment effects differed between sites, the treatment effects are given for Point Reyes first, then Tom's Point.

these two components allow a prediction for native species responses, which we test by examining actual responses of native species. This provides an assessment of whether functional traits and trait-based theory can contribute significantly to restoration ecology.

METHODS

Field

This field study was conducted at two coastal California grassland sites: the Pierce Point Ranch at Point Reyes National Seashore (38°11 N, 122°57 W), and Tom's Point (38°13 N, 122°57 W), a private nature reserve owned by Audubon Canyon Ranch. Both sites are dominated by exotic species, most notably the grasses *Holcus lanatus*, *Lolium perenne* and *Bromus diandrus*, but Tom's Point retains a greater native component than the Point Reyes site (taxonomy follows Hickman 1993). The two sites have been free from livestock grazing for at least 35 years,

though the Point Reyes site is visited frequently by native tule elk (*Cervus elaphus nannodes*). Soils at both sites may be N-enriched for two reasons. Each site has scattered individuals of *Lupinus arboreus*, a native shrub that has been shown to increase soil N in coastal California grasslands (Maron and Connors 1996). In addition, coastal California sites in this region receive approximately 5–7 kg/ha/year wet and dry N deposition (Fenn et al. 2003, Weiss 2006).

In 2005, we established 16 replicate mowing plots, 16 carbon addition and 16 control plots at each site. Plots were 5 × 5 m at Point Reyes and 4 × 4 m at Tom's Point, because of space limitations. Beginning in October 2005 and every six months thereafter, we applied the carbon addition treatment to the appropriate plots. Carbon was added as sucrose at 450 g/m^2 (189.5 g C/m^2), except the original application, which was 170 g sucrose/m^2 and 360 g sawdust/m^2 (approximately 240 g total C/m^2). Sucrose is the most widely used C source in such experi-

ments because it is readily available and enters the soil quickly, and this application rate is within the range of commonly used rates, based on a review of 55 studies of C addition (Alpert 2010). Plots in the mowing treatment group were mowed to ~10-cm height each spring in late March or early April and all clippings were removed from the plots. Half of the plots of each treatment type also received a mix of native grass seed each fall. Germination rates of these seeds were extremely low, and seed addition plots were lumped with unseeded plots in the following analyses.

We sampled the plant community at the end of the growing seasons of 2006–2009 (primarily in June, including sampling in late May or early July in some years). We assessed the presence or absence of all plant species within 16 50×50 cm subplots in the central 4 m^2 of each treatment plot. In addition, in the summers of 2008 and 2009, we estimated the percent cover of each plant species occurring in the middle four subplots. This allows two measures of a species' abundance within a plot: 1) a spatial prevalence measure, the occurrence frequency of the species in the 16 subplots, and 2) the relative abundance of the species, based on percent cover estimates. We also estimated the percentage of bare ground in the middle 1×1 m of each treatment and control plot in 2009. Finally, in 2008 and 2009, we counted the number of flowering stalks of each native grass encountered in the survey.

On March 31, 2006, shortly after the spring C addition, we collected three 15-cm deep, 2-cm diameter soil cores from carbon-treated and control plots, to assess N pools and net N mineralization rates. We bulked the samples, extracted half of each soil sample immediately with 2 M KCl, and incubated the other half in the lab for 14 days. Then, we extracted the remaining soil samples with 2M KCl. All extracts were analyzed for NO_3 and NH_4 concentrations by the UC Davis Agriculture and Natural Resources Analytical Lab using the flow injection analyzer method. Net N mineralization rate was calculated as the amount of $NH_4 + NO_3$ in incubated soils minus the amount in soils extracted immediately.

In July 2006, we clipped all standing biomass from two 50×50 cm squares within half of the treatment plots at each site (n = 8). We repeated this sampling in July of 2008 and 2009, except that clipping was done in two 25×25 cm squares in all plots (n = 16). We then dried and weighed these samples.

We eliminated one plot from all analyses (a control plot from Point Reyes) that was, by the end of the study, nearly completely covered by a very large *L. arboreus* shrub.

Trait sampling and composition

Between April and June, 2009, we collected data on plant functional traits. For species that were sufficiently abundant, we sampled one individual from each C addition treatment and control plot at each site. Mowed plots were not sampled, because the destruction of leaves by mowing made measuring leaf traits problematic. We sampled the first mature individual of each species encountered in a search beginning from a random corner of each plot. In this ideal case, we obtained 16 representatives of a species from each site for two treatments, for a total of 64 samples. However, many species were not present in all plots. In such cases, we took samples from up to two individuals from each plot where the species could be found, in order to come as close as possible to the goal of obtaining 64 samples per species.

