Yield–density functions as predictors of community structure in a serpentine annual grassland

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Summary

1 Two series of competition experiments involving the four annual plant species Bromus hordeaceus, Calycadenia multiglandulosa, Plantago erecta and Microseris douglasii were conducted in an experimental array of pots located at the Jasper Ridge Biological Preserve, San Mateo County, California, USA. One experiment was conducted during the 1988–89 growing season, the other during the 1989–90 growing season.

2 A four-species yield–density model was constructed using seed yield data from the 1988–89 experiment. Model predictions were tested against seed yield data from the 1989–90 experiment. A systematic bias in predicted seed yields was found. As a consequence, the original model was reparameterized to provide a better fit to the observed yields for the 1989–90 experiment.

3 Analyses were conducted to determine the importance of potential sources of bias in the original model, including (i) mis-specification of density effects at low densities due to the parameterization protocol; (ii) interaction effects among competing species; and (iii) year-to-year variability in competitive interactions. All three sources had a significant effect on at least one of the species in the experiment, although significant sources differed between species.

4 Using two forms of sensitivity analysis, a comparison was made between the original and modified versions of the yield–density model to determine how they differed in predictions of long-term plant community dynamics. Rank order of average densities among species did not differ between models; however, there were several important differences in their predictions with respect to overall community structure. Implications of these results with respect to the use of yield–density models in studying plant community dynamics are discussed.

5 The present study indicates that the effectiveness of the generally employed yield–density model at characterizing competitive interactions under different environmental conditions depends upon the criteria employed in making an assessment. One possible explanation is that competitive interactions within the serpentine community are highly sensitive to changes in environmental conditions and we found some evidence for this in Calycadenia and Plantago.

Keywords: competition, density effects, seed yield, serpentine grassland, temporal heterogeneity

Introduction

Many factors play a role in determining the long-term abundance of species in plant communities. Intraspecific density effects can regulate population size by affecting the performance of individuals at various life-history stages, potentially placing an upper bound on population size (e.g. Fowler 1986; Bergelson & Perry 1989; Thrall et al. 1989). Competitive interactions between plant species can also play a significant role in controlling species abundance, and can produce complex interconnected dynamics at the community level that depend upon the relative density...
Yield-density functions as predictors

and biomass of the various species in the community (Fowler 1981; Fowler 1986; Goldberg 1987; Gerry & Wilson 1995). Population size can also be affected by spatial and temporal variation in environmental conditions. This variability may not only affect individuals directly, e.g. altering their fecundity or survivorship, but may also alter the impact of intra- and interspecific density effects on individual performance (Fowler 1986; Watkinson 1990; Stone & Roberts 1991; Fowler 1995).

It is often difficult to follow populations over a long enough time frame, in enough detail, to determine how competitive interactions might affect the long-term dynamics of the plant community. Many studies therefore take short-term observations, build a model, and then use this model to predict community level dynamics at a broader spatial and/or temporal scale (Hobbs & Hobbs 1987; Pacala & Silander 1990; Silvertown et al. 1992; Wiegand et al. 1995; Jettsch et al. 1996; Moloney & Levin 1996; Pacala et al. 1996; Schwinning & Parsons 1996). This approach can provide insights into the long-term consequences of localized processes on community level dynamics, but a model parameterized from data collected under only a limited set of environmental conditions might have limited applicability. Year-to-year variability in environmental conditions could therefore play a fundamental role in determining the long-term dynamics of plant communities, unless biotic interactions constrain its impact.

The effects of competition in regulating plant communities have often been analysed through yield-density relationships (cf. Watkinson 1980; Coussens 1985; Firbank & Watkinson 1985; Pacala & Silander 1985; Silander & Pacala 1985; Coussens et al. 1987; Law & Watkinson 1987; Coussens et al. 1988; Pacala & Silander 1990; Turkington & Joliffe 1996). When the primary interest has been in understanding the role of competition in determining the long-term dynamics of a system, experiments have generally been conducted during one year, either in the field or under controlled experimental conditions (e.g. Firbank & Watkinson 1986; Law & Watkinson 1987; Pacala & Silander 1990), and the resulting relationships have then been used to develop a long-term model (although see the multi-year studies of Rees et al. 1996 and Law et al. 1997). Other studies, however, have shown that the outcome of competitive interactions is sensitive to environmental variation in space and time (e.g. Rees et al. 1996; Turkington & Joliffe 1996). We present a 2-year experimental study of the role of intra- and interspecific competitive effects among four species from a serpentine annual grassland community, which combines the two approaches and examines the importance of year-to-year environmental variability in being able to predict long-term community level dynamics. We also take a critical look at whether the typical methods used in parameterizing yield-density models significantly bias their predictive ability.

Study system

The ridge-top serpentine grassland in the core of the Jasper Ridge Biological Preserve (JRBP) of Stanford University, San Mateo County, California, has been the subject of a broad range of experimental and observational studies over the last 20 years (e.g. Gulmon et al. 1983; Hobbs & Mooney 1985; Mooney et al. 1986; Huenneke et al. 1990; Hobbs & Mooney 1995; Valentini et al. 1995). Most of the plant species are annuals and the composition of the plant community therefore responds quite rapidly to changing environmental conditions and, presumably, also to competitive interactions (Hobbs & Mooney 1991). Patterns of species dominance change markedly from year-to-year in response to variation in the timing and amount of precipitation within the mediterranean-style climate.

Primary productivity is quite low (100–200 g m\(^{-2}\) above-ground), reflecting a much stronger limitation by below-ground resources than by light. Soil depth and nutrient availability, however, vary dramatically at small spatial scales and in situ competition experiments may be very difficult to interpret. Although it is possible, when studying competition, to thin and supplement communities in the field (e.g. Reynolds 1995), it is quite difficult to establish large, well-replicated experiments with uniform below-ground resources. We therefore grew plants in deep pots at a site close to the serpentine grassland.

Numerous aspects of the grassland environment might play an important role in determining the outcome of species interactions and subsequent patterns of coexistence. We therefore attempted to replicate the effects of soil depth and profiles of soil type, moisture and temperature. The plants also received natural levels of sunlight and precipitation. Soil disturbance associated with soil mixing and filling the experimental pots, although potentially a problem, may mimic disturbance by gophers at Jasper Ridge (Hobbs & Mooney 1985, Hobbs & Mooney 1991; Moloney 1993).

