

## Comments

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### THE IMPORTANCE OF THE VARIANCE AROUND THE MEAN EFFECT SIZE OF ECOLOGICAL PROCESSES: COMMENT

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The recent paper by Benedetti-Cecchi (2003) makes the valuable point that the level of variance is an underappreciated ecological parameter that can and ought to be considered explicitly in experimental designs. Most experiments ignore the potential for manipulating levels of variance as a treatment, and some experiments have unfortunately used treatments that confound changes in mean effect with changes in the variance around the mean. This confounding is difficult to avoid in treatments that manipulate binomial processes, such as disturbances, because the mean and variance of a binomial distribution are intimately linked through shared parameters. However, many experimental treatments applied by ecologists allow orthogonal (independent) manipulation of mean effect sizes and the variance around the mean. I would like to point out advantages in certain experimental designs that were neglected in Benedetti-Cecchi's article. Using regression-based experimental designs or their multifactorial counterparts, response surface experimental designs, will allow ecologists to address the questions of when variance is likely to be important and the relative importance of changes in variance and in the mean effect size.

The logical foundation for a regression-based approach rests on the application of Jensen's inequality (Jensen 1906, Smallwood 1996, Ruel and Ayres 1999). This inequality states that, when  $f(x)$  is a monotonic nonlinear function of  $x$  and  $x$  is variable, the mean value of  $f(x)$ , denoted  $\overline{f(x)}$ , does not equal the function evaluated for the mean value of  $x$ ,  $f(\bar{x})$ . The sign of the inequality depends on whether the nonlinear function is convex ( $\overline{f(x)} > f(\bar{x})$ ) or concave ( $\overline{f(x)} < f(\bar{x})$ ). The magnitude of the inequality depends on the degree of

nonlinearity, which can be quantified by the second derivative of  $f(x)$  or through approximations, as in the scale transition approximation by Chesson et al. (*in press*). In other words, when an ecological response variable is a nonlinear function of the factors being manipulated in experimental treatments, a deterministic component of the importance of variance around the mean effect size can be predicted from an investigation of the shape of the relationship between levels of the treatment factors and the response. When a response is linearly related to the level of the treatments, variance in the mean effect size will not necessarily have any effect (but see discussion of behavioral responses to variance below). I still agree that direct experimental manipulations of variance treatments are essential, but encourage the use of more informative experimental designs as well.

Experimental designs based on analysis of variance (ANOVA) can provide powerful tests of hypotheses and have been responsible for many important conceptual advances in ecology. Benedetti-Cecchi (2003) concentrates on the use of ANOVA-based experimental designs as a tool for investigating the importance of variance around mean effect sizes and only briefly covers the use of alternative designs in Appendix B. Using the proposed factorial experimental design with small and large mean effect sizes crossed orthogonally with three levels of variance (Benedetti-Cecchi 2003: Fig. 4), an ANOVA design would allow the researcher to address the null hypothesis that the level of variance explains a significant proportion of variance in the response, either alone or through interactions with the mean effect size. Although it allows a test of the significance of variance around the mean, the power of this design is predicated on selection of appropriate levels of variance in the different variance treatments, and the ability to infer any pattern in the relative importance of changes in variance and changes in mean effect size is limited.

I contend that a regression-based experimental design may allow more rapid progress for researchers who wish to explore the importance of variance in effect size as well as mean effect sizes. For purposes of illustration, I follow Benedetti-Cecchi's (2003) lead and use predator density ( $x$ ) as the factor manipulated in the treatments and prey density ( $f(x)$ ) as the response of interest. The general principles would of course apply to any ecological system with a continuous gradient of densities. Rather than establishing two treatments with low and high average predator densities, a regression-based approach would establish treatments that cover a wide range of predator densities from zero to the upper bounds of observed predator densities in

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the field (within the constraints of biological realism and experimental logistics). Because the goal of the experiment is to characterize the shape of the relationship between predator and prey densities, an optimal design will usually allocate fewer replicates to each of a greater number of treatment levels, and so no more total effort is necessarily required than for an ANOVA-based experimental design that uses a smaller number of predator-density treatments but requires greater replication of each treatment. Note that in this experimental design variance in predator density within a treatment (i.e., predator density) is undesirable, even though the eventual goal may be to evaluate the effects of such variance. When the object is to characterize the nonlinearity of the relationship between predator density and a prey response, variance plays its traditional role of unwanted noise. Variance is not, however, limited to that role.

The relationship between predator and prey densities from the regression experiment can be fit by either parametric or nonparametric (i.e., spline [Wegman and Wright 1983] or quaslikelihood [Burnham and Anderson 1998]) methods. In either case, we can then calculate the second derivative of this relationship, although when splines are used, the second derivative will exist and be continuous only for splines of order 2 or higher. By comparing a plot of the second derivative  $f''(x)$  against predator density,  $x$ , and the plot of  $f(x)$  against  $x$ , we can observe directly whether variance in  $x$  will deterministically affect  $f(x)$ , and the range of predator densities over which variance in the mean effect size will have the greatest effect. Fig. 1A shows a hypothetical relationship between predator density and prey density and Fig. 1B shows the second derivative of this function against predator density. Because the effect of changes in predator density on prey density ( $f(x)$ ) is convex, Jensen's inequality states that variance in  $x$  will result in  $f(x) > f(\bar{x})$ . The plot of the second derivative of this function shows that a given level of variance in predator density will have a larger effect on prey densities when the mean predator abundance is low than when the mean predator abundance is high, because the relationship's second derivative is negligible for larger predator abundances.

