BIODIVERSITY AND STABILITY IN QUARRY RESTORATION
FINAL REPORT:

DIVERSITY AND RESISTANCE TO SIMULATED CLIMATE CHANGE

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Paul Richardson and Douglas W. Larson
Cliff Ecology Research Group
Department of Integrative Biology
University of Guelph

EXECUTIVE SUMMARY

1. Environmental fluctuations are intensifying globally, demanding that managers design perturbation resistance directly into anthropogenic ecosystems undergoing restoration; however, uncertainty over determinants of stability in different contexts limits such applications.

2. We hypothesized that in high-stress ecosystems emergent effects of species co-occurrence including facilitation enhance resistance, and tested this hypothesis by introducing native rock-barren plant species to abandoned limestone quarry floors in a design isolating co-occurrence from sampling effects by contrasting groups of communities differing in species number but not average species composition.

3. Diversity treatments were crossed with controlled installation of polycarbonate domes over plot communities to simulate severe drought and heat-wave conditions.

4. Strikingly, while low- and intermediate-diversity communities suffered steep cover losses under climate-change structures relative to watered controls, maximum-diversity communities remained completely unaffected.

5. Analysis of population patterns suggests multiple mechanisms including facilitation, complementarity, and compensation are responsible for diversity-enhanced community resistance, and thus potentially applicable to reconstructing stable ecosystems.

6. Implications of our results allow us to make several recommendations to managers of high-stress anthropogenic environments in general, and to managers of limestone quarry after-use in particular. First and foremost, we recommend that quarry managers ensure the stability of restored communities - whether mimicking natural alvars or an alternative target ecosystem - by introducing and facilitating establishment a broad diversity of target species. As stabilizing effects of biodiversity in our study were attributable to the *number* above and beyond the *identity* of species established, beneficial outcomes of introducing highly diverse species assemblages are unlikely to be replicated by focusing on just a few *particular* species.

7. Patterns of relationships between the resistance of individual species and the diversity of species comprising communities are consistent with both mechanisms relying upon competition among species, and different mechanism relying upon facilitation among species. This indicates that targeting high diversity without attempting to replicate particular species interactions may be the most appropriate approach for practical "on-the-ground" quarry restoration. Precise control of complex interactions may be impossible or impractical, but managers can "set the stage" for multiple potential interactions to play out, and allowing for such a diversity of stabilizing mechanisms to operate may itself produce robust and predictable species diversity-stability patterns.

8. Some of the alvar species introduced were certainly better colonizers of quarry floors than others; however five of the six best-performing species required the presence of

diverse neighbour species to realize their full functional potential, suggesting that targeting high diversity is necessary for effective population as well as community restoration. Best-performers included the wildflowers *Coreopsis lanceolata*, *Rudbeckia hirta*, *Solidago ptarmicoides*, and *Penstemon hirsutis*, and the grasses *Panicum virgatum* and *Elymus trachycaulus*.

9) Recommended methods and goals of quarry-to-alvar recommendations are provided, including substrate amendment strategies and suggested complementary addition of seeds and plant plugs directed toward achieving particular biodiversity targets.

10) Directions for critical future research are provided, primarily concerned with discovering and adopting new knowledge about biodiversity-stability relationships to achieving large-scale "on-the-ground" quarry-to-alvar restoration. The focus of this research will be on the role of scale on the application of alvar biodiversity to ecosystem functioning on quarry floors, from effects of spatial and temporal scales to effects of the different aspects of biodiversity considered and the variety of natural ecosystems represented, from alvar pavement to cliff-face, calcareous fen, and tallgrass prairie. Importantly, this research could be conducted through coupling of experimental design with adaptive management of quarry-to-alvar demonstration projects.

INTRODUCTION
General introduction
Effective management of ecosystems in human-created environments such as urban and industrial sites requires a theoretical framework that can accurately predicts the outcome of different management strategies under different environmental conditions. Challenges associated with deciding how many and which species to introduce to a particular degraded site, or to what extent soil and environmental conditions should be altered to create historical or other target conditions, exemplify this need. There are economic costs and benefits associated with the success or failure of alternative strategies, and similar decisions face mangers in a broad spectrum of heavily-altered ecosystems, from urban parks to abandoned mineral extraction sites. Abandoned limestone quarry floors are an ideal system in which to test and develop suitable guidelines for managing anthropogenic ecosystems in general, and extreme-stress aggregate extraction sites in particular. Thus while the results of the research reported here may be most directly applicable to the initiative of replicating alvar ecosystems on quarry floors (Larson et al. 2006) we encourage aggregate managers to think broadly about the utility of the main idea presented here: that biodiversity can be managed to achieve particular ecosystem goals such as stable vegetation cover in an increasingly fluctuating environment. To promote this objective the language of this Report will be as general as possible within the context of community and restoration ecology; however, we will conclude by making specific recommendations to quarry managers wishing to create stable alvar vegetative communities at post-extraction sites.

Biodiversity-stability relationships and restoration
The need to restore ecosystems such that communities are self-sustaining and resistant to future disturbances (Jordan et al. 1987, Palmer et al. 2005), and the hypothesis that ecosystem stability is influenced by the diversity of species coexisting in communities (McCann 2000), are two long-recognized but until now largely independent ideas in ecology. Only rarely has biodiversity been investigated as a general determinant of stability in anthropogenic ecosystems (Naeem 2006, Seabloom 2007), in part because the theoretical basis for restoration ecology remains undeveloped in general (Palmer et al. 1997) and in part because investigations into biodiversity-stability relationships have been primarily aimed at predicting consequences of biodiversity loss in existing ecosystems of high conservation value (Tilman 1999, Chapin III et al. 2000, Srivastava and Vellend 2005), not outcomes of biodiversity introduction in harsh degraded environments already barren of biodiversity and ecosystem functionality . Despite significant research effort in models of productive ecosystems targeted for conservation, the question of how biodiversity influences the stability of ecosystem properties such as biological production or vegetation cover remains unresolved (Cottingham et al. 2001, Loreau et al. 2001, Ives and Carpenter 2007). Some consensus is being reached that significant relationships between biodiversity and stability are possible, but the nature of such relationships varies extensively across systems and scales and the mechanisms underlying observed patterns are often unclear. Observed dependency of biodiversity-stability relationships on the environmental context (Cardinale et al. 2000, Zhang and Zhang 2006, Lloret et al. 2007) suggests that the nature of stabilizing mechanisms may

differ between young communities colonizing extreme-stress environments and long-established, relatively productive communities found in less stressful environments.

Developing strategies for creating self-sustaining communities is increasingly urgent given global climate change, under which environmental fluctuations are predicted to intensify (Palmer et al. 2005, Harris et al. 2006, Choi 2007). Understanding determinants of resistance, or functional constancy despite external perturbations (Grimm and Wissel 1997), in populations and communities colonizing high-stress environments may thus be crucial to restoring stable ecosystems. Species diversity is hypothesized to be one such determinant, but to date biodiversity-resistance relationships remain hotly contested and poorly understood (Givnish 1994, Tilman and Downing 1994, Tilman 1996, Huston 1997, Mulder et al. 2001, Pfisterer and Schmid 2002, Allison 2004, Zhang and Zhang 2006). This lack of consensus in the biodiversity-stability debate limits the abilities of land managers to both predict consequences of biodiversity loss and develop perturbation resistance directly into anthropogenic ecosystems undergoing restoration, rehabilitation of reconstruction. Only one previous study has investigated whether restoration success could be improved by applying diversity-stability relationships (Seabloom 2007); while species diversity was found to contribute positively to stability of restored communities, the experiment was conducted in California grasslands facing considerably different stress regimes than extreme anthropogenic wastelands such as exhausted hard-rock quarries.