Four common annual plant species, Bromus hordeaceus L., Calycadenia multiglandulosa DC, Plantago erecta Morris and Microseris douglasii (D.C) Sch.-Bip., encompass most of the observed range of variation in annual life-history traits. Nearly all the serpentine species found at Jasper Ridge germinate in the autumn after the first significant rainfall breaks the summer drought, and have little or no seed bank that carries over from year to year (Hobbs & Mooney 1985). One of the studied species, Bromus, is a non-native invading grass, while the other three are native forbs (Hobbs & Mooney 1985; Hobbs & Mooney 1991). Plantago flowers in March, Microseris in early April, Bromus in late April, and Calycadenia in July. Later flowering dates in this system tend to be associated with higher individual plant biomass at maturity and greater rooting depth (Gulmon et al. 1983;
Mooney et al. (1986). Differences in rooting depth may represent an important mechanism for avoiding competition in this semi-arid ecosystem, since soil moisture is an important limiting resource (Breshears et al. 1997; Goldberg & Novopansky 1997).

We characterized the relationship between planting density and yield in two experiments. During the 1988–89 growing season, we tested all possible single-species and two-species plantings of Bromus, Calycedena, Microseris and Plantago, whereas in 1989–90 all possible two-species, three-species and four-species combinations were tested. Data from the 1988–89 experiment were used to parameterize a four-species competition model, which was tested by comparing predicted and observed yields for the 1989–90 experiment. A second version of the competition model was then developed to fit the 1989–90 data. We determined whether systematic differences were due to environmental differences between years or to biases arising from two commonly employed assumptions used in fitting model parameters. Finally, we conducted a sensitivity analysis, using both models, in an exploration of the impact of differences in model fit on predictions of the long-term dynamics of the serpentine community.

Methods

Basic Design

Arrays of pots constructed from 1-m lengths of 10.2-cm diameter PVC pipe had been previously established at a site 1.5 km west of the serpentine grassland. Each array of 6 × 18 pots was housed in a wooden frame. The frames were arranged outdoors in two rows on a level concrete pad and were suspended above ground to allow sufficient drainage. The free space between the pots was filled with Styrofoam and expandable foam to allow formation of a natural soil thermal profile. The surface area of each pot was 0.008 m², large enough to support an average of seven to nine species (N. Chiariello, unpublished data) and over 200 individual plants (Huenneke et al. 1990) in undisturbed serpentine grassland.

Serpentine soil and subsoil were obtained from a grassland 40 km from Jasper Ridge. Subsoil and bedrock were crushed to 2.5 cm. Surface soil was transported to the JRBP, spread on a concrete slab, watered sufficiently to pregerminate resident seeds, allowed to dry, and then mixed. A wad of polyester wicking that extended into a drainage tube was placed at the base of each pot to simulate the matric potential of the soil and prevent pooling of water in the pot. Each pot then received 0.85 m subsoil and 0.15 m topsoil. Ratios of calcium to magnesium were 0.090 for the topsoil in the pots, compared with a ratio of 0.047 for topsoil on Jasper Ridge (P. Rundel, personal communication).

Fertilizer treatments had been applied to some of the pots in a previous experiment conducted during the 1987–88 growing season. All above-ground plant material, including litter, was removed from the pots and the variation in nitrogen availability reduced by watering until leachate concentrations of ammonium and nitrate from fertilized pots were reduced to the levels of unfertilized pots.

Seeds were collected from serpentine grasslands at JRBP and were given no pretreatment prior to planting. Two cultivars were planted during late September by sprinkling them on the soil surface and covering them with 2–4 mm of dry soil. High planting densities were used to allow for incomplete germination (Gulmon 1992) and pots were thinned to target densities after germination.

Competition Experiments

1988–89 Season

One-hundred single-species treatments (10 replicates at 10 target densities) were established for each of the four species. Density treatments ranged from one plant per pot (123 plants m⁻²) to 20 plants per pot for Calycedena, 100 plants per pot for Microseris and 400 plants per pot for Bromus and Plantago. Maximum densities exceeded typical field densities (Hobbs & Mooney 1985) by a factor of 9 for Calycedena, 20 for Plantago and 200 (75 on gopher mounds) for Bromus. One row of four frames (i.e. 6 × 72 pots) was used for single-species experiments. Each 6 × 9 section contained half the plantings (randomly assigned) for a single species and four empty pots.

All 12 possible focal species–competitor combinations were tested. Densities of the competitor species ranged from three to 10 plants per pot for Calycedena, 10 to 100 per pot for Microseris, and 10 to 300 per pot for Plantago and Bromus. The density of the focal species was one plant per pot when competitor densities were less than 100 plants per pot, or three per pot at higher competitor densities. The 35 plantings (seven replicates at five target densities) for each competitor–focal species combination were randomly assigned within a 6 × 6 block of pots (one blank per block) from within the second row of frames. Seeds were distributed evenly within the pot to avoid clumping, but we did not attempt to establish regular spacing of the focal species.

1989–90 Season

Single-species treatments were not repeated due to logistical constraints. High, medium and low densities were set for each species (Table 1a). Three density treatments were established for each two-species combination (treatments 1, 2 and 3, Table 1b), one density treatment for each three-species combination (treat-
Table 1 Planting design for the 1989–90 two-, three- and four-species competition experiments

(a) Key to densities (plants per pot)

<table>
<thead>
<tr>
<th></th>
<th>Low (L)</th>
<th>Medium (M)</th>
<th>High (H)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bromus</td>
<td>5</td>
<td>50</td>
<td>100</td>
</tr>
<tr>
<td>Calycadenia</td>
<td>3</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Microseris</td>
<td>10</td>
<td>25</td>
<td>45</td>
</tr>
<tr>
<td>Plantago</td>
<td>3</td>
<td>50</td>
<td>100</td>
</tr>
</tbody>
</table>