The existence of a nonlinear relationship between  $x$  and  $f(x)$  logically implies that variance around the mean effect size will affect  $f(x)$ , but is not the same as an experimental demonstration of the importance of variance around the mean. Experimental manipulations of variance, as called for in Benedetti-Cecchi (2003) should still be attempted. It could also be useful to apply the regression-based approach before attempting any direct experimental efforts at demonstrating an effect of variance in mean effect size. From Fig. 1B it is obvious that a manipulation of variance in predator

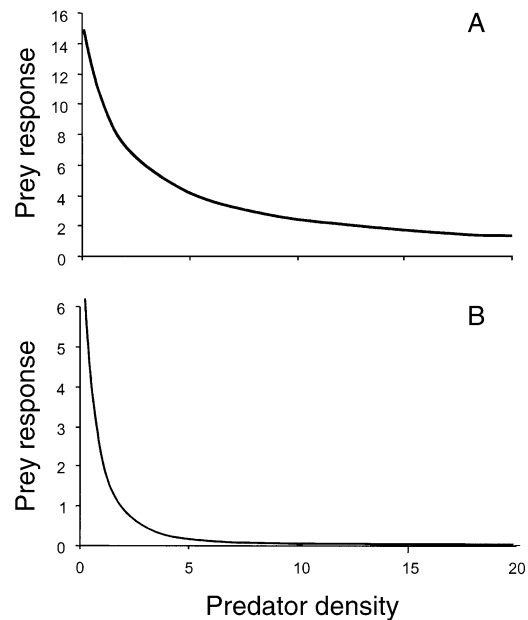


FIG. 1. (A) A typical monotonic saturating function,  $f(x) = 15 - 15x/(3 + x)$ , that may relate predator density and a prey response; and (B) the second derivative of this function. Note that the second derivative,  $f''(x)$ , becomes quite small while  $f(x)$  is still appreciably above its asymptotic value, indicating that the degree of nonlinearity in  $f(x)$  is quite small. Variance in  $x$  has a much larger effect on  $f(x)$  when the mean values of  $x$  are small and the absolute value of  $f''(x)$  is large than when the mean value of  $x$  is large and the absolute value of  $f''(x)$  is small.

density would have a much larger deterministic effect at low predator densities than at high predator densities. Using the design from Fig. 4 in Benedetti-Cecchi (2003) and the function relating predator and prey densities shown in Fig. 1A, the “large variability, small mean” predator treatment shows a 30% increase in the prey response compared to the “constant” treatment, whereas the “large variability, large mean” treatment shows only an 18% increase over the “constant” treatment. The effect of variance decreases further for even higher mean predator densities (Table 1). For saturating nonlinear functions such as this example, experiments that use designs like Fig. 4 and Fig. 5 in Benedetti-Cecchi (2003) should be expected to find a significant interaction between mean effect and variability, and the absence of a significant interaction would be more striking than its presence.

An important reason to conduct direct experimental manipulations of variance, in addition to inferring effects of variance from nonlinear functions, is that some species may respond to a variable environment by changing their behavior or through phenotypic plasticity (Werner and Peacor 2003). This kind of interaction modification or trait-mediated interaction that is ex-

TABLE 1. Effects of mean density and variance.

Variance	Mean predator density		
	2	4	8
None (0)	7.5	5.0	3.0
Low (3.82)	9.2 (18.6%)	5.6 (10.3%)	3.1 (3.8%)
High (8.73)	10.7 (29.8%)	6.1 (17.9%)	3.3 (8.2%)

*Notes:* The average prey density,  $\bar{f}(x)$ , given the nonlinear relationship in Fig. 1A, depends on both mean predator density and the variance in predator density. Results are shown as the expected average prey density, and the percentage change from the no-variance treatment,  $f(\bar{x})$ , is shown in parentheses. Each treatment consists of a series of 12 predator densities. The series with means of 2 and 4 are from Benedetti-Cecchi (2003: Fig. 4), except that the "small mean" treatments each had a pair of numbers changed to increase the variances from 3.64 and 5.27 to 3.82 and 8.73, in order to match the variances of the orthogonal mean densities. The treatments with a mean density of 8 are low variance (10, 5, 8, 10, 9, 8, 7, 6, 10, 5, 11; variance = 3.82) and high variance (5, 11, 4, 12, 5, 11, 7, 9, 6, 10, 5, 11; variance = 8.73).

pressed in a variable environment is separate from the effect of variance predicted by Jensen's inequality, which assumes that the underlying nonlinear relationship is stable. Behavioral responses to variation will be more common for some species than others. If prey can remember predator densities or respond to unpredictability in predator densities, their behavioral responses are more likely to reflect effects of variation in predator densities that are separate from those predicted by Jensen's inequality.