We measured the height of the highest photosynthetic surface from each individual, and collected one fully-expanded, green, leaf. We measured the thickness of the leaf lamina using a high-precision caliper, avoiding any major leaf veins. Each leaf was stored, refrigerated, for at most 24 hours. We photographed each leaf flattened against a white background and determined the surface area of each leaf using ImageJ (Rasband 2009). Leaves were oven-dried at 50°C for at least 48 hours, then weighed individually to a precision of 0.01 mg. In addition to directly measuring height, leaf thickness, leaf area and leaf mass values, we calculated specific leaf area (leaf area per unit mass) and leaf density (leaf mass per unit area, divided by leaf thickness). For each species and each trait, we then calculated a species mean trait value from all control plot samples, all C addition plot samples, and all samples combined. Trait values based on all samples were used for calculating plot mean trait values (below), while control- and C addition-specific values were used to assess

trait plasticity. All quantitative trait values were log-transformed prior to analysis.

Species were also classified according to several categorical traits, including growth form (graminoid or not), lifespan (annual or not), nitrogen fixing ability and origin (native or exotic). Finally, we supplemented these data with data on species' mean seed sizes from the Kew Gardens Seed Information Database (Liu et al. 2008); most seed size data for the Californian species in this database are originally from Baker (1972).

To summarize shifts in community composition with the restoration treatments, we used weighted community trait means (Garnier et al. 2004). These community trait means were calculated by taking the mean trait value of all species occurring within a plot, weighted by each species' abundance within the plot. Two kinds of abundances were used. The first was the spatial prevalence measure, the proportional occupancy of a species within 0.25 m^2 subplots within the sampling plot. The second was the relative abundance measure based on visual estimates of percent cover for all species, taken in 2008 and 2009.

Analysis

Plot-level responses were assessed using repeated-measures ANOVA, with site and treatment as fixed factors. Three measures (percent bare ground, inorganic N pool and net N mineralization rate) were available only for a single year, so a simple ANOVA was used in these cases. In this manner, we assessed how the restoration treatments affected N pools, net N mineralization, bare ground, aboveground biomass, the abundance of native species (using both spatial prevalence and relative abundance measures) and community mean trait values for each trait. For categorical traits, plot mean trait values were square root-arcsine transformed prior to analysis. For all of the following tests, C addition-control comparisons were conducted independently of mow-control comparisons, because the comparison of C addition to mowing treatments was not of particular interest to us.

We tested for overall differences between species mean trait values of native and exotic species. Considering one trait at a time, we performed t-tests comparing the trait means of native species to exotic species. For categorical traits, we instead performed a chi-squared test. In addition, we tested for multivariate differences between native and exotic trait means using the multi-response permutation procedure (MRPP, Mielke and Berry 2001).

We also examined how species' traits differed between control and C addition plots. For each species and trait, we calculated a treatment effect size (plasticity treatment effect size, PTES) by taking the difference between that species' log mean trait value in carbon plots and the log mean value in control plots. We used only species with measurements from at least two individuals in each plot type. For each trait, we then performed a one-sample t-test to determine whether these PTES differed collectively from zero. For example, a significantly negative PTES for a trait indicates that species generally had reduced values for a particular trait in C addition plots compared to control plots.

We investigated whether species with higher trait plasticity (PTES) performed differently from those with low plasticity. These tests were analogous to the repeated-measures ANOVAs described above, but used PTES for each trait and each species (rather than trait means) to calculate plot means. If no species within a plot showed trait shifts with C addition, or a plot contained equal abundances of species whose traits shifted with C addition in each direction, the plot mean plasticity would be zero. On the other hand, if plots contained mostly species whose trait values (for a particular trait) decreased with C addition, the plot mean would be negative.

Responses of individual species to C addition and mowing were assessed using a Monte Carlo permutation test. For each species, we took the mean occurrence frequency of that species in 50×50 cm subplots within a particular site and treatment. We then randomly shuffled treatment labels among plots within each site and recalculated these mean occurrence rates. We ranked the observed rate for the species against rates derived from 5000 random shuffles. This provides a distribution-free test of the effect of the treatments on each species' abundance.

