Using Constraint Lines to Characterize Plant Performance

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Ecologists and evolutionary biologists are searching for ways to understand the organization of complex systems. Individual organisms, populations, communities, and ecosystems all contain many components that differ from each other. Each of these components interact with one another and with their extrinsic abiotic and biotic environment to produce complex structures and dynamics. When studying such systems, it is difficult to sort through the complex patterns of variation to identify the effects of fundamental processes. Application of traditional univariate statistics is often unsatisfactory, because no single hypothesis or variable is able to account for a large proportion of the variation. Attempts to test multiple hypotheses are complicated by the fact that they are rarely mutually exclusive. Results of multivariate statistical analyses are difficult to interpret because they fail to elucidate the functional interdependencies among the multiple processes that have produced the complex patterns of variation.

Recently, Brown and Maurer (1987, 1989, Brown 1995; see also Maller et al. 1983, Maller 1990, Enquist et al. 1995, Hubert et al. 1996, Thompson et al. 1996) have suggested that the effects of fundamental processes may often be revealed as constraints on the observed patterns of statistical variation. The exercise of fitting constraint lines to enclose the observed distribution of values within constraint envelopes can be a useful aid in developing and evaluating mechanistic hypotheses. Like most approaches, this one is not entirely new. There is a long history of recognizing, at least implicitly and qualitatively, the limits on variation. For example, there have been many discussions of “threshold effects” and “boundary conditions” (see Goldberg and Scheiner 1993, Thompson et al. 1996) but these have rarely been quantified, or predicted by mathematical models.

There are both practical and conceptual difficulties in describing any complex pattern of variation. Consider the approaches that have been applied to even a relatively simple case: the distribution of variables in bivariate space shown in Fig. 1. Such distributions are often obtained, for example, when some measure of plant
productive effort, or biomass, is plotted as a function of performance, such as survivorship, growth rate, reproductive effort, or biomass, is plotted as a function of some measure of intra- or interspecific competition, such as the density, size, and/or distance of neighboring plants (e.g. Pacala and Silander 1985, 1990, Firbank and Watkinson 1987, Goldberg 1987, Goldberg and Fleetwood 1987, Goldberg and Scheiner 1993, Lindquist et al. 1994, Rees et al. 1996, Thompson et al. 1996). Here we discuss approaches that have been applied to this and more complex patterns reflecting the influence of competition and other environmental conditions on plant performance. Then we show how explicit mechanistic mathematical models can be used to define constraint lines that bound the observed distribution of data points. One value of such a modeling approach is that it develops an explicit hypothesis for each constraint line, and each hypothesis is potentially subject to an empirical test. To the extent that the hypotheses are supported by empirical evidence, they suggest fundamental mechanisms that powerfully constrain the performance of plants, despite the complexities and the magnitude of unexplained variation.

Traditional approaches

Patterns of variation, such as the one shown in Fig. 1, typically have been treated in several ways. Some investigators simply have fitted a linear or curvilinear regression (e.g. Pacala and Silander 1990, Lindquist et al. 1994; see also Goldberg and Scheiner 1993). If there are large numbers of data points, such a procedure will often yield a highly significant relationship, even though it accounts for only a small proportion of the variation and it violates parametric assumptions about homogeneity of variance.

Alternatively, one of several multivariate techniques (e.g. multiple or partial regression, principal components analysis, analysis of covariance, or multivariate analysis of variance) can be applied to the data, provided that the investigator has measured other variables that could potentially account for some of the variation (e.g., Rees et al. 1996, Thompson et al. 1996). Often, however, as in the case of many ecological experiments, additional variables have not been measured. Even when they have, the results of the multivariate analyses provide assumption-laden descriptions of the relationships among the variables, and these can be difficult to interpret in terms of the underlying mechanisms that have produced the pattern.