Underlying mechanisms
Several recent studies have reviewed potential mechanisms underlying biodiversity-stability relationships (Tilman 1999, Cottingham et al. 2001, Ives and Carpenter 2007, van Ruijven and Berendse 2007, Isbell et al. 2009), but such studies have focused on causes of long-term constancy within closed systems at equilibrium, not short-term resistance to catastrophic disturbance within necessarily non-equilibrium communities colonizing damaged landscapes. While statistical mechanisms contributing to long-term stability (Doak et al. 1998, Tilman et al. 1998) cannot explain short-term resistance, theory concerning the "insurance" value of biodiversity may be well-suited to restoration given the robustness of insurance mechanisms to non-equilibrium conditions (Yachi and Loreau 1999, Loreau 2000). In this framework the diversity of functional traits in a community may influence resistance of aggregate community properties through a variety of mechanisms stemming from either i) sampling effects, or ii) emergent properties of species co-occurrence.

1. Sampling effects
Sampling effects occur when randomly-constructed communities are more likely with increased diversity to contain particular species with strong effects on community resistance; sampling effects are additive in that effects of particular species in mixture can be predicted from patterns observed in monocultures (Loreau 2000). Sampling effects underlie some resistance mechanisms hinging on compensatory dynamics among species, such as when diverse communities by chance contain particularly resistant species which grow to replace more sensitive neighbors following perturbation (Yachi and Loreau 1999). Whether such compensation is construed as resistance or resilience depends in

practice upon the temporal scale over which observations are made (Grimm and Wissel 1997).

2. Co-occurrence effects

Co-occurrence effects depend upon species occurring together spatially and cannot be predicted solely from the performance of individual species in the absence of neighbors. At least four different co-occurrence mechanisms could drive diversity-dependent resistance in communities: compensation resulting from competitive release in the wake of perturbation (Lehman and Tilman 2000, Seabloom 2007); 2) perturbation-dampening via interspecifc facilitation (Stachowicz *et al.* 2008); 3) increased use-efficiency of strongly fluctuating resources due to niche complementarity (Kahmen *et al.* 2005); 4) altered resistance due to indirect effects of overyielding (Pfisterer and Schmid 2002) . Facilitation is an overlooked mechanism of diversity-resistance relationships which may be particularly important to restoration given increased importance of facilitation with abioitic stress (Callaway et al. 2002, Michalet et al. 2006), and demonstrated benefits of facilitation for population stability (Padilla and Pugnaire 2006).

General predictions

Co-occurrence-dependent resistance predicts perturbations will have less-severe impacts on high-diversity communities than on groups of low-diversity communities constructed via exhaustive sampling of a species pool consisting of only and all species comprising the high-diversity communities (Benedetti-Cecchi 2004). Where facilitation underlies such effects, particular perturbed species should suffer damage in the absence but not in the presence of diverse neighbor species. Where competitive compensatory dynamics contribute to community resistance, some species should be perturbation-sensitive regardless of neighbors while others experience growth limitations alongside perturbation-sensitive neighbors under control conditions, but accelerated growth alongside these same neighbors following perturbation, approaching but not exceeding performance in the absence of neighbors and perturbations. Finally, efficient use of resources associated with perturbations predicts some species will grow optimally when perturbed in the presence of diverse neighbors.

This study

Here we investigated biodiversity-resistance relationships in novel high-stress ecosystems undergoing experimental reconstruction: abandoned limestone quarry floors colonized by vegetation from rare natural limestone pavements called alvars (Schaefer and Larson 1997). We controlled species diversity, composition, and density of introduced communities in a design that enabled isolation of co-occurrence from sampling effects, and we simulated a severe climate change perturbation to determine how species co-occurrence influenced resistance of restored vegetation cover. We found that while placement of transparent polycarbonate domes over quarry communities for nine weeks in summer drastically increased air temperature and depleted soil moisture, perturbed communities suffered net cover loss in communities of low and intermediate diversity only, while maximum-diversity communities remained strikingly unaffected. Population-level patterns among species suggest that complementarity, compensation, and facilitation all simultaneously contributed to this effect. These findings suggest that

adapting ecosystem management to climate change may require maximizing species diversity with emergent benefits for community resistance within anthropogenic ecosystems.

MATERIALS AND METHODS
Study system

Limestone quarrying is a major economic industry, producing materials necessary for human life but dramatically restructuring landscapes in the process. Extensive removal of vegetation, soils, and underlying bedrock has created vast pits lined with steep-sloped exposed bedrock walls and flat expansive pavement floors that are highly heterogeneous at fine scales due to cracks, fissures and microtopographic variability. Substrates suitable for vegetation establishment are scarce and of poor quality, often unstable, infertile, and prone to flooding and drought because of bedrock's tendency to shed or pool precipitation rapidly (Larson et al. 2000). Substrates found in Ontario quarries are typically sandy loams with mineral fractions consisting largely of crushed limestone from quarrying; substrates are basic (pH = 7.68) , shallow (2.57 cm deep), and relatively infertile (0.31 % nitrogen, 6.31 mg/Kg of phosphorus , 11.51% carbon, and 8.46% organic material by weight) (Tomlinson et al. 2008). Harsh abiotic conditions inhibit spontaneous recovery of quarry floors, however, long-abandoned sites may be colonized by diverse assemblages including both stress-tolerant ruderal species typical of urban environments and native rock-outcrop specialists otherwise confined to alvars (Tomlinson et al. 2008). Alvar are of gloabl conservation value as refugia for high biodiversity including rare and threatened species (Catling 1995, Znamenskiy et al. 2006) and reconstructing alvar ecosystems on quarry floors is a novel rehabilitation initiative prompted by analogous biophysical conditions at quarries and alvars (Richardson *et al.* 2009). It is in this context that we performed a biodiversity experiment, introducing to randomly chosen patches of quarry floor various combinations of alvar plant species recently discovered to colonize quarry floors successfully with minimal need for substrate remediation. We performed the experiment at Waters Quarry, a site near Georgetown, Ontario that has remained unaltered since extraction ceased 35 prior to our experiment (UTM coordinates, NAD83 datum: 17T 583885 4837749). This site is representative of other abandoned quarry sites in Ontario and was selected primarily for its security from demonic intrusion relative to other similar sites in the region.

Biodiversity experiment – seed addition

We designed an experiment to enable comparison among groups of communities featuring different levels of species and functional group diversity but equivalent average species composition, such that differences among groups represent effects of species co-occurrence divorced from sampling effects (Benedetti-Cecchi 2004). In this experiment species and functional group diversity were altered in parallel to maximize differences in underlying trait diversity among treatments (Naeem 2002). One-hundred 0.3 m x 0.3 m plots were sown with seeds of alvar species in mid-October 2005, two weeks following glyphosphate application ("Round Up ®: Grass and Weed Killer", Monsanto, USA), and immediately following removal of all living and dead plant material from plots. At each plot seeds were intermixed thoroughly with any substrate present and with 2 L of a substrate amendment designed to mimic low-nutrient, high organic material substrate

found on alvars. Added substrate consisted of sterilized "Horticultural"-grade silicaceous sand (Nu Gro Technologies, Brantford Ontario) and mushroom compost (President's Choice, Brampton Ontario) mixed at a 1:1 ratio by fresh weight and combined with 15 mL/plot of a polyacrylamide tackifier ("HydroPAM ", Polymers Inc., Hot Springs, AK USA) to help bind seeds and substrates to the bedrock quarry floor. Seeds of some species were cold-moist stratified for 30 days as recommended by suppliers, and all species were germination-tested using standard greenhouse radicle-protrusion tests.

Each plot was sown with the equivalent of 1200 viable seeds, but the number and identities of species varied according to 5 diversity treatments. Thirteen species in total, representing early-flowering forb, late-flowering forb, and grass functional groups, were arbitrarily grouped into three core pools, with no species shared among pools. The Early Forb pool consisted of 3 early-flowering forb species; the Late Forb pool consisted of 3 late-flowering forb species; the Grass & Forb pool consisted of 4 grass and 3 late-forb species. Pools were then combined in different ways to create the 5 diversity treatments: i) 3 Early Forb Species; ii) 3 Late Forb Species; iii) 6 Early + Late Forb Species; iv) 6 Grass & Forb Species; v) 12 Early Forb + Late Forb + Grass & Forb Species (Table 1).

Table 1. Number of viable seeds from 13 alvar species added to limestone quarry floors in the context of 5 species diversity treatments.