RESULTS
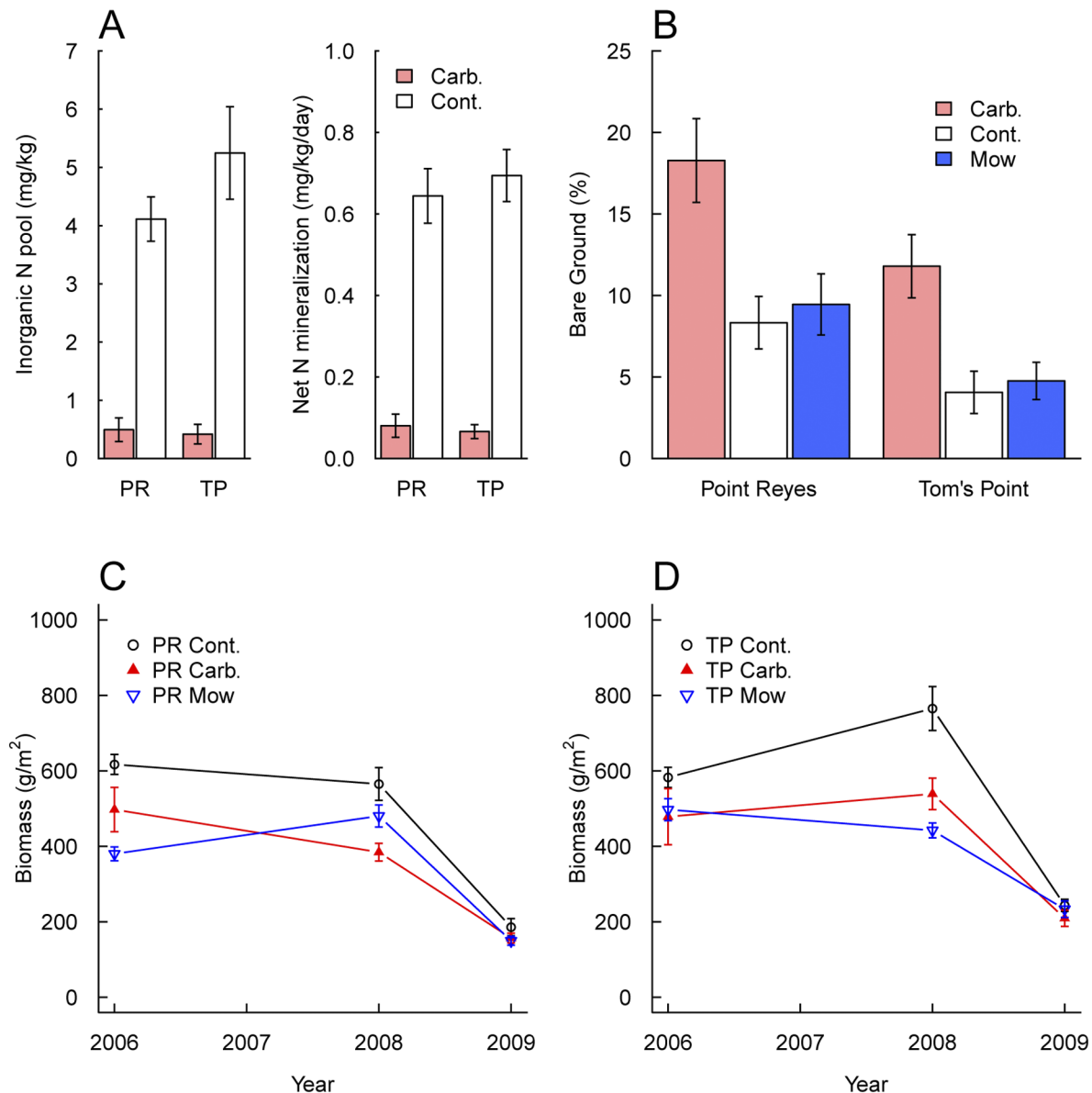
Carbon addition reduced standing pools of

Fig. 1. Responses (mean ± s.e.) of soil inorganic N amd net nitrogen mineralization rate (A), vegetative cover (B) and biomass at Point Reyes (C) and Tom's Point (D) to restoration treatments. Carbon addition greatly reduced standing N pools, N mineralization rates, increased bare ground and decreased plant biomass. Mowing reduced biomass, but had no effect on bare ground cover.