(b) Densities in two- and three-species treatments (all possible combinations)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Species 1</th>
<th>Species 2</th>
<th>Species 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>H</td>
<td>L</td>
<td>—</td>
</tr>
<tr>
<td>2</td>
<td>L</td>
<td>H</td>
<td>—</td>
</tr>
<tr>
<td>3</td>
<td>M</td>
<td>M</td>
<td>—</td>
</tr>
<tr>
<td>4</td>
<td>M</td>
<td>M</td>
<td>M</td>
</tr>
</tbody>
</table>

(c) Densities in four-species treatments (numbers are plants per pot)*

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Bromus</th>
<th>Calycadenia</th>
<th>Microseris</th>
<th>Plantago</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
</tr>
<tr>
<td>2</td>
<td>0.5 M</td>
<td>0.5 M</td>
<td>0.5 M</td>
<td>0.5 M</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>2</td>
<td>14</td>
<td>33</td>
</tr>
<tr>
<td>4</td>
<td>33</td>
<td>2</td>
<td>14</td>
<td>33</td>
</tr>
<tr>
<td>5</td>
<td>33</td>
<td>2</td>
<td>3</td>
<td>33</td>
</tr>
<tr>
<td>6</td>
<td>33</td>
<td>2</td>
<td>14</td>
<td>3</td>
</tr>
</tbody>
</table>

*Numbers in bold typeface indicate the single species planted at lower density in a four-species treatment.

Germination, thinning of plants and data collection

Prior to germination, each bank of pots was covered with a 40% shade cloth to prevent seed loss to birds. All pots with 50 or fewer plants of a species were censused and thinned to target densities 2–3 weeks after germination, except for treatments combining Microseris and Plantago which are difficult to distinguish at the seedling stage. Every pot was fully censused in mid-December and thinning was completed where necessary. Pots with target densities of 50 or fewer plants were censused again 6 weeks later.

Plants were grown to maturity. Above-ground plant material was harvested after seeds were filled but before they dispersed. Harvest dates ranged between May and September, depending upon the phenology of the species. In multispecies treatments, species were harvested individually to minimize loss of seeds or biomass. For each pot we recorded the number of reproductive plants and dried and weighed above-ground biomass for each species. After the biomass was dried, we removed and weighed all seeds. For each pot and species, we weighed a random sample of 10 seeds and used this value to convert total seed biomass to total seed number. For Calycadenia, ray and disk achenes were handled separately.

Methods of analysis

Choice of model

A general model that has been successfully used to describe yield–density relationships in plants is given by the non-linear equation:

\[ y = (x + \beta x)^{-1/\theta} \]  

(1)

where \(\alpha\), \(\beta\) and \(\theta\) are parameters, \(x\) is plant density and \(y\) is yield per plant (Bleasdale & Nelder 1960; Watkinson 1980; Firbank & Watkinson 1985; Watkinson et al. 1989). Other yield–density models offer, at best, only minimal improvement over equation 1 (Cousens 1985; Silander & Pacala 1985; Turkington & Joliffe 1996). The single species model in equation 1 can easily be extended to account for density effects on yield among several species as follows:

\[ y_i = \left( x_i + \sum_{j=1}^{s} \beta_{ij} x_j \right)^{-1/\theta} \]  

(2)

Here, \(y_i\) is yield per plant for species \(i\), \(\beta_{ij}\) is a parameter characterizing the density effect of species \(j\) upon species \(i\), and \(x_j\) is the density of species \(j\) (cf. Firbank & Watkinson 1985; Watkinson 1986).

Equation 2 assumes that interspecific competitive effects are additive: this may not necessarily be the case. One study that explicitly investigated the importance of interaction effects found them to be not significant (Turkington & Joliffe 1996). Most studies implicitly assume non-significance by leaving inter-
action effects out of the modelling process (e.g. Fir-
bank & Watkinson 1985; Pacala & Silander 1990). This is
done in part because of the data requirements and the dif-
culty of parameterizing interactions in a non-linear model.
Although we could not investigate interaction effects
directly, since density treatments were not applied in a
completely crossed design in 1988–89, we did examine the
impact of ignoring these effects on the model’s predictiv-
ability.

Model parameterization
We parameterized a four-species version of equation
2 for *Calycadenia*, *Microseris*, *Plantago* and *Bromus*
using seed yield and species density data from the
1988–89 experiment.

The parameters *x*, *θ*, and *β* for each species *i* were
estimated by weighted, non-linear least squares
regression (SAS Institute Inc. 1985) using data from the
single-species experiments. A log transform was
applied to seed yield data prior to regression to sta-
bilize the variance, which is often greater at lower
densities (Seber & Wild 1989; Turkington & Joliffe
1996). The greater importance this gives to high den-
sity treatments may reduce model fit at lower densities
and thus affect the ability of the model to fit data
from different years.

Data from two-species competition experiments
were used to estimate *β* for each of the 12 possible
two-species models:

\[
S_i = (x_i + \beta_{ij}x_j + \beta_{ji}x_i)^{-1/\theta},
\]

where *i* ≠ *j*, and *S* is the predicted seed yield for an
individual of species *i*. Each analysis used data from
density treatments in which the focal species, *i*, was
planted at low density (one to three individuals) and
the competing species, *j*, was planted over a relatively
broad range of densities. Each datum from the two-
species experiments was used in only one analysis.
Parameters (denoted as *s*, *β*, and *θ*) estimated from
the single species experiments were substituted into
equation 3. Equation 3 was then linearized prior to
analysis to be of the form *S* = *β* *x*, where

\[
S^* = s^* - \hat{S}^* - \beta_{ij}x_j, \text{ by converting seed yields for the}
\]

focal species *S* to values of *S* prior to analysis. A
weighted least-squares approach, once again assuming a log transform, was used in fitting *β*’s
(Seber & Wild 1989).

In the third stage of model construction, the par-
parameters estimated in stages 1 and 2 were combined
into the final four-species model (hereafter referred to
as the original model).