Diversity Treatment	Number of seeds added per species*											
	Ac	Fv	Ph	Pa	Rh	Sp	Rb†	Cl	Bk	Et	Pv	Ss
3 SP. EARLY FORB	400	400	400									
3 SP. LATE FORB				400	400	400						
6 SP. [EARLY + LATE] FORB	200	200	200	200	200	200						
6 SP. [GRASS + FORB]							200	200	200	200	200	200
12 SP. EARLY + LATE + [GRASS + FORB]	100	100	100	100	100	100	100	100	100	100	100	100

*Two-letter codes correspond to the following species, clustered according to functional group and following nomenclature of Newmaster et al. 1998. Early forbs: *Aquilegia canadensis (Ac), Fragaria virginiana (Fv), Penstemon hirsutus (Ph)* . Late forbs: *Potentilla arguta (Pa), Rudbeckia hirta (Rh), Solidago ptarmicoides (Sp), Rosa blanda (Rb), Coreopsis lanceolata (Cl)* . Grasses: *Bromus kalmii (Bk), Elymus trachycaulus (Et), Panicum virgatum (Pv), Schizachyrium scoparium (Ss)* .

† Insufficient Rb seeds were available to seed all plots as planned, so for half of the plots requiring Rb, an alternate late forb alvar species was introduced instead - *Asclepias syriaca.*

Biodiversity experiment – plug addition

Seeds in plots germinated and grew over the 2006 growing season while spontaneously occurring species were removed regularly (Richardson and Larson 2009). In May 2007 plots were evaluated to determine the extent to which established communities represented the species introduced, and the extent to which vegetation cover varied among treatments. Given our goal of testing the relationship between biodiversity and resistance of vegetation cover, it was desirable that realized richness mapped closely onto introduced richness, and that community cover on average was equivalent among treatments prior to imposition of any experimental perturbation or disturbance (Allison 2004). By May 2007 many communities exhibited this pattern however several communities failed to establish due to flooding and other stressors. We expected such outcomes based on previous work on quarry floors and thus between October 2006 and May 2007 had grown all species under glasshouse conditions (20-22 C day/ 16-18 C night, full sunlight) via germination in monoculture trays followed by transplantation of "individual" plants (rooted stems, for wildflower species and the grass *Panicum virgatum*; 5 cm x 5 cm swards for remaining species) to 10 cm x 10 cm x 20 cm deep pots. In the field, the 10 plots in each diversity treatment that exhibited the greatest vegetation cover also exhibited establishment of all species seeded, and did not receive additional plant material. The remaining 10 plots in each diversity treatment received alvar species plugs as needed to ensure that species introduced as seeds were present and evenly abundant as adults, and that total vegetation cover in plots approximated 60%, as observed on average in plots not receiving plugs. Plugs were added 26 May 2007, immediately after which all plots began receiving water semi-regularly ($\approx$ 1 L / plot municipal tap water, 1-3 times per week depending on rainfall; no plot experienced more than 3 days without natural or artificial precipitation). Plugs that died within 10 days of the initial planting were replaced. Hand-weeding of undesired species every 2-4 weeks continued May - September 2007.

Simulated climate change perturbation

Diversity treatments were fully crossed with a controlled climate change perturbation treatment, in which control ("CON") plots were watered normally while test plots were not watered but rather covered by transparent polycarbonate domes ("climate change structures", or CCS) designed to stop rain infiltration of plot soil and increase air temperature. Plots received CCS from 29 June until 3 September, 2007, after which watering resumed for the remainder of the growth season (mid-October). Each CCS consisted of a 1.2 m x 1.2 m sheet of transparent 1.5 cm-thick polycarbonate ("Lexan", G.E. Polymershapes, London, ON) stretched into a half-cylinder shaped dome (76 cm wide at the base, 76 cm high in the middle, 1.2 m long) and bound across the flat open base using rubber tie-down straps (1.5 cm x 1.5 cm x 60 cm, unstretched) and pre-drilled holes located 25 cm from each end the CCS (Fig. 1). Each CCS was centered over a single plot and staked down; open ends were covered with transparent polyethylene sheets and small gaps were created for air circulation. CCS treatment was applied within each biodiversity treatment to five randomly-chosen plots that had received plugs, and five that had not.

We collected 30 mL of soil from areas immediately adjacent to each plot, outside of the vegetation canopy but inside the CCS if present, immediately prior to, 30 days

after, and 65 days after CCS installation; samples were weighed fresh and again after 5 days at 60 C. Gravimetric soil moisture was calculated for each sample as [100% x (fresh weight - dry weight)/fresh weight]. Thermistor-based DS1921G Thermochron iButtons (Dallas Semiconductor Maxim, California USA) were sealed within small plastic bags and suspended ≈ 10 cm above the quarry surface immediately adjacent to each plot, programmed to record and log temperature every 3 hours for the duration of the experiment. Temperature data was summarized for each day in each plot using mean, maximum, and coefficient of variation (CV, the standard error divided by the mean) of values measured. We measured photon density flux (PDF) of photosynthetically active radiation in each plot using photometers, sampling 30 cm above the plot surface, and simultaneously 1 m above a central open patch of quarry floor, within 2 hours of solar noon on a cloud-free day. We calculated relative light intensity at each plot as (100% x PDF_{PLOT}/$PDF_{OPEN.)}$ Relative air humidity was measured using digital hygrometers at 30 CCS and 30 control locations at mid-day in July 2006 during a preliminary trial of the CCS design (i.e. not plots included in the biodiversity experiment). Environmental variables were compared among CCS and CON plots using separate mixed linear models for each variable.

CCS installation had a massive impact on temperature and soil moisture content in plots (Fig. 2). Daily mean, maximum and CV values for air temperature varied extensively over the course of the experiment but all were consistently greater in CCS then in CON plots, with least-square mean temperature increasing from 22.7 ± 0.3 C to 26.2 ± 0.3 C (difference: $t_{94} = -82.54$, P<0.0001), maximum temperature increasing from 34.04 ± 0.07 C to 41.14 ± 0.07 C (difference: $t_{94} = -71.29$, P<0.0001), and daily temperature CV increasing from 0.329 ± 0.001 to 369 ± 0.001 (difference: $t_{94} = -36.31$, P<0.0001). CON plots experienced 9 days with absolute maximum temperature > 50 C while CCS plots experienced absolute maximum temperatures of 51-62 C on 41 days. Soil moisture decreased over the 65 day perturbation period in CCS but not CON plots; substrates with 12-16% soil moisture (back-transformed 95% confidence interval) prior to CCS installation exhibited 13-21% moisture 65 days later in CON plots but only 2-3% soil moisture in CCS plots (difference: $F_{1, 95}=113.77$, P<0.0001). Relative light intensity was higher in CON ($89 \pm 2\%$) than in CCS plots ($77\pm2\%$; difference: $F_{1,98} =24.15$, P<0.0001), while relative air humidity was greater in CCS ($48 \pm 1\%$) than in CON plots ($42 \pm 1\%$; difference: $F_{1,59} = 23.07$, P < 0.0001).

