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A NONLINEAR REGRESSION APPROACH TO TEST FOR SIZE-DEPENDENCE OF COMPETITIVE ABILITY

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Abstract. An individual's competitive ability is often dependent on its size, but the methods commonly used to analyze plant competition experiments generally assume that the outcome of interactions are size independent. A method for the analysis of experiments with paired competition treatments based on nonlinear regression with a power function is presented. This method allows straightforward tests of whether a competitive interaction is size dependent, and for the significance of experimental treatments. The method is applied to three example data sets: (1) an experiment where pairs of plants were grown with and without competition at five fertilization levels, (2) an experiment where the fecundity of two snail species were compared between environments at two densities, and (3) an addition series experiment where two plant species were grown in proportional mixtures at several densities. Competitive ability was size-dependent in two of these examples, which demonstrates that a wide range of ecologically important information can be lost when the assumption of size-dependence is ignored. Regression with a power curve should always be used to test whether competitive interactions are size independent, and for the further analysis of size-dependent interactions.

Key words: competition indices; competitive ability; nonlinear regression; power function; size dependence.

Introduction

Indices of the intensity, effect, or outcome of competitive interactions underlie much of the ecological literature (e.g., Connolly 1986, Osenberg et al. 1999, Williams and McCarthy 2001, Weigelt and Jolliffe 2003). These ratio-based indices are popular because they summarize the outcome of competition as a single measure by taking the relative difference in performance between an organism experiencing competition and a neighbor experiencing little or no competition. Ecologists have extensively discussed the relative merits of different indices, but have rarely addressed the broader question of the suitability of such indices for competition data (Osenberg et al. 1999, Weigelt and Jolliffe 2003). Ratio-based indices of competition data present two major problems: (1) ratios are generally inappropriate for statistical analyses such as ANOVA, and (2) these indices require the very restrictive assumption that competitive ability does not change depending on the size of the organisms involved.

The statistical issues associated with using ratio-based indices have been extensively reviewed and are not repeated here (e.g., Atchley and Anderson 1978, Packard and Boardman 1988, 1999, Raubenheimer and Simpson 1992, Jasienski and Bazzaz 1999). Some of the more important issues raised in these reviews are that ratios have non-normal distributions, can be biased away from the true value, and have large confidence limits due to variation in both the numerator and denominator. These issues frequently result in both low power to detect significant treatment effects and falsely significant results when ratios are analyzed using ANOVA (Atchley and Anderson 1978, Packard and Boardman 1988, 1999, Jasienski and Bazzaz 1999). ANCOVA is the recommended alternative (Packard and Boardman 1988, 1999, Raubenheimer and Simpson 1992, Jasienski and Bazzaz 1999). In an ANCOVA of competition data, significant interactions involving the covariate indicate size dependence in competitive ability. Cahill et al. (2005) used ANCOVA in this context to study the impact of competition on seed production in *Arabidopsis thaliana*.

Although better statistically than ratios, ANCOVA still requires the biological assumption that competitive ability does not vary with size. This assumption is not

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TABLE 1. A general procedure for analysis of competition data using nonlinear regression with a power equation ($y = k_1 + k_2 x^{k_3}$).

Step	Description	Notes
1	Fit a single (global) curve.	
2	Determine whether $k_1 \neq 0$.	Compare the curve from step 1 to a global curve with the $k_1 = 0$. If $k_1 = 0$, proceed using a model with only k_2 and k_3.
3	Determine whether the relationship is nonlinear ($k_3 \neq 1$).	Compare the model retained from step 2 to one with $k_3 = 1$. If $k_3 = 1$, proceed using ANCOVA with the x variable as a covariate.
4	Determine if individual models are better than the global model (significant treatment effects).	Fit individual curves for each treatment and compare to the model retained from step 3.
5	Determine if treatments are best described by individual curves with a common parameter (the treatment affected only one parameter).	Fit individual curves to each treatment while holding one parameter to a common value across all treatments. Compare to the models retained in steps 2 and 4.