Model verification
We used data from the 1989–90 experiments to assess
the accuracy of the original model in estimating seed
production during a different growing season. Esti-
mated values of seed production per plant (*S* *) ) for
each species *i* in each pot *k* were obtained by entering
observed adult plant densities at the time of seed
production into the original model. Observed values of
seed production, *S*, were then regressed on the
estimated values *S*, after both *S* and *S* were trans-
formed using natural logs. This yields the regression
model:

\[
\log(S) = y_i + \xi \log(S) + \varepsilon_i
\]

which provides two tests of the model’s ability to
predict the observed data for each species. This can
be expressed through the two null hypotheses, *H* : *y* = 0
and *H* : *ξ* = 1.0. Rejection of either null hypothesis
indicates that predictions made by the parameterized
model differ in a systematic way from observed values.

One advantage of conducting the regression analy-
isis on log-transformed values was that we could take
the parameter estimates obtained through equation 4
and back-transform them to obtain a revised model
(modified model) that takes into account systematic
deviations of the seed yield estimates from the
observed values. The modified model then becomes:

\[
s_i = \left(\frac{a_i + \sum_{j=1}^{n} \beta_{ij}x_j}{\gamma_i + \xi \beta_{ij}}\right)
\]

where *s* represents the modified model estimate for
seed yield by an individual plant. (Equation 5 is
obtained by combining equation 4 with equation 2.)

Sources of systematic bias in model predictions
We tested three potential sources of bias in the orig-
inal model’s ability to predict 1989–90 seed yields.

1 Protocol effects: the weighting scheme used in par-
parameterization gives a better fit at higher densities,
i.e. a systematic bias in the prediction of 1989–90
data could be due to the average planting densities
being lower than in 1988–89.

2 Interaction effects: the model assumption that
interspecific competition does not involve sig-
ificant interactions among species, i.e. predictions
might be inaccurate because competition cannot be
adequately characterized by an additive model.

3 Year-to-year environmental effects: a model par-
parameterized during one growing season is unable to
predict seed yields during a subsequent year due to
a fundamental change in competitive relationships
in response to different environmental conditions.

We conducted three separate, two-way con-
tingency table analyses to determine which of these
effects might have biased the predictive ability of the
original model. Data were placed in two categories,
those where seed yields were more accurately pre-
dicted by the original model and those where seed
Yield-density functions as predictors

Protocol effects were examined by contrasting two subsets of data from the 1988–89 experiments: (i) Low Density subset—single-species and two-species treatments with normalized densities (calculated as \( d_i + \sum \beta_j x_j \)) falling within the range of densities used in the 1989–90 experiment; and (ii) High Density subset—treatments falling above the same range of densities (i.e. a normalized density above 0.17, 0.086, 0.19 and 0.14 for Bromus, Calycadenia, Microseris and Plantago, respectively). If the weighting scheme produced a systematic bias, we would expect the modified model to be a better predictor for the low density treatments and the original model to be better for the high density treatments.

We examined the effect of ignoring non-additive interactions among species in the original model by analysing two subsets of the 1988–89 low density data: (i) Intraspecific subset-data from the single-species experiments; and (ii) Interspecific subset-data from the two-species experiments. If non-additive competitive effects among species were significant we would expect the modified model to be a better predictor for the interspecific data subset, and the original model to be better for the intraspecific data subset. Potential biases produced by density effects and by year-to-year environmental variability were minimized by using only low density data from the 1988–89 experiment.

Year-to-year environmental effects were examined by comparing data from the two-species competition treatments (the only ones replicated) for the 2 years. Higher order interactions that may occur in the three- and four-species competition treatments did not therefore complicate the results. Only low density treatments were included in the 1988–89 data set. If year-to-year differences had a significant impact on competitive interactions, we would expect the modified model to be a better predictor for the 1989–90 treatments and the original model to be better for the 1988–89 treatments.

### Model comparisons

We used simulations based on the original and modified models to examine the implications of parameterization under different conditions in making long-term predictions of community level processes. Coupled sets of four difference equations were constructed by adding terms for germination rates \( g_i \) and survivorship \( f_i \) to the basic yield-density function to complete the life cycle:

\[
x(t + 1) = g_i f_i \left( \alpha_i + \sum_{j=1}^n \beta_{ij} x_j(t) \right)^{-1/	heta_i}.
\]  

Table 2; also see Hobbs & Mooney 1985; Hobbs & Hobbs 1987; Gulmon 1992).

Two forms of sensitivity analysis were conducted. The first analysis examined sensitivity to initial conditions by choosing the initial abundances for the four species at random, with equal probability, from the set of integers ranging from 1 to 500. A second analysis examined sensitivity to the choice of values for \( g_i \) and \( f_i \), because of the great variability of germination and survivorship rates observed in previous field and experimental studies. For each species, \( g_i f_i \) was multiplied by a random variable \( \delta_i \) (chosen from a uniform distribution ranging from 0.8 to 1.2) at the beginning of each replicate run. Initial population densities were set at 233 individuals m⁻² (approximately two individuals per species per pot in our experiments).

Five-hundred replicate runs were conducted for each sensitivity analysis for each of the two models. For each run, we iterated the model for 300 time steps, corresponding to a 300-year simulation. Population values were truncated to integers at the end of each iteration. Comparisons of community composition at the end of model runs were made using standard statistical techniques.

### Results

#### EXPERIMENTAL AVERAGES

The range of densities used in the two experiments was intentionally greater than the range observed under natural field conditions (Table 3). Average values for individual biomass and seed production were generally greater than field values, although values in 1989–90 for Bromus and Calycadenia were lower. For all species, individual plants in the 1988–89 experiment were up to four times larger and produced up to five times as much seed as plants in the 1989–90 experiment (Table 3). This could be due in part to differences in experimental design, although the lower total densities in 1989–90 would have been expected to lead to higher levels of individual production. Lower production during 1989–90 was therefore more likely due to differences in environmental conditions; the 1988–89 growing season was a near average year in terms of rainfall (514 mm of rain; 20 year average = 584 mm), whereas 1989–90 was a relatively dry year (369 mm of rain).