Plate 1. Photographs of quarry floor plots in the perturbation treatment receiving Climate Change Structures (CCS). Structures were installed at 50 plots randomly located across the Waters quarry site on 28 June 2007 (top panel) and removed on 2 September 2007. Each CCS, designed to block infiltration of precipitation and retain thermal radiation, consisted of a 1.2 m X 1.2 m sheet of transparent polycarbonate folded and bound into a half-cylinder shape using rubber straps and plastic cable ties, centered over experimental alvar-seeded plots, anchored using steel stakes and rocks, and covered-over at open sides with polyethylene sheeting (bottom panel).
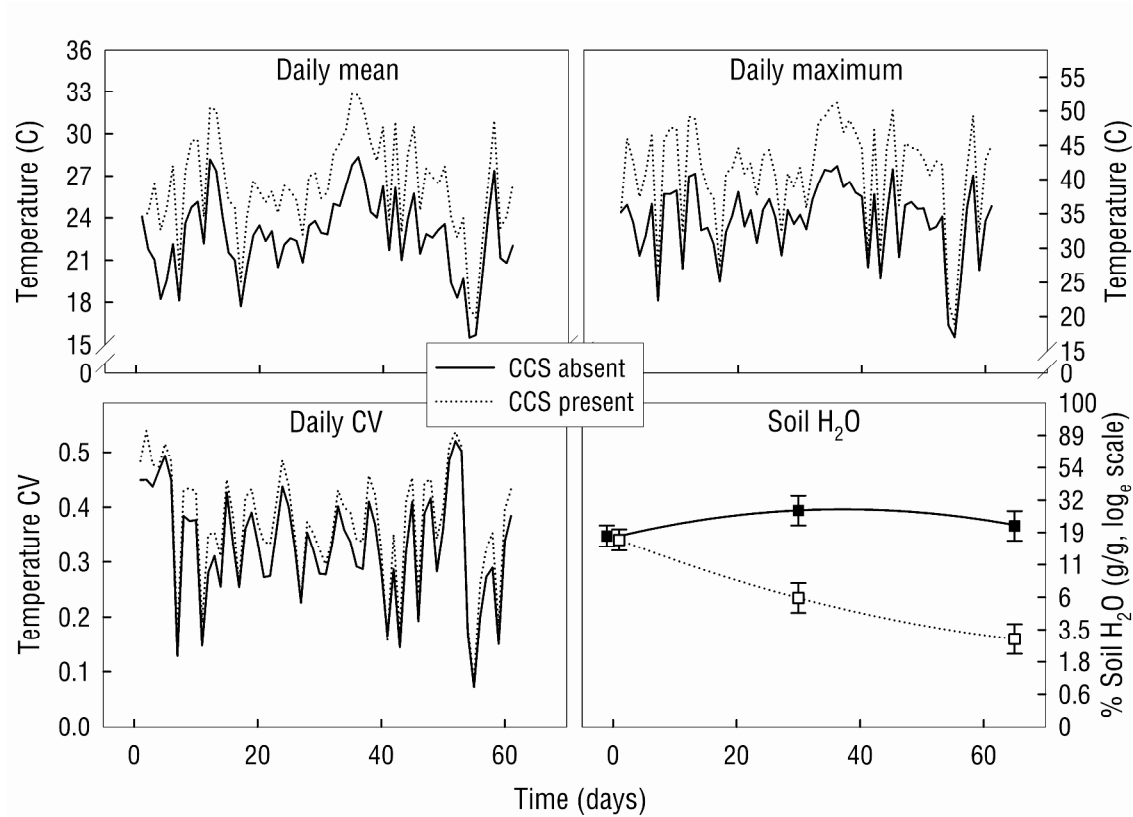
Figure 1. Effects of Climate Change Structures (CCS) on quarry floor microclimate conditions. Air temperature and soil moisture conditions were monitored in quarry floors experimentally colonized by alvar plant species and either watered regularly throughout the 2007 growth season (solid lines) or exposed to simulated climate change through installation of polycarbonate domes (CCS; dotted lines). Data is shown for the 65-day period over which CCS remained on plots. Temperature was measured every three hours in each plot (50 control + 50 CCS); effects of CCS on least-squared mean daily temperature mean, maximum, and coefficient of variation (CV: the standard deviation divided by the mean) are shown. Gravimetric soil moisture was log_e-transformed to enable comparison between treatments over time using ANCOVA; shown are back-transformed least-squared means and 95% confidence intervals for soil moisture in control (solid squares) and CCS (empty squares) plots on each day that soil was sampled.

Measurement of vegetation cover

Plots were repeatedly sampled for vegetation cover, a key metric of restoration success in this system, during multi-day surveys with mid-points 14 June, 14 July, 18 August, and 20 September 2007. The first sampling event occurred two weeks prior to CCS installation while the last occurred two weeks after CCS removal. Vegetation cover was sampled with high precision using a 0.3m x 0.3m quadrate subdivided into 225 (2 cm x 2cm) cells. Each cell was inspected and living plant biomass was determined to be either present or absent; where present, the species producing observed biomass was identified. Given these dimensions vegetation cover in each cell as was generally attributable to a single species, however for consistency cover in each cell was attributed to the first species contacted by a probe lowered into the center of the cell. Percent cover was calculated at the community levels as 100% x (number of cells with plant biomass present/225), and at the population level for each species *S* as 100% x (number of cells with cover attributable to *S* / 225).

Statistical analysis

Mixed linear models were used to analyze vegetation cover as a function of diversity treatment (factor DIV, 5 levels), climate change perturbation (factor PERT, 2 levels), number of days since first sampling (TIME, treated as a continuous variable), presence of plugs (factor PLUG, 2 levels), and interactions among variables. Plots were treated as subjects of repeated measures analysis to control for temporal autocorrelation. Stepwise backwards-elimination of model effects with P > 0.05 was performed to derive a final model for testing diversity-resistance hypotheses via contrasts among specific DIV x PERT x TIME combinations. Here we defined Resistance (RES) at the community level as the rate of change in plot cover over time in CCS plots relative to that in CON plots within the same diversity treatment. We tested the influence of species co-occurrence on resistance by contrasting RES values in 6 SP. [EARLY + LATE] FORB plots vs. the combination of 3 SP. EARLY FORB and 3 SP. LATE FORB plots, and by contrasting 12 SP. EARLY + LATE + [GRASS + FORB] plots against the combination of 6 SP. [EARLY + LATE] FORB plots and 6 SP. [GRASS + FORB] plots.

A similar approach was used at the population level; cover by each species population in each plot was analyzed as a function of plot DIV, PERT and PLUG treatments, TIME, and species identity (factor SPEC, 13 levels), plus interactions. The effect of species identity nested within plot identity was treated as a subject of repeated measures. Contrasts performed at the community level were also performed at each level of SPEC to test how co-occurrence influenced population RES within each species. All analyses were performed using Proc Mixed in SAS (the SAS Institute, Cary, NC); assumptions of general linear models were checked via visual inspection of residuals plots and standard tests for normality of residuals. Where residuals were found to deviate from the normal distribution and approximate the Poisson distribution, reanalysis using generalized linear models assuming the Poisson distribution, performed with Proc GENMOD in SAS, produced similar results as mixed linear models, and thus for simplicity only mixed linear model results are presented here. Estimates of means or effect sizes are reported as least-squared means ± standard error, unless noted otherwise.

RESULTS
Effects of CCS and co-occurrence on community resistance

Community cover over time in experimental quarry plots depended significantly upon multiple experimental factors including the three-way TIME x DIV x PERT interaction ($F_{4,290}$=18.48, P < 0.0001; Table 2), enabling contrasts required to test effects of species co-occurrence on community resistance to the simulated drought and heat wave. Community RES, or the difference in cover-time slopes between CCS and CON plots, was marginally more negative in 6 SP. [EARLY + LATE] FORB plots (-0.49 ± 0.05) than in the combination of 3 SP. EARLY FORB and 3 SP. LATE FORB plots (-0.36 ± 0.04; difference: $F_{1,94}$=3.85; P=0.0527). In contrast, RES was far more positive in 12 SP. EARLY + LATE + [GRASS + FORB] plots (0.08 ± 0.05) than in the combination of 6 SP. [EARLY + LATE] FORB plots and 6 SP. [FORB + GRASS] plots (-0.47 ± 0.04; difference: $F_{1,94}$=69.94; P < 0.0001).