Notes: At each stage competing models are generated, including global models where a single curve is fit to the entire data set and individual models where each treatment is modeled separately. Competing models are distinguished using the extra-sums of squares test and AIC, tests that determine whether a simple model or a more complex one best describes a data set (Bates and Watts 1988, Sokal and Rohlf 1995, Motulsky and Christopoulos 2004). See Appendix A for detailed instructions.

supported in the ecological literature. Asymmetric competition where larger individuals enjoy disproportionate access to resources is common in both plants and animals (Keddy 2001), and size-dependent changes in plant competitive ability are well documented (e.g., Howard and Goldberg 2001, Lamb and Cahill 2006). It is unclear why, when competition is so clearly size dependent, we have as a field continued to use metrics that assume size independence. In this paper, we propose a method based on nonlinear regression for detecting and analyzing size-dependent changes in competitive ability.

DESCRIPTION OF THE METHOD

Changes in competitive ability with size can be described through nonlinear regression using a power function. A power function takes the form

$$y = k_1 + k_2 x^{k_3}$$

The y variable is measures taken on an individual or population experiencing competition and the x variable is measures taken on a paired individual or population experiencing low or no competition. The resulting relationship is linear if $k_3 = 1$, a saturating curve if $k_3 < 1$, and an accelerating curve if $k_3 > 1$. The power function is commonly used in other aspects of biology, especially the description of allometric growth relationships (e.g., Niklas 1994).

Statistical inference with the proposed method requires the generation and comparison of successive candidate models. Experimental treatments can be tested by comparing the explanatory power of a single relationship for all treatments to that of more complex models where each treatment is described by a separate curve. Similarly, a curve where $k_3 \neq 1$ can be compared to one where $k_3 = 1$ to determine whether the relationship is significantly nonlinear. We recommend that a power-curve analysis follow the steps described in Table 1. Detailed instructions are available in Appendix A.

Interpreting a power function for competitive ability requires both examination of the coefficient values and checking for switches between competition and facilitation. The slope of the relationship (k_2) can be viewed as a measure of general competitive ability, with increasing values indicating declining competitive suppression and ultimately a switch to facilitation. The degree of deviation of the curve from a linear relationship (k_3) can be interpreted as a measure of how competitive ability varies with size. Switches between competition and facilitation can be identified by plotting a 1:1 line over the fitted curve. Any points where the confidence limits of the curve lie above the 1:1 line indicate facilitation, while any points below indicate competition. See Appendix A for detailed suggestions for the interpretation of ranges of coefficient values.

Methods similar to the one proposed here have been developed to detect nonlinear changes in competitive ability with density (Firbank and Watkinson 1985, Jolliffe 1988). Those methods make the assumption of size independence while testing for nonlinear changes in competitive ability across densities while the method proposed here assumes a linear relationship across densities while testing for nonlinear changes in competitive ability across sizes.

EXAMPLE APPLICATIONS

We present three examples to illustrate applications of the power-curve method. In the first example, we apply the method to a plant competition experiment designed to be analyzed with a ratio-based index. In the second example, we test whether the relationship between snail fecundity at high and low density is linear, and hence whether the data set is suitable for ANCOVA. In the final example, we apply the method to an addition series experiment, a variant of the replacement series design (Gibson et al. 1999). Nonlinear regressions were carried out using Proc NLIN in the SAS package (SAS System 8.02 for Windows; SAS Institute 2001), and P values for the extra-sums of squares test were calculated using the FDIST function