#### MODEL PARAMETERIZATION

The first step in the parameterization of the yield-density models, using the single-species experiments, was successful in capturing the general relationship between planting density and seed yield. The single species models predicted seed yields well, particularly at the higher densities (Fig. 1; parameters in Table 4). There was a slight tendency to overestimate seed
Table 2 Parameter values for germination rates (g;) and survivorship (f;) for each of the species i in the difference equation simulation models (equation 6) (see text for details)

<table>
<thead>
<tr>
<th>Species</th>
<th></th>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>Parameter</td>
<td>$Bromus$</td>
<td>$Calycadenia$</td>
<td>$Microseris$</td>
</tr>
<tr>
<td>$g_i$</td>
<td>0.98</td>
<td>0.78</td>
<td>0.80</td>
</tr>
<tr>
<td>$f_i$</td>
<td>0.49</td>
<td>0.58</td>
<td>0.80</td>
</tr>
</tbody>
</table>

Table 3 Comparison between field observations and experimental treatments at Jasper Ridge for average density, biomass and seed production for studied species (standard deviations are in parentheses). Field data are for undisturbed sites (Hobbs & Mooney 1985). Experimental data represent averages over all treatments within each of the 2 years of experiments (no field data were available for Microseris)

<table>
<thead>
<tr>
<th>Source of data</th>
<th>$Bromus$</th>
<th>$Calycadenia$</th>
<th>$Microseris$</th>
<th>$Plantago$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density of flowering plants (per m$^2$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field observations</td>
<td>240 (90)</td>
<td>290 (40)</td>
<td>NA</td>
<td>2550 (180)</td>
</tr>
<tr>
<td>1988–89 Experiment</td>
<td>10736 (13577)</td>
<td>474 (348)</td>
<td>3154 (3702)</td>
<td>12952 (16200)</td>
</tr>
<tr>
<td>1989–90 Experiment</td>
<td>5434 (3896)</td>
<td>317 (234)</td>
<td>3139 (1294)</td>
<td>6202 (4013)</td>
</tr>
<tr>
<td>Average biomass per flowering plant (mg)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field observations</td>
<td>39.6 (6.2)</td>
<td>98.6 (32.6)</td>
<td>NA</td>
<td>17.9 (4.4)</td>
</tr>
<tr>
<td>1988–89 Experiment</td>
<td>45.1 (99.4)</td>
<td>214.9 (168.0)</td>
<td>90.0 (146.7)</td>
<td>49.8 (80.7)</td>
</tr>
<tr>
<td>1989–90 Experiment</td>
<td>10.9 (9.9)</td>
<td>59.6 (59.1)</td>
<td>33.2 (18.5)</td>
<td>28.1 (19.5)</td>
</tr>
<tr>
<td>Average seed production per plant</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field observations</td>
<td>9.9 (1.1)</td>
<td>17.9 (2.8)</td>
<td>NA</td>
<td>3.7 (0.1)</td>
</tr>
<tr>
<td>1988–89 Experiment</td>
<td>15.5 (33.3)</td>
<td>21.4 (18.6)</td>
<td>41.1 (72.3)</td>
<td>18.6 (31.5)</td>
</tr>
<tr>
<td>1989–90 Experiment</td>
<td>3.2 (3.1)</td>
<td>3.7 (5.8)</td>
<td>10.2 (7.6)</td>
<td>5.7 (6.2)</td>
</tr>
</tbody>
</table>

Fig. 1 Seed production per plant and the yield–density function for Bromus, Calycadenia, Microseris and Plantago in the 1988–89 moniculture competition experiments. Standardized densities plotted are calculated as $\hat{\delta}_i + \hat{\beta}_i x_i$ for each species $i$ (see text for details). Standardizing the x-axis in this way allows direct comparison with plots of data from the multispecies competition experiments. The parameterized yield–density function for each species, $y_i = (\hat{\delta}_i + \hat{\beta}_i x_i)^{-1/\beta_i}$, is represented by the solid line.
Table 4 Parameter estimates for the yield-density equation involving only intraspecific competition (equation 1), corresponding to \( \alpha, \beta, \) and \( \theta \) in equation 2, as obtained through weighted, non-linear regression analysis. (See the methods for a detailed explanation of the analysis.) Parameter values of \( \beta, \) and the associated asymptotic standard errors were adjusted after analysis to express results in terms of densities of plants per m². The analysis itself was conducted using observed values of plant abundance in the pots.

<table>
<thead>
<tr>
<th>Species</th>
<th>( n )</th>
<th>( \alpha ) Estimated value ( \times 10^{-4} )</th>
<th>Asymptotic SE ( \times 10^{-4} )</th>
<th>( \beta ) Estimated value ( \times 10^{-5} )</th>
<th>Asymptotic SE ( \times 10^{-5} )</th>
<th>( \theta ) Estimated value</th>
<th>Asymptotic SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bromus</td>
<td>93</td>
<td>0.00</td>
<td>6.00</td>
<td>1.14</td>
<td>0.11</td>
<td>1.18</td>
<td>0.077</td>
</tr>
<tr>
<td>Calycadenia</td>
<td>99</td>
<td>23.00</td>
<td>63.00</td>
<td>7.38</td>
<td>0.51</td>
<td>1.00</td>
<td>-</td>
</tr>
<tr>
<td>Microseris</td>
<td>100</td>
<td>0.50</td>
<td>4.20</td>
<td>2.43</td>
<td>0.16</td>
<td>0.98</td>
<td>0.028</td>
</tr>
<tr>
<td>Plantago</td>
<td>98</td>
<td>0.01</td>
<td>6.00</td>
<td>0.98</td>
<td>0.12</td>
<td>1.33</td>
<td>0.113</td>
</tr>
</tbody>
</table>

*0 for Calycadenia was determined through a grid search (SAS Institute Inc. 1985) and then fixed for determining \( \alpha \) and \( \beta \).

Table 5 Parameter estimates for interspecific competitive effects (\( \beta \)) by four species on seed production in two-species competition experiments in 1988–89 (model in equation 4). Parameter values and the associated asymptotic standard errors were adjusted after analysis to express results in terms of densities of plants per m².