Still another approach to the kind of patterns shown in Fig. 1 is to fit an upper boundary that encloses all or nearly all of the data points, creating a constraint envelope. Most frequently, this is done qualitatively, either by discussing verbally the apparent existence of a boundary (e.g. Goldberg 1987, Goldberg and Scheiner 1993) or by fitting a line or curve by eye (e.g. Kodric-Brown and Brown 1978, Brown and Maurer 1987, Fowler 1990). Although such methods obviously lack quantitative rigor, they may lead to conceptual advances. While the hypothetical constraint line may be qualitative, it nevertheless represents a conceptually new way of thinking about the pattern of variation. Proposing the existence of a constraint line, either verbally or by a line fitted by eye, is often the first stage in developing and evaluating a mechanistic hypothesis. For example, Brown and Maurer (1987, 1989; see also Damuth 1991, Brown 1995) fitted lines by eye to the upper boundaries of log-log plots of population density as a function of body mass for a variety of animal species, and the similarity of the slopes to the exponents of well-established allometric equations suggested interesting hypotheses about mechanisms of resource allocation.

A more quantitative alternative is to use some standard statistical convention to isolate the data points near the boundary (e.g. some fraction of the highest points within equal increments along the abscissa) and then use parametric regression to fit a line or curve through these extreme points (e.g. Blackburn et al. 1992). This approach has the practical advantage of quantifying the extremes of variation. It has one serious conceptual shortcoming, however; it cannot characterize very precisely the limits set by the constraining mechanism. There will be approximately equal numbers of data points on either side of any fitted regression line; if the upper boundary is hypothesized to reflect some absolute constraint, however, then it should be logically impossible for data points to fall beyond the line.

Fig. 1. Examples of field data that suggest a complex, but constrained pattern of variation. Here we have plotted the survivorship of two species of desert annuals, *E. abertianum* and *H. gracilis*, as a function of the initial density of conspecific individuals. The distribution of data points suggests that maximal survivorship decreases with increasing density, implying that intraspecific competition sets an upper limit on the proportion of individuals that survive.
Mathematical models of constraint lines

Probably the most rigorous and productive way to draw constraint lines and to begin evaluating hypothesized mechanisms is to use mathematical models. One example in plant ecology is the application of Yoda’s thinning equation to show the effects of competition in constraining local density (Yoda et al. 1963, Osawa and Siguta 1989, Zeide, 1991, Osawa and Allen 1993). We will use this relationship to model survivorship as a function of density. Charnov and Skinner (1984) provide another and elegant example of this modeling approach. They used Lack’s theory of clutch size to derive a predicted maximal brood size for the parasitic wasp Nasonia, and then showed that the vast majority of data points fell below this theoretical constraint line. Here we use a similar approach to define hypothesized constraints of competition on the performance of plants.

Source of data

We use field data on survivorship of annual plants on our Chihuahuan Desert study site as the basis for this modeling exercise. A close relationship between modeling and data is appropriate, because the effects of fundamental constraining processes will vary with the environmental conditions, and will most readily be interpreted in the context of a specific sampling regime or experimental design.

At our long-term study site near Portal, Arizona, where the annual precipitation is distinctly bimodal, most annual plant species are present as vegetative individuals during either the winter or summer rainy seasons. During the last decade, densities of annuals and perennials on 384 0.25-m² permanent quadrats were censused at the end of both the winter (April–May) and the summer (August–September) seasons, so as to coincide with the period of cessation of growth, highest biomass, and maximal flowering and fruiting (for additional details, see Guo and Brown 1997).

For the purpose of this study, we analyzed data for two species, Eriogonum abertianum Torr. (Polygonaceae) and Haplopappus gracilis (Nutt.) A. Gray (Asteraceae) in the winter and summer of 1992. Among the annual plants at the study site, these are two common species that are unusual in having a biseasonal life history (Inouye et al. 1980, Fox 1989). They germinate after the winter rains, and grow and occasionally flower during the spring. However, the critical phase of their life history is survival through the spring drought; such survival is influenced by plant size and root development attained before the drought while competing with other winter-active annual and perennial species. These biseasonal annuals usually suffer high mortality during the May–June drought, but surviving plants grow rapidly, flower, and produce seeds following the onset of summer rain, and then die during the next drought (Fox 1989). Our models are based on two measures of population-level performance: (1) survivorship during the spring drought, measured as the number of individuals present in each quadrat at the end of the summer season divided by the number present on that quadrat at the end of the winter season (i.e., final density/initial density); and (2) final density, measured as the number of individuals in each quadrat at the end of the summer season.