Comparison of community cover over time in each perturbation and diversity treatment sheds light on this pattern. While cover, averaging 57 ± 1% per plot, did not differ among any treatments at the onset of the experiment (both DIV and PERT were non-significant predictors of cover outside of their interaction with TIME; Table 1), cover increased significantly in CON plots over the 2007 growing season to 79 ± 2% regardless of diversity treatment (P>0.05 for Tukey-Kramer adjusted comparisons among groups). As expected given the extreme drought and heat stress imposed by CCS treatment (Fig. 1), community cover in most CCS plots decreased over the growing season, including plots in the 3 SP. EARLY FORB and 3 SP. LATE FORB treatments (dropping to 41 ± 3%), the 6 SP. [EARLY + LATE] FORB treatment (dropping to 32 ± 4%), and the combination of 6 SP. [EARLY + LATE] FORB and 6 SP. [GRASS + FORB] treatments (dropping to 33 ± 3%). It was striking therefore that vegetation cover actually increased in 12 SP. EARLY + LATE + [GRASS + FORB] CCS plots, reaching 92 ± 4% in a trend not significantly different from 12 SP. CON plots (difference: $F_{1,94}$=2.40, P=0.1243) (Fig. 2). CCS installation thus had strong negative effects on communities at low and intermediate levels of species diversity, but no effect on maximum-diversity communities. Given that the same species were present at intermediate and high levels of diversity, species co-occurrence rather than sampling effects are implicated in diversity-dependent resistance observed here. Absence of a PLUG effect (P > 0.05) indicated that biodiversity-resistance relationships were independent of whether diversity and cover resulted from seed addition alone or seed addition supplemented by plug addition.
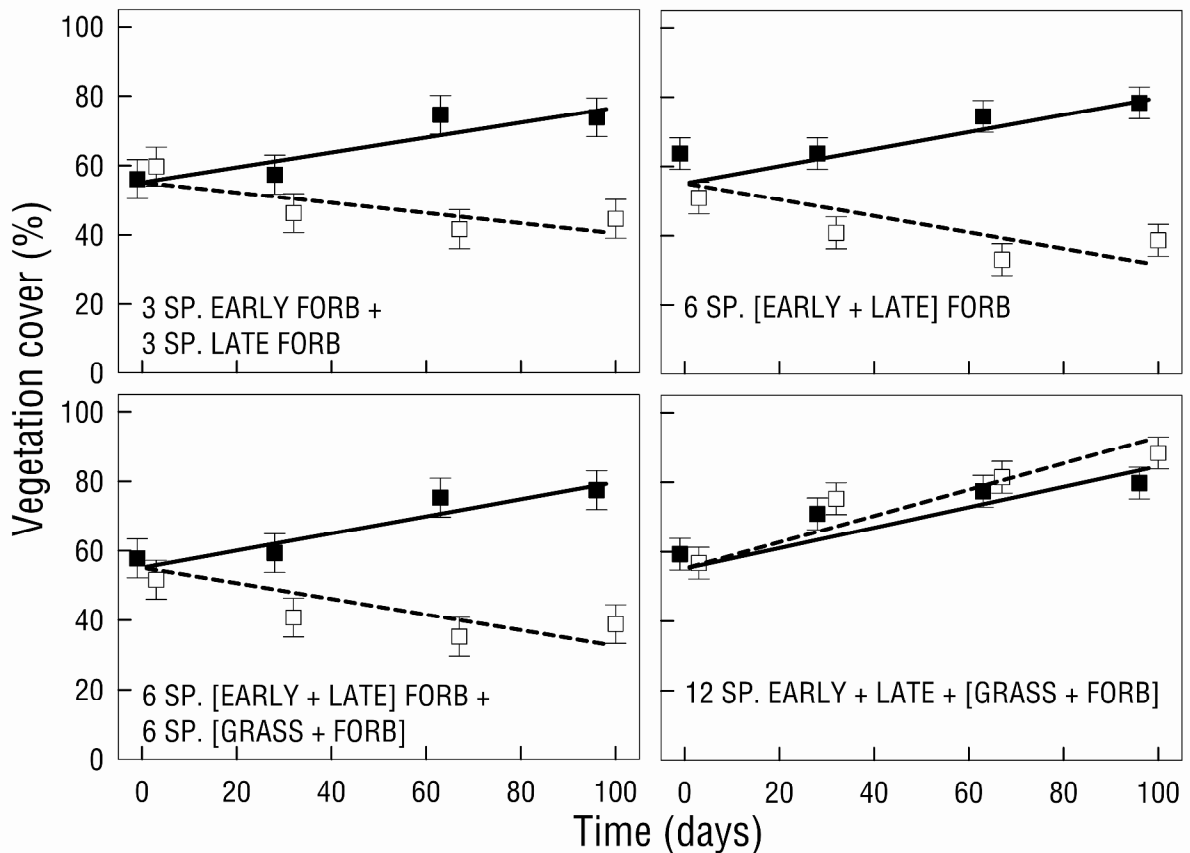
Figure 2. The effects of species diversity, climate change perturbation, and time on vegetation cover in communities of alvar plant species experimentally established on abandoned limestone quarry floors. Plot communities received either regular watering throughout the 98-day experiment (solid squares and solid lines, indicating least-squared means, 95% confidence intervals, and results of linear regression) or simulated microclimate change for 65 days. Trends in vegetation cover over time in perturbed relative to control plots ("RES", see text) were compared *within* groups of plots established using a pool of either 6 species (top panels) or 12 species (bottom panels), but *among* groups receiving either one-half of the species pool per plot, with both halves represented equally overall (left-hand panels), or the entire species pool per plot (right-hand panels).

Table 2: Vegeation cover in seeded quarry floor communities and populations in response to species diversity and simulated climate change.

Effect	DF	F	Pr > F
Community-level ANCOVA			
Time	1, 290	17.81	< 0.0001
Time*DIV	4, 290	30.17	< 0.0001
Time*PERT	1, 290	170.30	< 0.0001
Time*DIV*PERT	4, 290	18.48	< 0.0001
Population-level ANCOVA			
Time	1, 3770	3.85	0.0497
Species	12, 1235	74.39	< 0.0001
Time*DIV	4, 3770	6.97	< 0.0001
Time*PERT	1, 3770	91.74	< 0.0001
Species*DIV	52, 1235	87.32	< 0.0001
Time*Species*DIV	48, 3770	2.65	< 0.0001
Time*Species*PERT	12, 3770	4.18	< 0.0001
Time*Species*DIV*PERT	52, 3770	7.84	< 0.0001

Covariance parameters for residuals of subjet:

Plot	Z=13.95 Pr > Z	< 0.0001
Species(Plot)	Z=50.02 Pr > Z	< 0.0001

*Results from repeated-measures ANCOVA treating 'plot' as the subject repeatedly measured in community-level analysis, and "species" nested within 'plot' as the subject repeatedly measured in population-level analysis.
TIME=number of days from 14 June (continuous variable); DIV=diversity treatment (5 levels); PERT=perturbation treatment (2 levels); SPECIES = taxonomic species identity (13 levels).

Effects of CCS and co-occurrence on population resistance

Vegetation cover at the population level depended significantly upon multiple interacting factors including the four-way TIME x SPEC x DIV x PERT interaction (Table 2), enabling within-species contrasts of population RES in plots with HIGH vs. LOW diversity (e.g. 6 SP. vs. 12 SP. plots). While no species exhibited differences in population RES when occurring in 3 SP. vs. 6 SP. plots, five species exhibited significantly greater RES in 12 SP. EARLY + LATE + [GRASS + FORB] plots than in the combination of 6 SP. [EARLY + LATE] FORB plots and 6 SP> [GRASS + FORB] plots (Fig. 3; Table 3). As at the community level, DIV and PERT only influenced cover through interaction with TIME, indicating that populations of the same species did not differ with respect to initial cover among perturbation and diversity treatments.

The five species exhibiting positive diversity-dependent population resistance did so in varying ways, suggestive of different underlying mechanisms (see Discussion). Cover produced by the grass *Elymus trachycaulus* increased in CON plots at both diversity levels but dropped in 6-species CCS plots while increasing in 12-species CCS plots. Cover by the late forb *Rudbeckia hirta* increased in CON plots, more so in 6-species than 12-species plots, but decreased in 6-speceis CCS plots while increasing in 12-species CCS plots. The early forb *Penstemon hirsutus* increased in cover in 6-speceis CON plots while remaining mostly unchanged in 12-species CON plots, and experienced cover loss under CCS in 6 species plots but surprisingly steep gain in cover in 12-species plots. The late forb heliophyte *Solidago ptarmicoides* exhibited a similar pattern to *Penstemon*, and while the grass *Panicum virgatum* exhibited this same pattern at the 6-species level, vegetation cover increased significantly in 12-speceis plots under both CON and CCS conditions. Of the 8 species that did not exhibit increased population resistance with community diversity, 2 species exhibited strongly decreased cover over time in CCS relative to CON plots at both diversity levels (the grass *Bromus kalmii* and the early forb *Fragaria virginiana*), while 3 species lost no cover in CCS plots but rather exhibited lower rates of cover growth in CCS relative to CON plots (the grass *Schizacharium scoparium*, the early forb *Aquilegia canadensis*, and the late forb *Coreopsis lanceolata*; Fig. 3).