<table>
<thead>
<tr>
<th>Target species</th>
<th>Competing species</th>
<th>Estimated value ( \times 10^{-4} )</th>
<th>Asymptotic SE ( \times 10^{-4} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bromus</td>
<td>Bromus</td>
<td>33 1.22</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>Calycadenia</td>
<td>34 0.26</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>Microseris</td>
<td>34 0.26</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Plantago</td>
<td>34 0.26</td>
<td>0.03</td>
</tr>
</tbody>
</table>

\( s_p = (0.10 \times 10^{-5} + 0.12 \times 10^{-5} \cdot x_b + 0.43 \times 10^{-5} \cdot x_c + 0.36 \times 10^{-5} \cdot x_m + 0.98 \times 10^{-5} \cdot x_p)^{-0.75} \) (10)

Subscripts \( b, c, m \) and \( p \) in equations 7–10 represent the species Bromus, Calycadenia, Microseris and Plantago, respectively.

MODEL VERIFICATION

The original model did not do a particularly good job of predicting individual seed yields in the 1989–90 experiment. The predicted yields were higher than the observed yields for all four species (Fig. 2). Regression analyses of observed yields on predicted yields (both log-transformed) indicated that only one of the four intercept terms differed significantly from zero (Table 6) and we were therefore able to conduct a second regression analysis for each species, using a no-intercept model. All were highly significant, explaining between 61% and 95% of the variance in the data (Table 6). More importantly, the slope terms were significantly less than the expected slope of one \( (P < 0.0001 \) in all four cases; Table 6).

We used the estimated slope terms \( (\hat{\beta}) \) from the
Fig. 2 Seed yields predicted by the original model from 1989–90 plant densities and plotted against the observed seed yields in 1989–90 after log transformation. The solid line represents the expected regression relationship: a line with slope 1 and intercept 0. The broken line is the best fit, no-intercept, regression model (Table 6).

Table 6 Regression coefficients for intercept and no-intercept models examining the relationship between realized seed yield and predicted seed yield in the 1989–90 experiment. Observed values of individual seed yield were regressed on the predicted values after converting both to natural logarithms. Significance levels associated with $R^2$ represent significance levels for the overall model. Levels associated with the intercept and slope are significance levels for the individual parameters, with slope being tested for a significant difference from the expected value of 1.00.

<table>
<thead>
<tr>
<th>Species</th>
<th>Intercept model</th>
<th>No-intercept model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>d.f.</td>
<td>Intercept</td>
</tr>
<tr>
<td>Bromus</td>
<td>87</td>
<td>0.22</td>
</tr>
<tr>
<td>Calycadena</td>
<td>64</td>
<td>0.40</td>
</tr>
<tr>
<td>Microseris</td>
<td>87</td>
<td>−0.87**</td>
</tr>
<tr>
<td>Plantago</td>
<td>88</td>
<td>−0.10</td>
</tr>
</tbody>
</table>

* $P < 0.05$; ** $P < 0.01$; and *** $P < 0.001$.

SOURCES OF SYSTEMATIC BIAS IN MODEL PREDICTIONS

The source of bias in the original model differed markedly among species (Figs 4–6). For two of the species, Bromus and Plantago, a bias was introduced through the weighting protocol: the modified model did a better job of predicting seed yields at low densities, whereas the original model did a better job at the higher densities (Fig. 4). The original model appeared to fit the observed data for Microseris somewhat better at higher densities, although the results were not significant (Fig. 4).

For three of the four species, Bromus, Calycadena and Microseris, data suggested that competitive effects among species on seed yields were non-additive (Fig. 5). For Bromus, seed yields in the two-species treatments were fit better by the modified model, whereas both models did equally well at fitting the single-species treatments. For Calycadena and Microseris, the original model was only a good predictor for single-species results.
Fig. 3 Seed production per plant for the 1989–90 mixed-species experiments plotted against standardized community density $\delta + \sum_{i=1}^n \beta_i x_i$. The solid line represents the values predicted by the original version of the yield–density model and the dotted line represents the predictions made by the modified model.

Fig. 4 Number of cases where the original or modified model provided the better prediction of observed seed yields for *Bromus*, *Calycadenia*, *Microseris* and *Plantago* in low density and high density plantings from the 1988–89 competition experiments. $\chi^2$ values and their significance levels for an analysis of the corresponding two-way contingency tables are indicated.
Only two of the four species, *Calycadenia* and *Plantago*, exhibited a significant effect of year-to-year environmental variability on the ability to predict individual seed yields (Fig. 6). As expected, the modified model was the better predictor for the 1989–90 experiment. However, the improvement over 1988–89 results was only marginal for *Plantago* ($P < 0.04$ for the $\chi^2$ analysis comparing model fit across years; Fig. 6), and using a Bonferroni correction, to allow for each low-density two-species datum being used in two comparisons, gave an even more conservative estimate of $P < 0.08$ (Snedecor & Cochran 1980). However, if we included the three- and four-species treatments from the 1989–90 experiment in our analysis, the significance of the year-to-year bias for *Plantago* was greatly increased ($\chi^2 = 13.13; P < 0.0004$ for a contingency table analysis including all the 1989–90 treatments). This result could be due to the effects of higher order interactions rather than year-to-year environmental variability. However, of the four species in the experiment, *Plantago* was the only one that did not exhibit a significant interaction effect in comparing the single-species and two-species experiments (Fig. 5).

**COMPARISON OF THE TWO MODELS**

Predictions concerning species densities varied substantially between the original model and the modified model (Table 7). In the modified model, *Microseris* exhibited higher abundances and greater ability to persist compared to the original model, whereas *Bromus*, *Calycadenia* and *Plantago* declined in mean abundance. There was also less variability in species richness at the end of 300 iterations for model runs involving the modified model, particularly those runs exploring sensitivity to changes in parameter values (Fig. 7).

Long-term predictions made by both models were relatively insensitive to changes in initial conditions, as can be seen in the small standard deviations associated with variable initial conditions in Table 7. The only species with a moderate degree of variation was *Bromus*, which can be attributed to the fact that it was either extinct, or on the verge of extinction, in all runs. (In an extended analysis, we found that *Bromus* went extinct before the 319th iteration in all runs employing variable initial conditions.) Model outcomes were much more sensitive to alterations of the compound parameter $gf_n$ as evidenced by greater variability in mean abundance, than to alterations of initial conditions (Table 7). However, with the exception of *Bromus*, mean abundances for the species were quite similar in both sensitivity analyses (Table 7).