Models of survivorship

We first consider the effect of the population density of neighbors on the survival of a target species. Assume the following experimental or observational design. We have a large number of replicated quadrats, similar in soil, water, nutrients, and other abiotic conditions, but varying in the initial number and/or spacing of seedlings. Further assume that some fixed quantity of limiting resource, constant across all quadrats, is available to support the growth and survival of the seedlings.

This design fits our field data set well. The limiting resource is the water supplied by winter rains, and depletion of soil moisture during the spring drought is a major cause of mortality. Plots of survivorship of E. abertianum and H. gracilis as a function of initial density of conspecifics in all 384 sample quadrats are shown in Fig. 1. In each graph the points all fall within a space that is roughly triangular but has a distinct curvilinear upper boundary, which appears to reflect some maximum limit on survival as a function of initial density. We will now apply the well-known allometric thinning law in plant ecology to characterize this constraint of interspecific competition on survival.

Changes in plant size and survivorship under competition for a limiting resource can be modeled by the allometric thinning law described by Yoda et al. (1963). This is usually written as

\[ M \propto c_1 N^b \]  

where \( M \) is the average mass of an individual plant, \( N \) is the density of plants in the neighborhood, \( b \) is the slope of the thinning relationship and \( c_1 \) is a fitted constant that varies with species and local environmental conditions. Yoda et al. (1963) and some subsequent authors have suggested on theoretical grounds, based on the geometry of plant growth and competition, that the value of \( b \) should be \(-3/2\). Empirical studies, however, have typically obtained values of \( b \) closer to \(-4/3\) (Lonsdale 1990), and B. J. Enquist et al. (unpub.) have derived a theoretical model, based on plant energetics and resource use, that predicts this value.
Nevertheless, as will be shown below, the values of $b$ and $c_1$ do not affect the generality of our results. While the thinning law has most often been applied to intraspecific competition in forestry and other monocultures, it is very general and can often be used to characterize the combined effects of intra- and interspecific competition in forests and other polycultures (White 1980, Westoby 1984, Guo and Rundel 1998, Enquist et al. in press).

Although the thinning law has traditionally been used to assess the effect of density and competition on population biomass, because of interest in timber yield in forestry and similar applications, it can also be used to model survivorship. As mentioned above, traditional studies have usually focused on the trajectory and slope of the thinning relationship. Instead, the emphasis in this study is on the final density attained. The simple model presented here assumes that for any initial density, $N_i$, plants will grow in size until resources become limiting (see Fig. 2). At this point the thinning line is reached and competition for resources begins. Further increase in size is only possible if some plants die. Others will then continue to grow at their expense. If populations are grown at various densities, high-density plots will reach the thinning line sooner than low-density plots.

In this model, we have further assumed that since we have samples (stands) of plants growing under identical conditions of resource limitation, except for their initial densities, they are subject to the same thinning line. Now, as populations experience greater time under thinning conditions, mortality will continue to occur. If the thinning process is allowed to continue, eventually all populations will reach a similar uniform density ($N_f$) (i.e. see Kays and Harper 1974, Harper 1977, Chapin 1993). This density appears to be set by species-specific requirements for space and resources, and the rate at which resources are renewed (not a factor in our application of the model, but see Chapin 1993, Enquist et al. in press). It is at this point that no further increase in size is possible because resources are exhausted.

If the final density of all populations is roughly similar, then it is possible to predict the maximal survivorship at a given initial population density. Given a fixed amount of time (i.e. the growing season), high-density plots will experience larger changes in density (lower survivorship), due to longer time experiencing thinning conditions, than low-density plots (higher survivorship). Thus, in our example (Fig. 2), high-density plots experience proportionally more thinning (mortality) than low-density ones. The maximum survivorship value for a given population can then be shown as

$$S = N_f/N_i.$$  

If all populations varying in initial density $N_i$ thin to a final density ($N_f$) that is species and environment specific, characterized here by the constant $c_1$, then maximum survivorship values can be rearranged as

$$S = c_1(N_i)^{-1}. \quad (3)$$

Maximum values of population survivorship depend upon the initial population density, $N_i$, and the species- and environment-specific constant $c_1$. The exponent $-1$ simply reflects the fact that all populations attain the same final density.