Derived vegetation cover (%)

Time (days)
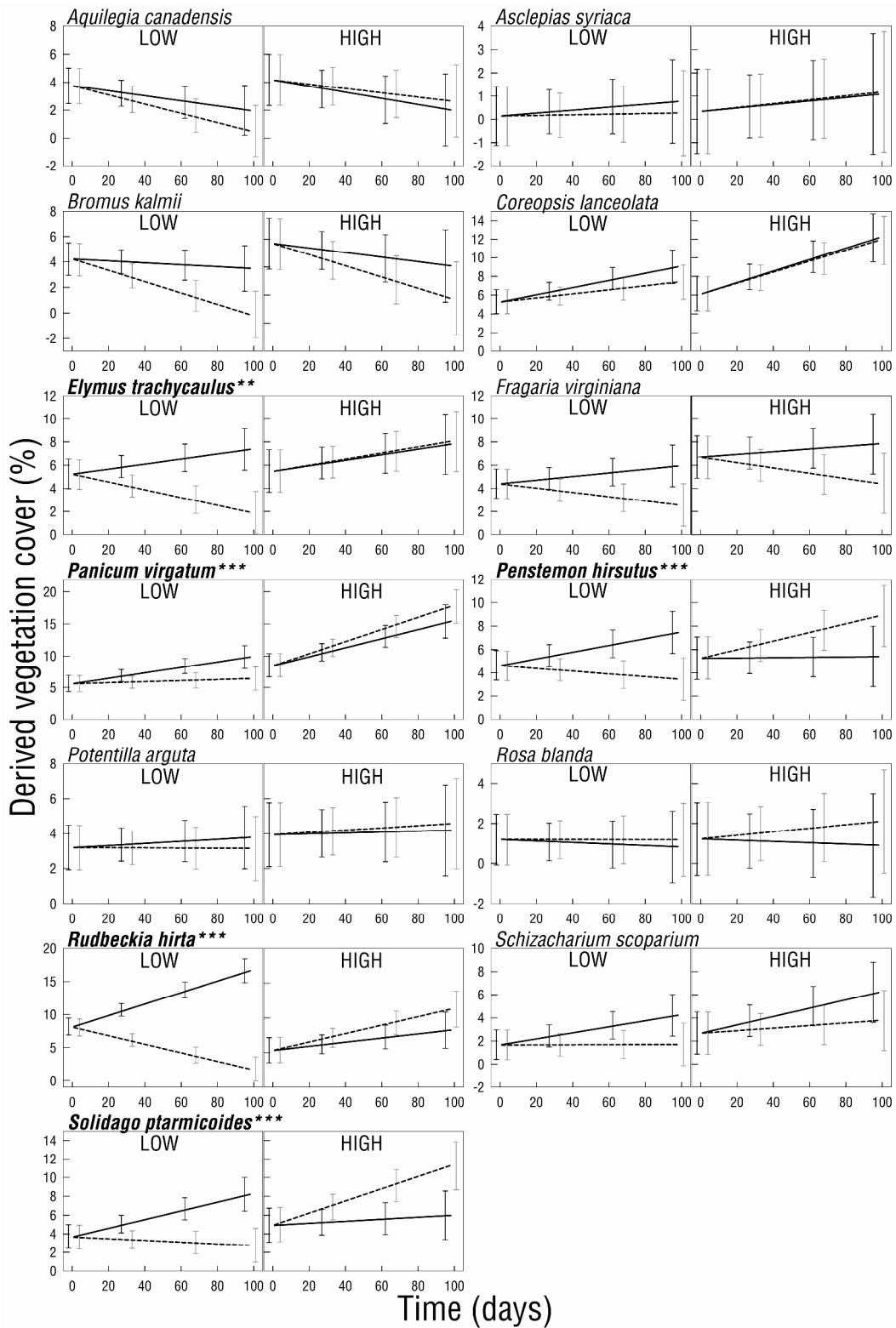
Figure 3. Effects of biodiversity treatments on degree of change in vegetation cover over time in populations corresponding to 13 different species established in multi-species communities on limestone quarry floor plots either watered regularly (solid lines, representing regression coefficients derived from repeated-measures ANCOVA) or exposed to simulated climate change (dotted lines). ANOVA-predicted 95% confidence intervals for cover values at each sampled time point are shown to illustrate the certainty associated with regression coefficients for each species in each diversity and perturbation treatment (black error bars = control plots; grey error bars = CCS plots). For each species, Population Resistance values (i.e. rates of population cover change over time in CCS plots relative to control plots) were contrasted between plots with relatively low diversity (the combination of 6 SP. [EARLY + LATE] FORB and 6 SP. [GRASS + FORB] treatments) vs. plots with high diversity (the 12 SP. EARLY + LATE + [GRASS + FORB] treatment). Bold-face print and asterisks denote species in which this contrast resulted in a statistically significant difference (** P < 0.01; *** P < 0.0001; see Table S1for contrast statistics).

Table S1: Rates of change in population cover over time in perturbed relative to unperturbed plots (Resistance) in LOW vs. HIGH diversity treatments.

Species	Functional group	Resistance LOW	Resistance HIGH	DF	Contrast F	Pr > F
Aquilegia canadensis	Early forb	-0.02 ± 0.01	0.01 ± 0.02	1, 1235	1.03	0.3115
Asclepias syriaca	Late forb	-0.01 ± 0.01	0 ± 0.02	1, 1235	0.10	0.7512
Bromu kalmii	Grass	-0.04 ± 0.01	-0.02 ± 0.02	1, 1235	0.71	0.3993
Coreopsis lanceolata	Late forb	-0.03 ± 0.01	0 ± 0.02	1, 1235	1.32	0.2504
Elymus trachycaulus	Grass	-0.06 ± 0.01	0 ± 0.02	1, 1235	9.81	0.0018
Fragaria virginiana	Early forb	-0.03 ± 0.01	-0.03 ± 0.02	1, 1235	0.00	0.9865
Panicum virgatum	Grass	-0.05 ± 0.01	0.02 ± 0.01	1, 1235	10.84	0.0010
Penstemon hirsutus	Early forb	-0.04 ± 0.01	0.04 ± 0.02	1, 1235	12.66	0.0004
Potentilla arguta	Late forb	0 ± 0.01	0 ± 0.02	1, 1235	0.05	0.8262
Rosa blanda	Late forb	0 ± 0.02	0.01 ± 0.02	1, 1235	0.21	0.6493
Rudbeckia hirta	Late forb	-0.13 ± 0.01	0.03 ± 0.02	1, 1235	55.40	< 0.0001
Schizacharyium scoparium	Grass	-0.03 ± 0.01	-0.02 ± 0.02	1, 1235	0.07	0.7986
Solidago ptarmicoides	Late forb	-0.04 ± 0.01	0.05 ± 0.02	1, 1235	18.75	< 0.0001

*Contrasts performed using repeated-measures ANCOVA of population cover over time as a function of community diversity treatment, perturbation treatment, and species identity; C-T slopes shown represent changes in vegetation cover over 98 days in perturbed plots relative to changes in control plots, for populations in plots with LOW diversity (the combination of 6 SP. [EARLY + LATE] FORB and 6 SP. [GRASS + FORB] treatments) vs. HIGH diversity (the 12SP. EARLY + LATE + [GRASS + FORB] treatment).

DISCUSSION

We manipulated species diversity and microclimate conditions on limestone quarry floors to determine the form of the relationship between species diversity and perturbation resistance in high-stress ecosystems undergoing reconstruction, and we compared community and population-level patterns to identify mechanisms potentially responsible for such relationships. The simulated drought and heat wave was severe and inflicted steep cover losses in 6-species communities but surprisingly no change in 12-species communities of equivalent composition. Population-level patterns suggest that the observed positive effect of species co-occurrence on community resistance arises from several mechanisms operating simultaneously, including facilitation, complementarity, and compensation. Incorporating knowledge of these mechanisms into ecosystem management may improve rehabilitation efficacy in harsh and disturbance-prone environments.