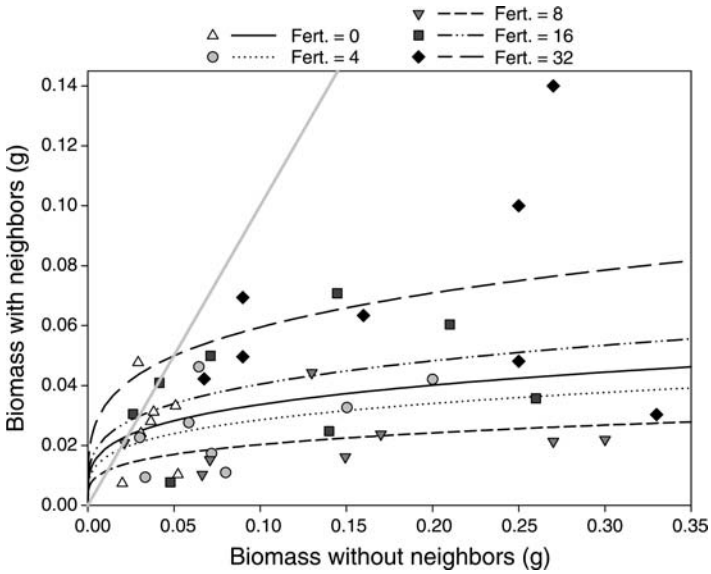

FIG. 1. Power curves for the five fertilization treatments (in g NPK/m^2) from the *Linum* experiment with the raw data points overlain. Facilitation occurs above the gray 1:1 reference line, and competitive suppression below. Values on the *x*-axis are the mass of the plant without neighbors while values on the *y*-axis are the mass of the plant with neighbors.

in Microsoft Excel 2003 (Microsoft, Redmond, Washington, USA). SAS scripts and raw data for the first example are available in the Supplement.

Example 1

In the first example, we examined the effect of fertilization on the competitive response of *Linum lewisii* Pursh, a small grassland forb (S. W. Kembel and J. F. Cahill, *unpublished data*). Two *Linum* seedlings were grown in each of 39 29 $\times$ 32 cm tubs with a simulated plant community of nine species. One plant in each tub had both root and shoot competition eliminated through netting holding back neighboring shoots and a root exclusion tube, while the other plant experienced both root and shoot competition. The experiment was arranged in a blocked design with one replicate of each of five fertilization treatments (0, 4, 8, 16, 32 g/m^2 NPK) in each of eight blocks. An analysis of this data set using a ratio-based index is presented in Appendix B for comparison.

The power-curve analysis identified size-dependent changes in competitive ability and significant fertilization effects (Fig. 1; Appendix B). Only the k_2 and k_3 parameters were included since the seedlings in the *Linum* experiment were all of similar starting size (randomly drawn from a relatively homogeneous population). Models were developed and compared following the steps in Table 1. A model with individual curves for all treatments was better than the single-curve model but not significantly so ($F_{8,29} = 2.21$, $P = 0.056$), while the model with a common k_3 parameter was significantly better than the single-curve model ($F_{4,33} = 4.94$, $P = 0.003$). The relationship was significantly nonlinear because the model with a common k_3 parameter was better than a model with $k_3 = 1$ ($F_{1,33} = 20.45$, $P < 0.001$). Pairwise tests between fertilization treatments revealed two overlapping subsets (0, 4, 8, 16 and 0, 4, 16, 32 g/m^2), though with Bonferroni correction only the comparison of the 8 and 32 g/m^2 fertilization treatments were significant.

The power curve analysis revealed three important features of the competitive response of *Linum*. First, the k_3 parameter was less than 1, demonstrating that ANCOVA would be inappropriate for these data. Biologically, this result indicates that the negative effects of having neighbors increased as plants grew larger. Second, the shape of the curve (k_3) was the same between fertilization treatments indicating that the treatments did not affect the size-dependence relationship. Finally, fertilization affected the slope of the relationship (k_2), with *Linum* a poorer competitor at moderate fertilization levels and a superior competitor at high fertilization levels.

Example 2

The second example is an experiment where the net fecundity of two sympatric snail species (*Lymnaea peregra* and *Lymnaea ovata*) was compared between two water level treatments (constant and decreasing) at densities of either two or four snails per container (Ward et al. 1997). The experiment included eight replicates of the eight treatment combinations in four blocks (two replicates per block). Since the density treatments within each block could be objectively paired (C. Goater, *personal communication*), eight replicates per treatment combination were available.