In the case of desert annuals where all of the limiting resource is used and the initial densities are sufficiently high that all (or nearly all) populations experience thinning mortality, we expect the exponent of this relationship to approximate $-1$. Together, thinning mortality and the attainment of a similar final density for each population set the conditions under which maximal survivorship can be achieved. Equation 3 predicts that for any value of $c_1$ all values of $S$ will lie along a concave line as a function of $N_i$ (Fig. 3).
Our survivorship function, based on a simple model of growth and thinning predicts a maximum survivorship value for a given population size. The maximum survivorship value is that which would occur if all mortality were associated with thinning. In order to apply the thinning law to define a constraint line for our data on desert annuals, we assumed that for the existing conditions of resource limitation, intraspecific competition sets only an upper boundary on survivorship. Many other factors, such as physical stress, disease, disturbance, herbivory, and interspecific competition, could cause mortality and result in values of survival below the upper boundary. Therefore, we fitted the position of the constraint line by varying the constant \( c_f \), so that the line just encloses the most extreme values (Fig. 3).

The model provides a robust mathematical description and offers a mechanistic hypothesis for the constraint of resource-based competition on the observed pattern of variation in survivorship. In particular, the allometric thinning process appears to accurately predict maximal survivorship over several orders of magnitude of variation in initial density. Further, the model leads logically to several additional testable predictions. If we had data on growth rates of individual plants – which we do not – we could make and test predictions about plant size as a function of both initial and final density. We do have data on the densities of other plant species, however, so we can extend the approach to assess interspecific competition.

If plants of all species are competing for a common resource – a reasonable assumption in this water-limited arid ecosystem (Went 1948, Beatly 1967, Kemp 1983), then we should see the outcome reflected in similar constraint lines defining similar patterns of variation in survival as a function of initial density of heterospecific, as well as conspecific, individuals. That is just what we observe for both *E. abertianum* and *H. gracilis* (Fig. 4). Even though both species differ in many evolutionary and ecological aspects the slope constraint line appears identical. It is only necessary to

fit the constant \( c_f \) to obtain a function describing the upper maximum survivorship boundary that fits the data quite well. This indicates that all populations experienced a similar thinning survivorship boundary that fits the data quite well. This indicates that all populations experienced a similar thinning process, and thinned to a unique species-specific final density. Since the sizes and competitive effects of different species vary, different values of \( c_f \) have to be fitted to define the constraint of density of neighbors on the maximum survival of the target species.

The differing \( c_f \) values observed for each target species are due in part to their unique requirements for space and resources. Variation among species in their final densities provides insight into their relative requirements for resources and their tolerance for competition. Some of the variation in \( c_f \) will also be due to the competitive environment, the quality of resources available, and especially the resource requirements of the competing species. Note the differences in \( c_f \) in the scaling of the abscissa in Fig. 3 is due to the varying per capita effects on the target species of different kinds of competitors: intraspecific vs interspecific, annuals vs perennials.

Further, interspecific competition can be hypothesized to account for some of the variation in survivorship within the constraint envelope set by intraspecific competition. This leads to the testable prediction that a significant component of the as yet unexplained survivorship in Fig. 3 should be inversely correlated with the initial density of heterospecific individuals. We
tested this prediction by fitting a regression to the log-transformed data on survivorship as a function of density of conspecifics, and then regressing the residuals on the densities of all other annual plants. The regressions were highly significant (E. abertianum - survivorship vs density of conspecifics: \( r = -0.67, P < 0.0001 \); residuals vs density of all other annuals: \( r = -0.36, P < 0.0001 \); H. gracilis: survivorship vs density of conspecifics: \( r = -0.61, P < 0.0001 \); residuals vs density of all other annuals: \( r = -0.20, P < 0.0006 \)). Thus, much of the variation in survival not explained by intraspecific competition can be attributed to interspecific competition. Together, these analyses show that between 40% and 60% of the variation in survival can be explained by competition. Hypotheses about effects of other factors, such as herbivores, physical stress, and disturbance, could be tested in a similar way if one had independent estimates of these sources of mortality.

Models of density and biomass

When other variables are used to measure plant performance, different patterns of distributions of data points can be obtained and different models can be developed to define the constraint lines. For example, in plots of the density of one species of annual as a function of the density of the other species (Fig. 5), the points appear to fall within a triangular constraint envelope. This suggests that interspecific competition causes a linear trade-off in maximal densities of the two species.