Varying parameter values had a greater effect on the number of species surviving to the end of a model run than varying initial conditions did (Table 7 and...
Yield–density functions as predictors

![Graphs showing yield–density functions for Bromus, Calycadenia, Microseris, and Plantago for original and modified model comparisons.](image)

Fig. 6 Prediction of seed yields in the 1988–89 and 1989–90 two-species competition experiments.

Table 7 Species survival and mean abundance at time step 300 in sensitivity analyses of the original and modified versions of the simulation model. Standard deviations in mean abundance are in parentheses and were calculated using the results from model runs where the species was still present at the end of the simulation.

<table>
<thead>
<tr>
<th>Variable initial conditions</th>
<th>Runs surviving (out of 500)</th>
<th>Mean density (individuals m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Original model</td>
<td>Modified model</td>
</tr>
<tr>
<td><strong>Bromus</strong></td>
<td>478</td>
<td>0</td>
</tr>
<tr>
<td><strong>Calycadenia</strong></td>
<td>500</td>
<td>500</td>
</tr>
<tr>
<td><strong>Microseris</strong></td>
<td>500</td>
<td>500</td>
</tr>
<tr>
<td><strong>Plantago</strong></td>
<td>500</td>
<td>500</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variable parameter values</th>
<th>Runs surviving (out of 500)</th>
<th>Mean density (individuals m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Original model</td>
<td>Modified model</td>
</tr>
<tr>
<td><strong>Bromus</strong></td>
<td>280</td>
<td>5</td>
</tr>
<tr>
<td><strong>Calycadenia</strong></td>
<td>500</td>
<td>493</td>
</tr>
<tr>
<td><strong>Microseris</strong></td>
<td>416</td>
<td>494</td>
</tr>
<tr>
<td><strong>Plantago</strong></td>
<td>500</td>
<td>500</td>
</tr>
</tbody>
</table>

Fig. 7. In varying parameter values, total community richness ranged from two to four species for both model versions, although only five modified model runs resulted in a two- or four-species community. In contrast, all of the model runs in the analysis employing variable initial conditions would have resulted in a three-species community comprised of *Calycadenia*, *Microseris* and *Plantago*, if the model was extended a little beyond 300 iterations, due to the extinction of *Bromus*.

Significant negative correlations in mean abundance were found for three of the six possible species pairs in model runs involving variable parameter values, i.e. *Bromus* and *Plantago*, *Plantago* and *Microseris*, and *Microseris* and *Calycadenia* (Table 8). These relationships indicate that improved conditions...
for one species (mediated through a change in germination and survivorship rates) lead, through competitive interactions, to poorer conditions for the other species, and vice versa. We also found a significant positive correlation between *Microseris* and *Bromus*, but only in the simulations involving the original model.

**Discussion**

The present study indicates that the effectiveness of the generally employed yield–density model at characterizing competitive interactions under different environmental conditions depends upon the criteria employed in making an assessment. The yield–density model fit to 1988–89 seed yield data generally overestimated yields in the 1989–90 experiment. One possible explanation is that competitive interactions within the serpentine community are highly sensitive to changes in environmental conditions, some evidence of which we found for *Calycadenia* and *Plantago*. This is not necessarily a problem nor is it particularly surprising; in fact, if we can adequately parameterize yield–density relationships across a range of environmental conditions, yield-density models could be used to study community dynamics under competition linked to historical weather patterns or other environmental processes. A nice example can be found in an elegant study by Turkington & Joliffe (1996). They examined the yield–density relationships between the clonal plants *Trifolium repens* L. and *Lolium perenne* L. and were able to demonstrate that inter- and intraspecific competitive effects were highly dependent upon time of harvest (within-season changes), age of the source pasture for clones (interpreted as being indicative of an evolutionary response to competitive interactions over varying lengths of time), and an interaction between these two factors. However, they did not attempt to use these relationships to explore long-term community dynamics explicitly, but were primarily interested in determining if there was a significant evolutionary response to past competition.

Turkington and Joliffe’s methodology could be used to parameterize yield–density models that include some measure of environmental variability as an independent variable. The impact of processes such as climate change on long-term community level dynamics could then be explored through simulation experiments. This approach, however, would require repeating yield–density experiments over the range of expected environmental conditions (over a number of years or using direct environmental manipulation). More importantly, the utility of the yield–density approach for studying long-term dynamics in plant communities may face other potential problems, notably the inability to predict yields equally well at low and high densities and the need to account for interaction effects among species.

Although we have not shown this directly, comparison of the predictive abilities of the two models

---

**Table 8** Pearson correlation coefficients for species abundances in the variable parameter sensitivity analyses of the original and modified simulation models. Significance levels were based on a Bonferroni correction for multiple comparisons among groups.

<table>
<thead>
<tr>
<th></th>
<th><em>Bromus</em></th>
<th><em>Calycadenia</em></th>
<th><em>Microseris</em></th>
<th><em>Plantago</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Original model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bromus</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td><em>Calycadenia</em></td>
<td>–0.11</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td><em>Microseris</em></td>
<td>0.39***</td>
<td>–0.27***</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td><em>Plantago</em></td>
<td>–0.62***</td>
<td>0.01</td>
<td>–0.75***</td>
<td>–</td>
</tr>
<tr>
<td><strong>Modified model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bromus</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td><em>Calycadenia</em></td>
<td>–0.08</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td><em>Microseris</em></td>
<td>0.05</td>
<td>–0.29***</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td><em>Plantago</em></td>
<td>–0.13*</td>
<td>0.01</td>
<td>–0.78***</td>
<td>–</td>
</tr>
</tbody>
</table>


*P < 0.05; ***P < 0.0001.*
Yield-density functions as predictors

suggests that for *Bromus, Calycadenia* and *Microseris* a significant bias in model predictions (at least at low densities) may be introduced by implicitly assuming that competitive effects among species are strictly additive (i.e. non-linear competitive interactions among species can be ignored). Improvement in the predictive ability of the model, which came through a reparameterization, may be a response, in part, to non-additive interaction effects among species. The only other studies that we know of, which examine the possibility of interaction effects influencing yield-density relationships in a multispecies experiment, are ones by Turkington & Joliffe (1996) and Suehiro & Ogawa (1980). No significant interaction effects between species were found. All of the other studies we have seen implicitly assume that competitive interactions are strictly additive, either because the interest is in looking at the impact of weed species on crop plants, with the density of the crop plant being held constant, or because the possibility of significant interactions is not explicitly considered. The importance of interactions among species in determining yield-density relationships clearly needs to be explored further.