Community patterns

The suite of microclimate changes imposed on test plots, including a 91% reduction in soil moisture, and 12%, 15% and 21% increases in daily CV, mean, and maximum air temperatures, respectively (Fig. 1), reduced vegetation cover and limited plant growth by 20% relative to controls in 6-species communities, but had no effect on 12-species communities (Fig. 2). Given that all species had equal opportunity to establish and contribute to community resistance whether planted within 6-species or 12-species communities, and that communities at all diversity levels exhibited equivalent cover immediately prior to the perturbation, our results demonstrate clearly that species co-occurrence can promote community resistance independent of sampling effects or the occurrence of overyielding prior to perturbation. Low resistance in both three and six-species communities suggests that species diversity may need to exceed a threshold of six or so species before effects on resistance emerge, consistent with patterns observed in this system in the wake of natural drought (Submitted Manuscript). While sampling effects associated with the insurance hypothesis (Yachi and Loreau 1999) may link biodiversity to stability in important ways, our results suggest such mechanisms must be considered within a conceptual framework also accounting for stabilizing roles of facilitation, complementarity, and other outcomes of species co-occurrence (Hughes and Stachowicz 2004, Stachowicz et al. 2008).

Patterns reported here agree with previous reports of positive diversity-dependent resistance to natural drought (Tilman and Downing 1994, Tilman 1996, Lloret et al. 2007), however, earlier studies were unable to unambiguously attribute resistance to biodiversity vs. "hidden treatments" including experimental and environmental drivers of biodiversity (Givnish 1994, Huston 1997). In contrast, our results contradict diversity-dependent instability observed in one of the few field experiments where species richness, composition, and perturbation were fully controlled (Pfisterer and Schmid 2002). High-stress ecosystems may select for particular stabilizing mechanisms such as facilitation while more productive grasslands select for competition-dependent mechanisms, although this hypothesis requires experimental testing. Experimental results from aquatic algal microcosms manifesting positive diversity-stability relationships under low-nutrient but not high-nutrient conditions (Zhang and Zhang 2006), and from

positively-interacting laboratory bryophyte communities exhibiting diversity-dependent productivity only under drought stress in (Mulder et al. 2001), are consistent with this idea, highlighting the need to better understand environmental context-dependency of biodiversity-stability relationships (Cardinale et al. 2000).

Population patterns and potential mechanisms

Previous insights into mechanisms linking biodiversity and community stability have resulted from analysis of population-level patterns and processes (Tilman 1996, Vogt et al. 2006, van Ruijven and Berendse 2007). Here we identify potential mechanisms for co-occurrence-dependent community resistance by investigating four properties within each species: the relationship between population RES and co-occurrence with neighbor species; relative influence of reduced mortality vs. enhanced growth with diversity; evidence for competitive suppression or release; and the capacity for perturbed populations to outperform unperturbed controls. Of the 13 alvar species planted on quarry floors, none showed increased sensitivity to drought when planted alongside 11 rather than 5 neighbor species, but five species clearly exhibited the opposite trend of enhanced resistance where more neighbors were present. Two species experiencing increased population RES with neighbor diversity did so via reduced mortality, indicated by steep cover loss under CCS in 6- but not 12-species plots, while three species exhibited increased RES due to enhanced growth, indicated by diversity-dependent steepening of initially neutral or positive cover-time relationships under CCS (Fig. 3). Given this pattern it seems likely that the species experiencing reduced mortality with neighbor diversity - the grass *Elymus trachycaulus* and the late forb *Rudbeckia hirta* – did so as an outcome of facilitation dampening the local intensity of the perturbation, possibly through provision of shade or retention of soil moisture by benefactor species (Padilla and Pugnaire 2006).

  In contrast, the late forb *Solidago ptarmicoides* and the early forb *Penstemon hirsutus* exhibited resistance patterns more consistent with compensatory release from competition. In unperturbed plots these forbs grew less in 12-species than in 6-species communities, suggesting competition suppressed growth at higher diversity (Fig.3) (Lehman and Tilman 2000). However, in 12-species perturbed plots cover attributable to these species increased significantly over the experiment, outperforming populations in 12-species unperturbed plots and approaching maximum cover expansion, observed in 6-species unperturbed plots. In contrast, grass species *Bromus kalmii* and *Schizachyrium scoparium* grew well under unperturbed conditions at low and high diversity, but suffered sharp cover loss under CCS regardless of neighbors. As these grass species co-occur with *Solidago* and *Penstemon* species in 12 SP. but not 6 SP. plots, release from competition following CCS-induced grass mortality may explain enhanced forb growth in high diversity perturbed communities.

  The fifth species to exhibit increased population RES with diversity, *Panicum virgatum*, experienced greater growth in perturbed 12-species plots than in any other treatment combination (Fig. 3). This increase in cover helped compensate for perturbation-induced cover loss experienced by other species, but the pattern of growth by *Panicum* across treatments is inconsistent with competitive release. Rather, *Panicum* appears to have experienced strong benefits from co-occurrence that outweighed marginal negative impacts of the perturbation treatment: maximal cover gain in high-

diversity perturbed communities suggests this species utilized resources associated with the perturbation treatment, and did so more efficiently at high than low diversity. While such phenomena may result from facilitation, increased niche complementarity would be the outcome at the community level (Kahmen et al. 2005).

Implications for theory and management

Responses to diversity and disturbance within experimental rock-barren communities demonstrated that species co-occurrence can promote functional resistance in the context of reconstructing high-stress ecosystems. Patterns at the population level suggest complementarity, facilitation, and competitive compensatory dynamics simultaneously contributed to community-level resistance, highlighting the need for theory and future experiments to be updated to account for multiple concurrent and potentially interacting population-level mechanisms of community stability. Certainty regarding mechanisms responsible for observed patterns would be strengthened by controlling for effects of different initial population densities among diversity levels, a potentially confounding factor that our experiment was not designed to rule out (Benedetti-Cecchi 2004). Given the strong variability in diversity-stability relationships observed across systems and scales, it is possible that more robust patterns will emerge once the diversity of stabilizing and destabilizing mechanisms is better understood.

High-stress ecosystems predominate anthropogenic landscapes, but as potential refugia for biodiversity they provide hope that the need to exploit natural resources can be reconciled with the need to conserve biodiversity and ecosystems (Larson et al. 1999) (Rosenzweig 2003). Based on the experiment reported here, we conclude that introducing a high diversity of suitable species to severely degraded environments will increase the likelihood that restored communities will persist and function stably, despite environmental fluctuations expected to intensify given climate change and legacy effects of historical exploitation regimes. Human adaptation to global climate change may therefore be quickened by rethinking biodiversity management strategies to maximize resistance of populations, communities, and ecosystems to both predicted and unpredictable future challenges.

RECOMMENDATIONS FOR QUARRY MANAGERS

In the work presented here we experimentally altered both the number of alvar plant species established on abandoned limestone quarry floors and the degree of disturbance experienced by the replicated alvar communities, and assessed the influence different combinations of these factors on production of vegetation cover over a single growing season. Based on our findings in this experiment, and in the context of our previous work in this system, we confidently make the following recommendations to land managers seeking to rehabilitate abandoned or exhausted quarry sites.

1. Given that communities with 3 or 6 species suffered >30% losses in vegetation cover in climate-change disturbed relative to control plots but 12-species communities increased in vegetation cover whether exposed to a simulated climate change (including drought and heat wave conditions) or not, the diversity of species established in quarry-to-alvar restoration appears to play a strong role in the capacity for restored communities

to maintain vegetation cover in the face of extreme environmental fluctuations - notorious sources of restoration failure only expected to intensify under global climate change scenarios. We therefore recommend that quarry managers ensure the stability of restored communities - whether mimicking natural alvars or some alternative target ecosystem - by introducing and facilitating establishment of a broad diversity of target species.

2. Given that contrasted high- and low-diversity communities contained the same species on average and exhibited equivalent cover among all treatments prior to the experimental climate change, differences in resistance among treatments must be due to species co-occurrence rather than sampling effects. This increases our confidence that it is the *number* of species, above and beyond the *identity* of species, underlying stabilizing effects of biodiversity in this system, and thus outcomes of following Recommendation 1 – more species – cannot be duplicated by focusing on just a few *particular* species.