inorganic N and net N mineralization rates in soils at both sites by approximately 90% ($F_{1,27} = 81.5$, $P < 0.0001$, $F_{1,27} = 147.6$, $P < 0.0001$, Fig. 1A). This reduction led to a decrease in productivity in these plots, with C addition plots typically showing 20–30% reductions in aboveground biomass ($F_{1,27} = 13.0$, $P = 0.0012$, Fig. 1C, D). In 2009, there was 2.5 fold increase in bare ground in C addition plots relative to control plots ($F_{1,59} = 25.0$, $P < 0.0001$, Fig. 1B). Mowing decreased aboveground biomass at the end of the growing season by 5 to 40% relative to controls ($F_{1,27} = 30.9$, $P < 0.0001$, Fig. 1C, D) but had no significant effect on the percentage of bare ground ($F_{1,60} = 1.0$, $P = 0.33$, Fig. 1B). Productivity in 2009 was unusually low, and both
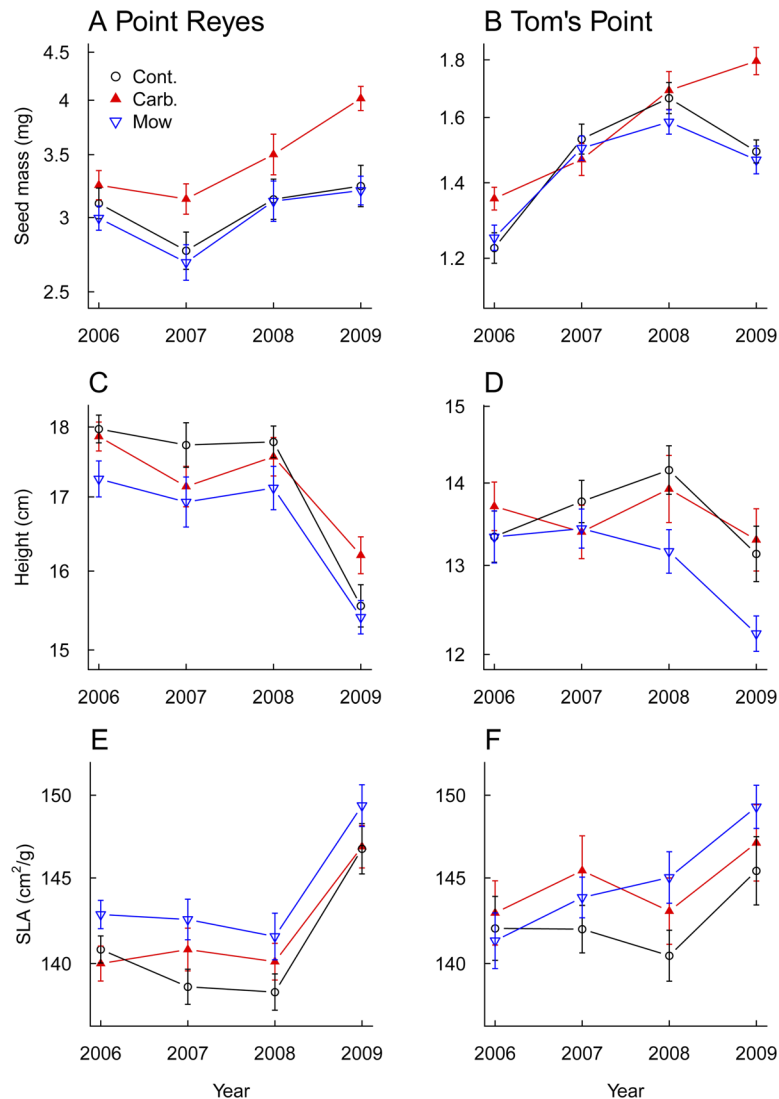
Fig. 2. Shifts in community trait composition induced by restoration treatments. Trait data are community trait means (means ± s.e.), weighted by each species' occupancy rate within the plot. Mowing favored shorter species (A, B) and species with high specific leaf area (E, F). Carbon addition favored large-seeded species (C, D).

treatments produced very small reductions in productivity in that year (treatment-by-year interactions $P < 0.05$). Here and throughout, interactions of site or year with treatment are not noted unless they were significant.

Community trait composition

The restoration treatments produced directional shifts in community composition along all trait axes. Carbon addition led to an increase in plot mean seed mass relative to control plots ($F_{1,59} = 9.1$, $P = 0.0038$, Fig. 2). This was especially true at

Point Reyes, with increasingly strong effects through time (treatment-by-year interaction, $F_{3,185} = 9.5$, $P < 0.0001$). At Point Reyes, C addition favored thick- and large-leaved species, while at Tom's Point, thin-, small-leaved species benefitted (treatment-by-site interaction: thickness, $F_{1,59} = 4.4$, $P = 0.0400$, area, $F_{1,59} = 4.7$, $P = 0.0344$, Fig. 2). In some years, C addition produced a shift towards shorter species (treatment-by-year interaction, $F_{3,177} = 4.3$, $P = 0.0056$).

Mowing produced a decrease in plot mean height ($F_{1,59} = 6.3$, $P = 0.0145$) and an increase in
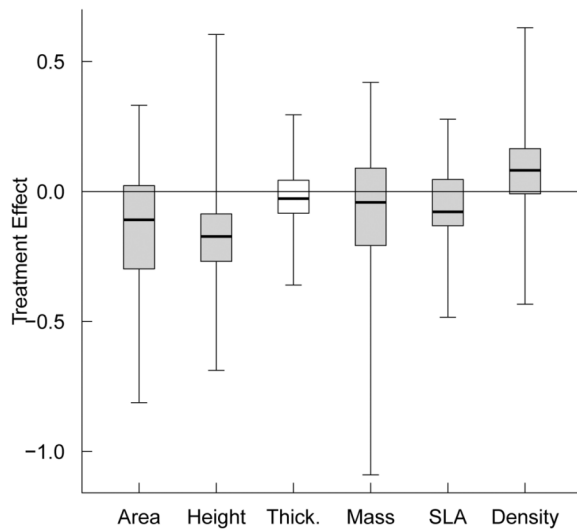
Fig. 3. Intraspecific trait shifts induced by carbon addition. For each species and each trait, the treatment effect size is the species' log mean trait in control plots minus the log mean trait in carbon addition plots. For a particular trait, the heavy bar shows the median treatment effect size across 39 species, while the box shows the 25% and 75% quantiles and the whiskers show the extreme values. Traits for which treatment effects differed collectively from zero are shaded grey.

mean SLA ($F_{1,59} = 5.1$, $P = 0.0272$) that tended to become more pronounced through time (year-by-treatment interaction $F_{3, 177} = 2.7$, $P = 0.0464$, Fig. 2). This change in SLA was caused by an increase in species with low-density leaves ($F_{1,59} = 4.8$, $P = 0.0325$), rather than thinner leaves ($P > 0.6$).