In terms of our study, this trade-off can be modeled very simply. It is only necessary to assume that within each replicate quadrat some quantity of limiting resource, \( W \), has been divided among individuals of two species, \( A \) and \( B \), such that

\[
W = c_a N_a + c_b N_b
\]  

where the \( N \)'s are the final (after competition) densities of each species; and the \( c \)'s are species-specific constants that reflect the influence of such characteristics as initial seedling size, growth rate, and root system on the rates at which resources can be taken up from the environment and converted into numbers of plants. For a design such as ours, it is convenient to reparameterize eq. 3, as

\[
1 = N_a/c_a - N_b/c_b
\]  

where the \( c_a \) and \( c_b \) give the maximal number or density of species \( A \) and \( B \), respectively, when each is growing in monoculture (Fig. 5A). Differences in these constants among species reflect variation in per capita resource demand and resulting asymmetries in competitive effects. Thus, interspecific competition for these resources sets the upper boundary on the joint maximal densities of each species. Other sources of mortality (abiotic stresses, interspecific interactions, and intraspecific thinning) will cause the observed densities to be less than the maximal possible values.

The same kind of model can be applied to any kind of linear resource division between competing plants. For example, when plotted against each other, the densities of annual and perennial plants on our study quadrats fall within triangular-shaped constraint envelopes (Fig. 5B), suggesting that they reflect the outcome of a similar linear competitive process of resource division. The observed species-specific constants convey the relative interspecific competitive impact per individual. In this case, widely different values of \( c_a \) and \( c_b \) presumably reflect the asymmetrical constraint of competition from established perennials on the densities of annuals.

Very similar linear trade-off models can be used to characterize the constraints on biomass of competing species. For example, Goldberg (1987) conducted field experiments in which she assessed the effect of competition from intra- and interspecific neighbors on growth rates and biomass of single target plant individuals. When she plotted biomass of the target individual at the end of the growing season as a function of the combined biomass of its neighbors, she obtained triangular distributions of data points similar to those we obtained for population density in Fig. 5. This is con-
sistent with a simple linear model of competition for some limited resource that is used to produce plant biomass (see also Firbank and Watkinson 1987).

Discussion

This paper is about the use of models of constraint lines and constraint envelopes as a conceptual approach to investigate complex patterns of variation and the mechanistic processes that influence them. We have illustrated this approach by presenting examples of how mechanistic models of intra- and interspecific competition can be applied to characterize limits on the performance of annual plants. Many applications of this approach to both perennials and annual plants in differing habitats, and to other kinds of systems are possible.

The advantage of fitting constraint lines is that, on the one hand, the lines quantify hypothesized effects of important processes on the structure and/or dynamics of the system, but, on the other hand they do not attempt to account for all of the variation in those structures or dynamics. This point is well illustrated by studies of the effects of intra- and interspecific competition on plant performance. In the laboratory (and sometimes in manipulative field experiments) it is possible to analyze the effects of competition by designing experiments to vary the identity, density, size, or distance of neighbors and to hold constant effects of other potentially confounding variables such as other kinds of competitors, herbivores, and abiotic characteristics of the microsite. The effects of the variable of interest can be assessed by appropriate statistical techniques, such as analysis of variance, analysis of covariance or regression analysis (linear or non-linear) (see Goldberg and Scheiner 1993). The experimental design has effectively simplified the system by removing or holding constant all of the variables that might potentially affect plant performance except for competition. Thus, it should not be surprising that in well-designed and carefully conducted laboratory experiments it is often possible to find by regression analysis that a measure of competition, such as neighbor density or biomass, accounts for a large proportion of the variation in a measure of plant performance, such as growth or survival (e.g. Waller 1981, Firbank and Watkinson 1987, Goldberg 1987).

Field systems, including many experimentally manipulated ones, are much more complex. Many factors other than competition can affect the performance of plants (Harper 1977). These include variation in: (1) limiting resources (e.g. water, nutrients, light); (2) physical disturbance (e.g. animal activities, fire, flood); and (3) non-competitive interactions with other organisms (e.g., herbivores, granivores, seed dispersers, pollinators, pathogens, mycorrhizal fungi). Thus it is not surprising that some measure of the competitive neighborhood often fails to account for more than a small proportion of the variation in plant performance (e.g. Turkington and Aarssen 1984, Goldberg 1987, Stadt et al. 1994, Guo and Rundel 1998). In part for this reason, there has been a long-standing debate over the importance and general role of competition within and across plant communities (see Fowler 1986, Schoener 1986, Tilman 1987, Wilson and Tilman 1991, Campbell and Grime 1992, Goldberg and Barton 1992). Oftentimes, the highly variable results of such experiments are often interpreted as indicating that competition “is not very important” in the field. This may not be true, especially when there is good evidence for the existence of a constraint line, such as in Fig. 1. In some of these systems, competition on resources does play an important role in the system by setting the ultimate deterministic limits on plant performance and ecological variation.