The general yield-density model may not provide an equally good fit to yield data across the entire range of densities that are of interest. In fact, there may be a systematic bias in predictions across a subset of densities, as we found for *Bromus* and *Plantago*. The systematic bias at low density for these species can be traced to the weighting scheme used in parameterizing the yield-density equations. This scheme is a commonly employed technique used to correct for a generally recognized problem with yield-density data; variance in yield data is often negatively correlated to plant density, making estimation at low density difficult and parameterization with low-density treatments problematic (cf. Seber & Wild 1989; Pacala & Silander 1990; Turkington & Joliffe 1996).

We know of only one other study that has explicitly compared the predictive ability of yield-density models across a range of densities (Law & Watkinson 1987). In this study, model fit was biased at some densities, depending upon the specific yield-density model used and the species being considered. Unfortunately, very few studies that parameterize yield-density models provide much detail concerning the statistical methods used, other than mentioning the general technique employed, e.g. non-linear regression or maximum likelihood. Even fewer provide a plot of predicted and observed yields together as a function of density. And, in most of these cases, the observed-yield data are too sparse to assess the fit at different densities visually (although see Pacala & Silander 1985; Silander & Pacala 1985; Pacala & Silander 1990). Even so, there is often a suggestion of some systematic bias over a subset of the densities studied.

Does it matter if yield-density models do a poorer, and perhaps biased, job at predicting yields across a subset of densities? It may not matter so much for the present study, if the primary goal is to predict long-term community-level dynamics for naturally occurring plant populations, since serpentine populations are generally found in the higher range of densities over which the models provide a reasonably good estimate of seed yields (cf. Hobbs & Mooney 1985). However, a biased fit at low density could present a problem for long-term predictions if conditions characterized by low population density occur periodically. Our results suggest that this may not be a problem for the four species studied here, since predicted densities of the different species were almost completely insensitive to changes in initial population size.

Can this experiment and the subsequent analyses shed any light on the ecological dynamics of *Bromus, Calycadenia, Microseris* and *Plantago* at Jasper Ridge? Predictions made by the two versions of the model can be compared and interpreted in light of what is already known about the Jasper Ridge system. Average species densities predicted by the two versions of the yield density model were, generally, an order of magnitude greater than natural densities observed in the field (cf. Tables 3 and 7). This may be due to a number of factors, including differences in soil depth, seed predation by ants and other organisms, and number of species interacting within the natural serpentine community. However, a more qualitative comparison of rank order densities (*Plantago* > *Calycadenia* ≈ *Bromus* for the variable parameter value analysis) suggests that there are similarities between model predictions and patterns generally observed in the field (Tables 3 and 7; no field data were available for *Microseris*).

Although there were subtle differences in the predictions made by the two models regarding species richness, both predicted that the three native species, *Calycadenia, Microseris* and *Plantago*, generally coexist, whereas the invading species, *Bromus*, is much more likely to go extinct, a pattern that is also seen in the field (Hobbs & Mooney 1991). Negative correlations among pairs of species observed among model runs examining sensitivity to changes in rates of germination and survivorship (Table 8) are also suggestive of a general pattern in the field; different years can be characterized by changes in the species that are most dominant, due to a demographic response to varying environmental conditions.

Perhaps the most tantalizing result from this study is the difference between the two models in their predictions of long-term survival probabilities for *Bromus. Bromus* is a non-native species that is successful at invading the serpentine grassland at Jasper Ridge during wet cycles, but declines dramatically in abundance during dry cycles (Hobbs & Mooney 1991). The original model was parameterized from an experiment conducted during a near-average rainfall.
year, whereas the modified model was parameterized after a relatively dry year. As would be expected, the original model predicted higher rates of survivorship for Bromus than the modified model, suggesting that the models capture the impact of environmental differences between the 2 years (Table 7). Unfortunately, the weighting scheme used in fitting parameters to the model and non-linear effects of interspecific competition appeared to be more important than year-to-year environmental differences in contributing to the systematic bias in the original model. We interpret the greater survivorship of Bromus in the original model as being indicative of the fact that Bromus does better under circumstances characterized by a model optimized for conditions of high density and low levels of interspecific competition. An intriguing aspect of this is that, in the field, these factors could be strongly correlated with environmental conditions. For example, population densities and the relative strengths of interspecific and intraspecific competition would be expected to vary as patterns of rainfall and temperature change, particularly since most of the species in the Jasper Ridge serpentine community are annuals that can respond rapidly to environmental variability through direct changes in germination and survivorship response. However, the manner in which density and the strength of competition relate to rainfall and other environmental variables is not clear, and is most likely quite complex. As a result, we can view the patterns of survivorship for Bromus predicted by our two versions of the model as being only suggestive of a potential environmental relationship. Without a complete study of the correlation between density, relative strengths of competition and environmental conditions we cannot know if the relationship we found is indicative of a true pattern.

It is clear that the two versions of the simulation model make different predictions about long-term dynamics of the Jasper Ridge serpentine annual grassland community, at least for the four species examined here. If these differences are indeed due to year-to-year environmental effects impacting the outcomes of competition, we could develop competition models appropriate for different environmental conditions. These could then be used in a simulation model where the competition model was allowed to vary according to changing environmental patterns, such as annual variation in timing and amount of rainfall (cf. Wiegand et al. 1995; Jeltsch et al. 1996; Wiegand & Milton 1996). We could then use this coupled model to explore community dynamics in an environmentally variable ecosystem. However, before we can do this, we must address the technical issues of how to build a model that accurately characterizes the effects of competition across a broad range of densities and one that accounts for potential non-additive competitive effects among species, as well as accounting for year-to-year variability in environmental patterns.

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