Neither the total abundance of annual species nor grasses changed with C addition for either occurrence-based ($P > 0.45$) or cover-based analyses ($P > 0.30$). Nitrogen-fixing plants responded positively to C addition ($F_{1,59} = 20.1$, $P < 0.0001$). This effect became increasingly apparent through time (treatment-by-year interaction $F_{3, 177} = 6.1$, $P = 0.0005$), and was particularly strong at Point Reyes (treatment-by-site interaction $F_{1,59} = 5.7$, $P = 0.0206$). Annual abundance increased in mowed plots relative to controls, particularly in the third and fourth year of the experiment (year-by-treatment interaction $F_{3, 177} = 3.3$, $P = 0.0225$).

Traits of individual species were plastic in response to C addition. Plants growing in C addition plots tended to have smaller individual leaf area ($t_{38} = -3.6$, $P = 0.0010$), leaf mass ($t_{38} = -2.1$, $P = 0.0461$) and SLA ($t_{38} = -2.2$, $P = 0.0349$), reduced height ($t_{38} = -4.8$, $P < 0.0001$), and higher leaf density ($t_{38} = 2.9$, $P = 0.0066$, Fig. 3). However, the magnitude of species' trait plasticity did not predict their response to C addition for any of the quantitative traits we considered.

Native and exotic species did not differ significantly in mean values for any of the quantitative species traits ($P > 0.05$), nor were they separable in multivariate space ($P > 0.49$). Native species were not more or less likely than exotic species to be grasses or N fixers ($P > 0.1$), but were more likely to be perennial ($\chi^2 = 10.7$, $P = 0.0011$).

Consistent with the absence of trait differences between native and exotic species, neither C addition ($P > 0.71$) nor mowing ($P > 0.33$, Fig. 4A, B) changed the relative abundance of native species as a group, calculated from either occurrence frequencies or percent cover. However, detailed stem counts of native grasses at Tom's Point did reveal a positive response of *Bromus carinatus* ($F_{1,30} = 4.0$, $P = 0.054$) and *Danthonia californica* ($F_{1,30} = 6.8$, $P = 0.014$) to C addition, and a tendency for *B. carinatus* ($F_{1,30} = 3.8$, P = 0.060) to increase with mowing (Fig. 4C). There were no effects of treatments on native grass stem counts at Point Reyes ($P > 0.1$), largely because native grasses were very rare at this site.

Species-specific responses

Species responses to the C addition ranged from strongly positive to strongly negative. At Point Reyes, species that increased include the native N-fixer *Lupinus bicolor* and exotic N-fixers *Trifolium subterraneum* and *Vicia sativa* Species that strongly decreased in abundance included *Bromus hordeaceus* and *Geranium dissectum*, an exotic annual grass and forb, respectively. At Tom's Point, increasing species included the native forb *Eschscholzia californica*, native perennial grass *Danthonia californica* and native N-fixers *Lupinus bicolor* and *Trifolium microdon*. Some exotic species benefitted from C addition as well, including the exotic annual grass *Bromus diandrus*, exotic perennial grass *Festuca arundinacea* and exotic forb *Erodium botrys*. *Pteridium aquilinum*, a native fern, and *Rumex acetosella*, an exotic forb, decreased notably with C addition at
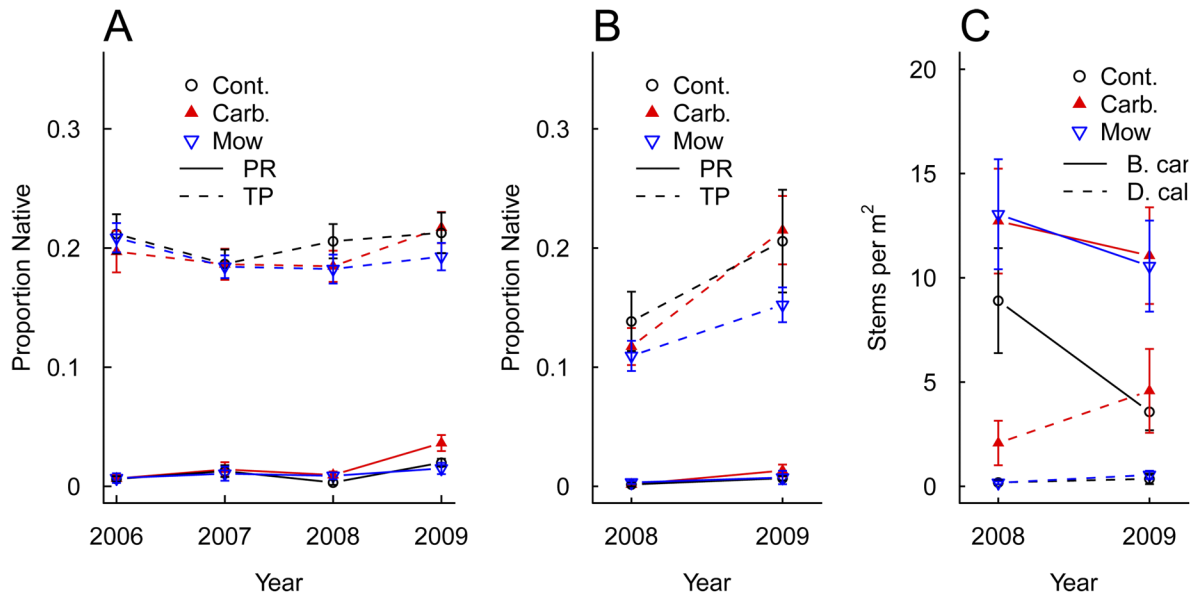
Fig. 4. Responses (mean ± s.e.) of native species to restoration treatments. Neither mowing nor carbon addition increased native abundance at either site, measured as either occurrence rates (A) or percent cover (B). However, detailed counts of stems of native grass species did reveal positive responses of some species to the treatments (C). *Bromus carinatus* increased with both mowing and C addition, while *Danthonia californica* benefitted only from C addition.