Given evidence for the existence of a constraint line and some limiting process, there are several advantages in trying to characterize them using mathematical models. Compared to a verbal or other qualitative description of the pattern of variation, the mathematical model has the obvious advantage of rigorously and quantitatively specifying the relationships among the variables. A statistical characterization of the variation (e.g. univariate regression or multivariate analysis) would also provide such quantification. Such a purely statistical model, of the sort advocated by Peters (1991), however, provides only a description of the system. A statistical description of a complex ecological system is of limited utility. For one thing, it is only valid within the range of variables used to create it; it cannot be used to make predictions beyond this range. Further, such statistical models are sensitive to assumptions about the distribution and independence of the data. For example, fitting regressions to the data in Fig. 1 is problematical for two reasons: (1) variance in the dependent variable, $S$, is not distributed homogeneously as a function of the independent variable, $N$, and (2) the dependent variable includes the independent variable in its denominator, because $S = N/N_0$, so that a negative relationship between $S$ and $N$ would be expected by chance alone. Note, that this is true only when $N_0$ is the initial density of conspecifics, as in Fig. 1, but not when it is the density of other species as in Fig. 4.

If constraint lines are to be used to describe quantitatively how critical processes limit variation, then it will be necessary to develop statistical procedures for fitting the lines to data. This raises a number of issues that have not been thoroughly addressed above or in the literature of statistics or biometry (E. Bedrick pers. comm.; see also Thompson et al. 1996). There are both conceptual and practical difficulties. For example, if the
line describes an absolute constraint, as is hypothesized by our models, then it should be theoretically impossible to have any data points outside the boundary. This implies that the line should be fitted so that the line passes through the most extreme values, as we have done in Fig. 3. Doing so also assumes, however, as does our model, that the replicate plots were all initially identical, so there was no effect of variation in initial conditions on the maximum observed values of survivorship. While this may be a reasonable assumption for a mathematical theory of thinning process, it is unlikely to be upheld in the field. Further, a reasonable sample of data points is usually required to fit a function statistically, but the very concept of an absolute constraint boundary implies that there will often be few points on or near the line.

Given these practical problems, one might ask why attempt to define constraint lines and envelopes at all, especially when standard regression techniques can “explain” 40–60% of the variation in the empirical measures of plant performance. There are two answers. The first is statistical. While standard parametric and non-parametric statistics are relatively good at describing central tendencies in data, they are not intended to characterize boundary conditions. When the limits of variation rather than the central tendency become the phenomena of interest, different statistical procedures are called for. Fortunately, statistics is an active and evolving discipline, so new techniques can be expected to be developed to meet the need (see also Blackburn et al. 1992, Thompson et al. 1996). The second reason for modeling constraint lines is conceptual. Statistical fits to data do not imply any mechanisms, they just describe quantitative relationships among the variables. In contrast, even our very simple mathematical models imply a particular mechanism and specify its functional form. When a model is fitted to data, the mathematical function and the fitted constants provide a precise quantitative description of the process. While the constraint lines that we have derived above must be regarded as hypotheses, they have the advantage of specifying a mathematical form and the quantitative limits of intra- and interspecific competition on annual plant performance.

The great advantage of an analytical mathematical model is that usually it implies a specific quantitative mechanism. This serves as an hypothesis that can be evaluated by some combination of analysis of existing data and collection of new experimental or observational data. The testing of such hypotheses about constraining processes and boundary conditions can form the basis of a productive research program designed to elucidate the fundamental processes that influence the structure and dynamics of complex systems. Elsewhere, Brown (1995) has suggested that the statistical distributions of large numbers of data points with respect to potentially important ecological variables may hold some of the best clues to the general, lawlike processes that underlie much ecological complexity.

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