The goal of this analysis was to determine if these data were suitable for an ANCOVA with high-density fecundity as the response variable and low-density fecundity as the covariate. A power function with $k_3 = 1$ was compared to one where k_3 was allowed to vary. The k_1 parameter (y intercept) was included since it is possible for snails at one density to produce eggs while snails at a second density may fail to reproduce. A global

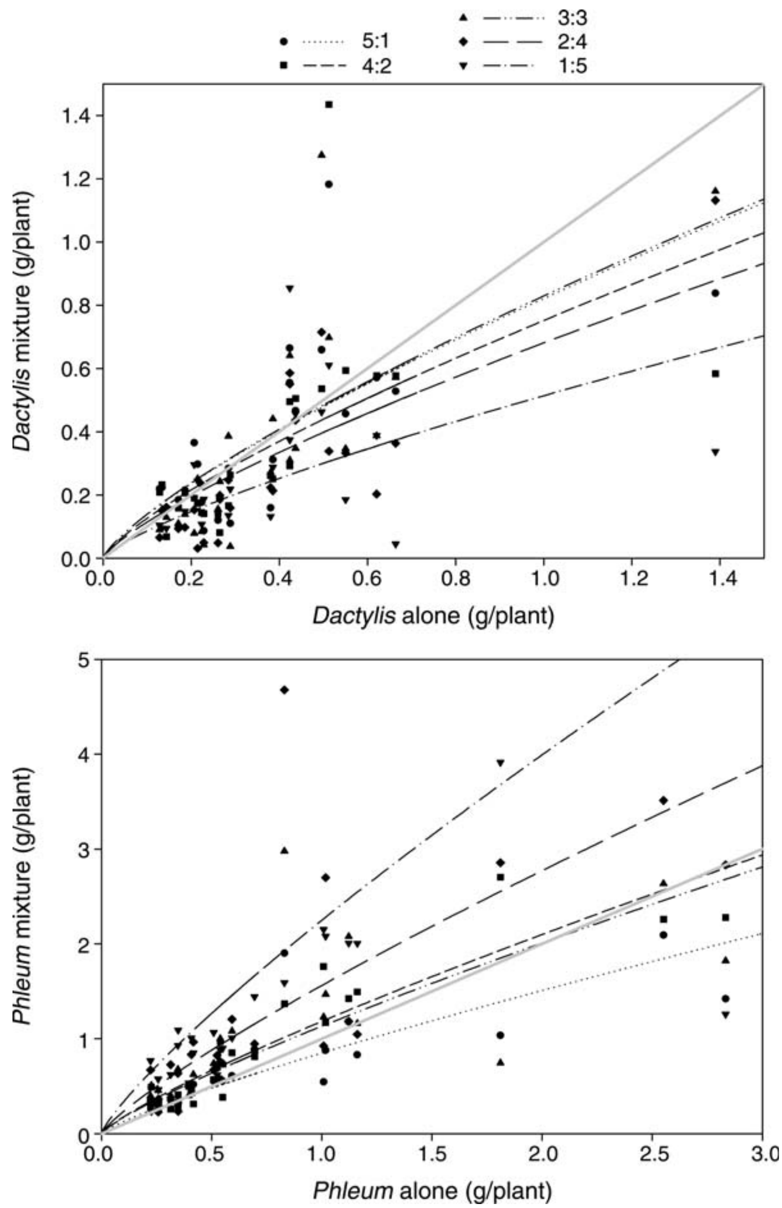

Fig. 2. Power curves for five mixture proportions of (a) *Phleum pratense* and (b) *Dactylis glomerata* with raw data points overlain. The first value in each of the species proportions in the legend refers to the focal species in each figure. Above the gray 1:1 reference line, species performed better in mixture than alone; below the line, species performed better alone than in mixture. Values on the x-axis are the average mass of individual plants grown in monoculture while values on the y-axis are the average mass of individual plants grown in mixture. Increasing values on the x-axis represent a gradient of declining population density since individual plants achieved larger sizes at lower density.

model including all three parameters could not be found because the model failed to converge. Overparametrization, indicated by very high correlations between parameter values, can cause convergence failure (Bates and Watts 1988). Since the correlation between k_2 and k_3 was −0.9997, we abandoned the three-parameter model and instead compared all three possible two-parameter models (k_1, k_2; k_1, k_3; k_2, k_3). All three two-parameter models converged, and, based on AIC, the best model included only the k_1 and k_2 parameters. The lack of a k_3 parameter indicates that the decline in egg production at high density was linearly related to fecundity at low density (Appendix B), and the analysis should proceed using the more powerful and flexible ANCOVA.