Tom's Point (see the Appendix).

Several species showed strong responses to mowing. *Rumex acetosella* increased with mowing at both sites, as did the exotic forb *Hypochaeris radicata* and exotic annual grass *Vulpia myuros*. *Geranium dissectum* increased strongly with mowing at Point Reyes. At Point Reyes, the native forb *Oxalis albicans* tended to decline with mowing, while the native forb *Achillea millefolium* L. declined at Tom's Point (Appendix).

Discussion

Carbon addition successfully decreased soil N cycling rates, and both treatments reduced above-ground biomass, as intended. Previous tests of these strategies in California grasslands and in other systems have yielded similar effects (reviewed in Alpert 2010, Perry et al. 2010).

Community trait composition

Our hypotheses for the directions of trait shifts were largely upheld, supporting the utility of functional traits in predictive screening for restoration treatments. Consistent with an in-creased importance of seed provisioning in low-nutrient environments, C addition favored large-seeded species. Nitrogen-fixers were also able to benefit from C addition, as their ability to obtain atmospheric nitrogen directly became more valuable as soil nitrogen was reduced. The increase in bare ground in C addition plots suggests that light competition may have become less important in these plots, as hypothesized, leading to the observed increases in short-statured species. Mowing, on the other hand, favored short, annual species, which are better able to either avoid or rapidly recover from destruction (Diaz et al. 2007, DiTomaso et al. 2007). Thin, low density leaves are cheaper to produce, reducing the cost to the plant when those leaves are lost to mowing (Craine et al. 2001). Thus, we detected an increase in species with high SLA. Our ability to correctly predict these responses indicates that our understanding of plant functional strategies is sufficiently mature to facilitate improved restoration decisions.

However, not all traits responded as predicted. The effects of C addition on certain leaf charac-

teristics that we had predicted to be important were weak or inconsistent across sites. We hypothesized that low-SLA species should benefit from C addition (Table 1), but observed no change in community composition in SLA. Leaf thickness, a trait that is closely related to SLA, showed the expected increase at Point Reyes but decreased at Tom's Point. In contrast, leaf area, a trait we expected to decrease with C addition, showed the expected response at Tom's Point, but the opposite response at Point Reyes. One possible explanation for this is that leaf thickness and area are well-correlated among species at our sites (r = 0.702). Thus, while C addition would be expected to favor small, thick leaves, the absence of species with this trait combination may have constrained the observed response. At Tom's Point, the decrease in leaf thickness with C addition may have been driven by an advantage of species with small leaf sizes despite a disadvantage of thin leaves, while the reverse occurred at Point Reyes. Our results suggest that height, seed mass and N-fixing ability, not leaf traits, are the most consistent predictors of response to C addition. Predictions of response to mowing, however, are improved when leaf traits are included.

Surprisingly, intraspecific trait variation and trait plasticity were not predictive of species' responses to C addition (McLendon and Redente 1992). Previous work (Berg and Ellers 2010, da Silveira Pontes et al. 2010) has suggested that species with more plastic traits should be able to occupy a wider range of conditions along abiotic gradients. While we did find large responses of species traits to C addition, variation among species in this response appeared not to drive community-level responses to treatments.

Carbon addition and mowing as restoration measures

Neither mowing nor carbon addition caused a consistent increase in native plant abundance. Though particular native species did benefit from the treatments, their gains were offset by reductions in the abundance of other native species. Thus, we do not recommend the widespread use of these restoration treatments without careful assessment of whether the treatments are appropriate to the target community. Our failure to detect general benefits for native species contrasts with some previous results (McLendon and Redente 1992, Zink and Allen 1998, Alpert and Maron 2000, Averett et al. 2004, Prober et al. 2005, Blumenthal 2009, Perry et al. 2010), but may be expected in systems like coastal Californian grasslands, where functional differences between some native and exotic species are small (Corbin and D'Antonio 2010). The utility of C addition and mowing as restoration measures depends on the existence of substantial functional differences between native and exotic species that could drive differential responses of the two groups. These conditions might be met in Midwestern prairies where the native prairie species are often slow-growing relative to exotic species (Averett et al. 2004), or when the native and exotic species represent clearly distinct functional groups, such as shrubs and grasses (Zink and Allen 1998). At our sites, native and exotic species were not well separated along functional trait axes, so it is not surprising that neither treatment benefited native species as a group.