3. Patterns observed in this and previous studies suggests that at least 6-12 species are required before beneficial effects of more diverse communities are detectable; we recommend a minimum of 12 species within relatively small-area patches of quarry floor (e..g > 1 m^2) be considered as a goal in quarry-to-alvar restoration practice. An upper limit of biodiversity establishment to strive for cannot be recommended at the present time due to lack of knowledge of biodiversity effects at very high levels of species richness (e.g. > 25 species / m^2); however, the maximum species richness observed in alvar-seeded quarry and natural alvar plots studied previously was approximately 30 species / 0.18 m^2 (Richardson et al. 2009). Given that such extraordinary species diversity is at least possible on "biodiversity hotspot" rock outcrops, $\approx$ 30 species / m^2 may represent a suitable interim upper target for alvar biodiversity restoration on quarry floors, until more information on the effects of spatial scale on biodiversity-stability relationships is obtained.

4. On average only about one-half of the species seeded to any given plot establish in this system (Richardson and Larson 2009), and at the site scale quarries are mosaics of different environmental "patches" containing conditions optimal for distinct sets of species. We therefore suggest that a considerably larger pool of species – perhaps on the order of 60-80 species total – must be at hand to achieve maximum diversity goals targeted (e.g. 20-30 species / m^2). For example, a single quarry site may consist of distinct patches particularly well suited to alvar pavement, calcareous fen, tallgrass prairie, or natural cliff-face species; a large species pool containing many species capable of specializing in each of these distinct habitat types would therefore be needed to achieve high biodiversity within each patch, as well as among patches. Fortunately, the economic costs associated with such intensive species introduction efforts should be offset by the conservation benefits of utilizing quarry sites as biodiversity refuges to their maximum potential, as well as the economic benefits of achieving high-functioning communities that are extremely resistant to future disturbance and climate change.

5. The variety of relationships observed at the level of individual species populations between the number of alvar species established and resistance of vegetation cover to simulated climate change is consistent with at least two different classes of mechanisms

operating simultaneously to induce observed biodiversity effects on community stability. Both classes depend upon species co-occurring in space, but they differ with respect to the nature of interactions among species. The first class relies upon diverse species competing intensely such that when perturbation damages one species population in a community, other species are released from competition with these dominant but perturbation-sensitive species, causing rates of plant growth or functioning to increase in the released species such that damage to the sensitive species is compensated for at the community level. The second class relies upon species interacting positively, such that the negative impact of disturbance on the survival or growth of individuals belonging to some species is dampened by the presence of other species due to facilitative effects such as shade provision and increased water availability. The fact that our results are consistent with both mechanisms operating simultaneously suggests that species interactions in this system may be complex, but positive impacts of diversity stability may be robust precisely because multiple mechanisms exist. This implies that focus need not be placed on introducing just species that interact either positively or negatively; both types of interaction can contribute to increased stability with diversity.

6. The patterns observed at the level of individual species populations provide some insight with respect to which particular species are likely to be successful colonizers of quarry floors. Of the 13 native alvar species planted here, six produced vegetation that covered at least 8-10% of experimental plot surfaces on average, with many instances of exceptional cover by the late summer wildflowers *Coreopsis lanceolata* (Lance-leaved Coreopsis) and *Rudbeckia hirta* (Brown-Eyed Susan), good cover by the grass *Panicum virgatum* (Switchgrass), and moderately high cover by the wildflowers *Solidago ptarmicoides* (Upland White Goldenrod) and *Penstemon hirsutis* (Hairy Beardtongue), and the grass *Elymus trachycaulus* (Slender Wheatgrass). However, an important lesson about the potential effectiveness of utilizing these species in practice comes from population-level diversity-resistance patterns: under climate-change conditions, maximum growth is in five of these six "best performing" species (i.e. all but the *Coreposis*) was obtained only where neighbour diversity was maximal. This implicates facilitation as important to the colonization success of these species and suggests that if they are to achieve their considerable full functional potential on quarry floors, a high diversity of neighbour species should additionally be established.

7. While the method of substrate addition used here to promote establishment of alvar biodiversity on quarry floors was not specifically tested in this study, the successful establishment of most species introduced and the relatively high vegetation cover achieved indicates that our approach of mixing the naturally occurring quarry subatrate with a blend of silica sand and low-nutrient vegetable or mushroom compost provides nutrient conditions sufficient for growth of alvar plant species. Addition of this substrate in the present and previous studies increased total substrate depth by approximately 2 cm, and provided substrate in patches otherwise barren, leading to more consistently successful quarry colonization than previous work where only seeds were added. This quantity of substrate was similarly effective for seeds and plugs planted, and on the grounds of the success observed here we recommend use of similar substrate remediation where quarry-to-alvar restoration is attempted at larger scales. Similarly, the inclusion of

polyacrylimide tackifier in the substrate amendment, designed to bind seeds and substrate to the quarry surface, was not specifically tested but in some cases the success of introduced communities on patches of particularly scarce or unstable substrate may well be due to this tackifier. While further research on the utility of such products may yield interesting results, given the relatively low cost of the tackifier, the low likelihood that it will negatively impact plant growth, and the likelihood that in at least some instances alvar species establishment was helped by the capacity of tackifier to adhere seeds and substrates to the frequently flooded and wind-blown quarry floors, we recommend further use of this product in quarry rehabilitation projects, at least in situations where there is moderate desire for broadcast seeds to establish in the particular location seeded.

8. The question of whether seeds or plant plugs are more effective methods of alvar species introduction was not specifically addressed in this study, but the experiment reported here follows one previous experiment where only seeds were added, and another experiment where only plugs were added, and represents the first occasion where both seeds and plugs were introduced to the same plots. Without formal analysis, both seeds and plugs were successful under some microhabitat conditions but not others, but while seed addition was generally sufficient to achieve moderate vegetation cover on quarry floors, plug addition was frequently necessary to achieve particular community structures such as a targeted number or composition of species. From this we recommend that larger-scale quarry restoration start with an initial broadcast of diverse species as seeds intermixed with alvar-like substrate (see above), but follow-up with addition of small plugs containing species that established poorly from seed but may have particular functional or conservation value. Plug addition may well be necessary to achieve communities that are sufficiently diverse to produce stabilizing effects on vegetation cover and other ecosystem properties.

9. Quarry floors have potential to serve as highly effective ecological "laboratories" as well as conservation habitat and aesthetically pleasing parks and nature preserves. We have to date used quarry-to-alvar restoration as a model system for testing fundamental theories about community assembly, biodiversity maintenance, environmental heterogeneity, ecosystem functioning, and functional stability in a globally-changing climate. Much potential exists for further pure and applied ecological research on quarry floors. Moreover, the results of such research will inevitably feed back on the usefulness and efficacy of ecosystem restoration or reconstruction in depleted quarries and other high-stress human-altered environments. In particular, for both theoretical and practical reasons the role of scale in determining community assembly rules and interrelationships among biodiversity, heterogeneity, stability, and ecosystem functioning must be better understood. For example, where quarries are mosaics of habitat patches ranging from cliff-faces and wetlands to pavement, scrubland, and grassland, how will multiple restored ecosystem properties over various practical timescales depend upon both the diversity of species introduced and the diversity of analogous natural ecosystems represented (e.g. site-scale effects of introducing 30 alvar pavement species vs. 10 pavement species plus 10 calcareous fen species plus 10 tallgrass prairie species)?

Expanding the potential colonist species pool to include groups such as mosses, mycorhizal fungi, and wetland vegetation may have powerful impacts on ecosystem stability and multi-functionality - topics of great theoretical interest, but also of practical concern given the extent to which established biodiversity appears to directly influence restoration success. We recommend that the best method for addressing such pressing research questions is to couple a simple but powerful experimental research design with large-scale "on-the-ground" quarry restoration projects.

Finally, strong research potential exists for exploiting the capacity of quarry floors to mimic extreme environmental conditions and variability in environmental conditions predicted to occur widely in the future as a result of global climate change. Further experimental work could enable better prediction of how different ecological communities will respond to climate change, enabling formulation of guidelines for adapting anthropogenic ecosystem management to ensuing climate change.

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