Example 3

In the final example, we used the power curve method to analyze an addition series experiment, a design where a replacement series is replicated at several densities (Gibson et al. 1999). Jolliffe et al. (1988) grew populations of two species (*Phleum pratense* L. and *Dactylis glomerata* L.) for 90 days in monoculture and varying proportional mixtures (5:1, 4:2, 3:3, 2:4, 1:5) at six densities (~650, 1300, 2000, 2650, 3300, and 4000 plants/m^2) in four replicate blocks. Mean aboveground biomass per planting was used as the x variable and the average plant size of that species at the corresponding density in each mixture treatment was used as the y variable.

Both *Phleum* and *Dactylis* were better described by nonlinear models than models with $k_3 = 1$ (*Phleum*, $F_{4,118} = 5.23$, $P < 0.0239$; *Dactylis*, $F_{1,118} = 10.34$, $P = 0.0017$) and models with a common k_3 parameter for each mixture treatment were significantly better than models with separate k_2 and k_3 parameters (*Phleum*, $F_{4,114} = 8.89$, $P < 0.0001$; *Dactylis*, $F_{4,114} = 2.60$, $P = 0.0398$). The k_2 values for *Phleum* increased as the proportion of *Dactylis* in the mixture increased, while for *Dactylis*, the opposite trend occurred (Fig. 2). Pairwise tests revealed three overlapping subsets of curves for *Phleum*, but the results were not significant for *Dactylis*.

The power curve analysis revealed two important features of the interaction of *Phleum* and *Dactylis*. The increasing value of the k_2 parameter for *Phleum* as the proportion of *Dactylis* in the mixture increased indicated that *Phleum* experienced stronger competitive suppression from other *Phleum* individuals than it did from *Dactylis*. This was supported by the concurrent decline in *Dactylis* k_2 values as the proportion of *Phleum* in the mixture increased. Second, for both species, the k_3 values were less than 1, indicating that at lower densities individual plants of both species performed better in monoculture than in mixture. The species proportions in mixture did not affect this relationship since the k_3 values were the same between mixture treatments.

This type of complex experimental design can be analyzed with a variety of nonlinear methods. For example, Jolliffe (1988) used a two-stage nonlinear regression procedure to model changes in yield per unit area between species mixtures for each density treatment in this experiment. Jolliffe's (1988) method is useful when changes in biomass production per unit area due to the relative abundance of each species in mixture are of interest. In contrast, when the response of individual plants to mixture and density are of interest the present method is advantageous. In particular, the information gained by comparing k_3 values between treatments is not readily accessible through other analytical methods.

CONCLUSION

Competitive ability frequently varies with the size of the organism, but current analytical methods require the assumption that competitive ability is fixed regardless of size. The power curve method provides both a test of the assumption of size independence and a method for analyzing datasets where the assumption is not met. Of the examples in this paper, only one (Ward et al. 1997) was suitable for analysis using ANCOVA. In the other two examples, the present method captured a wide range of ecologically important information on the size dependence of competitive ability that would otherwise have been lost. Size-dependent changes in competitive ability may be a general feature of competitive interactions; the use of statistical methods that allow these changes to be quantified is the first step toward understanding those interactions.

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APPENDIX A

Detailed instructions for implementing and interpreting a power curve analysis (*Ecological Archives* E087-083-A1).

APPENDIX B

Three tables and one figure showing the full results of the analysis of the *Linum* experiment and a figure showing the results of the analysis of the *Lymnaea* data set (*Ecological Archives* E087-083-A2).

SUPPLEMENT

The *Linum* data set and a text file containing instructions and SAS scripts for analysis of the data set (*Ecological Archives* E087-083-S1).