Those native species that did benefit, however, tended to possess traits that we predicted would be advantageous. For example, *Danthonia californica* (which increased with C addition) is short, with low SLA, high leaf density and small leaves. *Lupinus bicolor*, one of the species with the strongest positive responses to C addition, is a large-seeded N-fixer. Considering the responses of particular exotic species to the mowing treatment, *Geranium dissectum*, a short, annual forb with high SLA and *Vulpia myuros*, a short, annual grass with small, thin leaves and small seeds, showed the strongest positive responses. Thus, it is possible to use functional trait-based predictions not only for species groups, but to predict the responses of particular species within groups. This should be useful to managers who wish to make more specific predictions regarding, for example, how particular rare native species or particular noxious exotic species might respond to restoration.

Interannual variability in plot mean trait values was substantial, even in control plots. This is unsurprising, given California's highly variable climate and the potential for high turnover in the annual portions of these communities (Reever Morghan et al. 2007). 2008–2009 stands out as a particularly unusual year, with a

relatively late start to the growing season and low productivity. Species with low average height and high SLA may have benefitted from the climatic conditions in that year in a way that they did not in seasons with other climatic conditions, because of their ability to rapidly obtain returns on growth investments. Though little studied, efforts to restore habitats with high inter-annual climatic variability may be further complicated by variation in the effects of specific restoration methods depending on climate (Vaughn and Young 2010; G. F. Hayes and K. D. Holl, *unpublished manuscript*).

These results contribute to our understanding of the basic mechanisms by which mowing and C addition alter community composition, thereby increasing their utility as restoration methods. Though we detected no increase in native species abundance in response to either treatment, our results indicate the conditions under which one would expect to observe such increases. There are, however, other problems with the large-scale implementation of these restoration strategies that may make their application difficult, even in suitable communities. Sucrose is expensive, and while sawdust may provide a cheaper C source, its low density makes it difficult to spread the necessary quantities over a larger area. Further, the reduction of soil N by C addition is temporary (Sandel 2010), and it remains to be seen how long community changes induced by C addition last after treatments cease. Despite these challenges, though, C addition does hold promise in small-scale restoration projects if the community trait context is suitable (Alpert 2010, Perry et al. 2010).

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APPENDIX

Table A1. Prevalence rate of all species at Point Reyes, summarized by site and treatment, with permutation test results for treatment effects.

Species	Carbon	Control	Mow	Rank Carb.	Rank Mow
Agrostis stolonifera	0.009	0.044		0.281	0.059
Aira caryophyllea	0.006	0.009	0.025	0.278	0.849
Anagallis arvensis	0.185	0.170	0.220	0.744	0.911
Avena barbata	0.080	0.069	0.057	0.525	0.438
Baccharis pilularis			0.001		0.754
Briza maxima	0.045	0.015	0.011	0.849	0.380
Briza minor		0.001		0.251	0.251
Bromus carinatus	0.001	0.002	0.007	0.304	0.891
Bromus diandrus	0.996	0.995	0.998	0.612	0.807
Bromus hordeaceus	0.352	0.559	0.532	0.056	0.411
Carduus pycnocephalus	0.047	0.030	0.058	0.703	0.791
Cirsium vulgare	0.001	0.001	0.002	0.506	0.696
Claytonia perfoliata			0.001		0.742
Cynosurus echinatus	0.009	0.004	0.008	0.842	0.744
Erodium botrys	0.196	0.180	0.251	0.696	0.914
Erodium cicutarium		0.001		0.245	0.252
Geranium dissectum	0.355	0.500	0.675	**0.014**	**0.988**
Holcus lanatus	0.115	0.176	0.233	0.263	0.722
Hordeum brachyantherum	0.019	0.020	0.027	0.474	0.512
Hordeum murinum	0.376	0.367	0.477	0.544	0.850
Hypochaeris glabra	0.025	0.046	0.052	0.110	0.612
Hypochaeris radicata	0.008	0.003	0.011	0.866	0.957
Lolium perenne	0.757	0.721	0.720	0.729	0.504
Lupinus arboreus	0.002	0.019		0.367	0.250
Lupinus bicolor	0.099	0.026	0.039	**1.000**	0.878
Marah fabaceus	0.001	0.003		0.377	0.249
Medicago polymorpha	0.003	0.005	0.009	0.231	0.704
Oxalis albicans	0.019	0.031	0.009	0.247	0.071
Plantago lanceolata	0.005		0.003	0.874	0.945
Ranunculus californicus			0.001		0.750
Raphanus sativus	0.816	0.787	0.828	0.806	0.913
Rubus ursinus	0.001	0.002		0.310	0.121
Rumex acetosella	0.890	0.833	0.903	0.899	0.960
Silene gallica	0.042	0.062	0.073	0.202	0.657
Sonchus asper	0.001	0.008	0.016	0.037	0.859
Trifolium subterraneum	0.116	0.038	0.075	0.919	0.722
Triphysaria pusilla	0.000	0.000	0.000		
Vicia hirsuta	0.034	0.028	0.018	0.578	2.000
Vicia sativa	0.734	0.588	0.566	**0.999**	0.361
Vulpia myuros	0.956	0.964	0.986	0.390	0.822

Notes: The abundance shown is the proportion of 0.25 m^2 plots occupied by each species, across all years within the site and treatment. The permutation rank shows the results of the Monte Carlo permutation test, in which treatment effects were assessed by randomly scrambling treatment labels among plots at each site. The value shows the proportion of random permutations in which the observed abundances in the named treatment exceeded the randomly generated abundance. Values greater than 0.975 indicate significant increases in the treatment relative to the control, while values less than 0.025 indicate significant decreases, at $\alpha = 0.05$. For clarity, species with no occurrences within a site and treatment are left blank.

Table A2. Prevalence rate of all species at Tom's Point, summarized by site and treatment, with permutation test results for treatment effects.

Species	Carbon	Control	Mow	Rank Carb.	Rank Mow
Achillea millefolium	0.043	0.063	0.009	0.308	0.057
Aira caryophyllea	0.553	0.615	0.770	0.241	0.964
Anagallis arvensis	0.348	0.286	0.364	0.797	0.909
Avena barbata	0.038	0.002		0.921	0.249
Baccharis pilularis	0.045	0.079	0.053	0.190	0.250
Briza minor	0.038	0.032	0.045	0.543	0.663
Bromus carinatus	0.584	0.458	0.659	0.893	**0.981**
Bromus diandrus	0.789	0.646	0.580	0.974	0.203
Bromus hordeaceus	0.930	0.870	0.974	0.855	**0.993**
Carduus pycnocephalus	0.137	0.223	0.326	0.072	0.935
Carex sp.	0.394	0.456	0.315	0.214	**0.021**
Cirsium vulgare	0.002	0.020	0.019	**0.021**	0.483
Claytonia perfoliata	0.001			0.748	
Cynosurus echinatus	0.004			0.877	
Danthonia californica	0.098	0.028	0.020	0.969	0.253
Daucus pusillus	0.188	0.133	0.229	0.729	0.827
Elymus glaucus	0.341	0.444	0.393	0.145	0.271
Erodium botrys	0.100	0.031	0.063	**0.995**	0.899
Eschscholzia californica	0.099	0.025	0.060	**0.991**	0.955
Festuca arundinacea	0.045	0.002	0.017	**0.976**	0.951
Galium aparine		0.004	0.001	0.058	0.147
Geranium dissectum	0.583	0.753	0.729	**0.002**	0.267
Gnaphalium purpureum	0.003	0.001	0.006	0.753	0.634
Heracleum lanatum		0.003	0.001	0.250	0.372
Holcus lanatus	0.924	0.967	0.989	0.176	0.741
Hordeum murinum		0.001		0.251	0.244
Hypochaeris glabra	0.325	0.249	0.381	0.862	0.966
Hypochaeris radicata	0.603	0.501	0.700	0.866	**0.992**
Lactuca serriola		0.003		0.057	0.055
Linum bienne	0.063	0.018	0.004	0.686	0.367
Lolium perenne	0.646	0.696	0.729	0.341	0.606
Lupinus arboreus	0.002	0.003	0.002	0.356	0.370
Lupinus bicolor	0.096	0.039	0.069	**0.983**	0.956
Marah fabaceus	0.001	0.001		0.499	0.251
Medicago polymorpha	0.003			0.943	
Monardella villosa	0.021	0.026	0.030	0.370	0.566
Oxalis albicans	0.207	0.162	0.123	0.720	0.217
Phalaris aquatica	0.001		0.007	0.751	0.943
Plantago lanceolata	0.363	0.472	0.510	0.119	0.659
Pteridium aquilinum	0.160	0.342	0.218	**0.014**	0.075
Ranunculus californicus	0.017	0.033	0.037	0.152	0.600
Rubus ursinus	0.414	0.597	0.545	0.102	0.369
Rumex acetosella	0.921	0.987	0.997	**0.007**	0.971
Silene gallica	0.141	0.055	0.037	0.882	0.352
Sisyrinchium bellum	0.009	0.006	0.002	0.568	0.370
Sonchus asper	0.001	0.009	0.009	0.039	0.505
Trifolium albopurpureum	0.004	0.011	0.003	0.125	0.053
Trifolium bifidum	0.008	0.003	0.003	0.878	0.492
Trifolium microdon	0.042	0.006	0.011	0.994	0.794
Triphysaria pusilla	0.040	0.009	0.020	0.784	0.564
Vicia sativa	0.839	0.806	0.798	0.800	0.428
Vulpia myuros	0.902	0.941	0.979	0.095	**0.974**

Note: See notes to Table A1 for details.