Because Jensen's inequality has been extended to many cases beyond the original class of monotonic functions (e.g., by Fink and Jodeit [1990]), this approach of plotting second derivatives in order to infer the importance of variance or plan more robust experiments that manipulate variance directly is widely applicable. My conjecture is that any nonlinear function  $f(x)$  that lacks a point of rotational or translation symmetry at the center of mass of the distribution of  $x$  implies that  $\bar{f}(x) \neq f(\bar{x})$ . Simple monotonic functions such as the Michaelis-Menton function in Fig. 1A will always have a correspondingly monotonic second derivative, but more complex nonlinear functions can have second derivatives with maximum magnitude at intermediate values.

The use of second derivatives to predict the importance of variance around mean effect sizes can also be extended to experiments that have more than one factor. In this case, one would use a response-surface experimental design (Inouye 2001) in place of univariate regression. For example, one may be interested in the effects of two alternative predators ( $x$ ,  $y$ ) on a prey response. A response-surface experimental design would use treatments that manipulate the densities of each of the two predators independently over a range of appropriate densities for each species. As for the case with a single predator, either parametric or non-parametric methods could then be used to fit a surface that describes the joint effects of the two predators ( $x$ ,

$y$ ) on prey density,  $f(x, y)$ . Partial second derivatives of the surface with respect to the two predators would reveal effects of variance around mean densities in either species independently, and the joint derivative could be used to investigate effects of simultaneous variance in both predators' densities and the covariance in their densities. Given a response surface where  $f(x, y)$  is linear with respect to  $x$  but nonlinear with respect to  $y$ ,  $f(x, y)$  would not be affected by variance in  $x$  alone but would still be affected by both covariance in the densities of  $x$  and  $y$  and variance in  $y$ . This approach can of course be extended to higher dimensions, although visualization of the response surface is difficult and experiments to describe the surface require more effort. While response surface experimental designs are an efficient way to investigate effects of multiple factors simultaneously, they can require a large amount of effort and will not always be logistically feasible.

Although ecologists have recognized the important roles of temporal and spatial heterogeneity, we have been slow to appreciate the effect of variance as a factor distinct from effects of changes in the mean level of experimental factors. Experiments that manipulate levels of variance while holding the mean effect size constant will be helpful in firmly establishing the significance of variance in its own right. A wider use of regression-based and response-surface experimental designs can help to make qualitative and quantitative predictions about the importance of variance. Examining second derivatives of regressions and surfaces can provide important insights into the conditions under which variance in mean effect size will be more important and can help guide future experimental work by ensuring that treatment levels are chosen efficiently.

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**THE IMPORTANCE OF THE VARIANCE  
AROUND THE MEAN EFFECT SIZE  
OF ECOLOGICAL PROCESSES:  
REPLY**

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Inouye (2005) makes constructive comments on my paper on the variance of ecological processes (Benedetti-Cecchi 2003), drawing attention to empirical and

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mathematical issues that I have not addressed explicitly in my analysis. Inouye (2005) proposes an approach for investigating the ecological consequences of changing the variance of a process that combines the power of regression-based designs with the mathematical property of monotonic nonlinear functions known as Jensen's inequality (Jensen 1906, Ruel and Ayers 1999). The main point is that, in principle, it is possible to examine the effect of the variance of a predictor variable by characterizing the relationship between levels of intensity of this variable and the response variable of interest. If this relationship is a nonlinear monotonic function, then Jensen's inequality can be used to infer the effect of the variance of the process on the mean value of the response variable, with no need of manipulating the variance directly.

Since experiments in ecology have focused mainly on the mean intensity of predictor variables, emphasis on variance provides a new and exciting slant to explore linkages between pattern and process. Progress in this direction relies on the identification of appropriate experimental and analytical techniques to deal with effects of variance and intensity of processes simultaneously. I believe that regression-based designs and Jensen's inequality, as suggested by Inouye (2005), provide an important addition to the more explicit approach of manipulating levels of variance and intensity of ecological processes directly, as advocated in my paper (Benedetti-Cecchi 2003). I also believe, however, that some caution is necessary before using this indirect approach for anticipating the consequences of changing the variance of predictor variables, either in isolation or concomitantly to changes in mean intensity. Though valid in principle, the ability of the indirect approach to provide realistic predictions must be assessed with respect to (1) the precision and accuracy with which regression-based designs describe the relationship between predictor and response variables and (2) the degree to which the mathematical determinism inherent in Jensen's inequality retains its predictive capabilities when confronted with natural variability.

Inouye (2005) makes the valuable point that regression-based designs are more powerful and informative than ANOVA-based designs when examining relationships between predictor and response variables. Though the choice of a particular design should be dictated primarily by the specific hypothesis under investigation and by the nature of predictor variables (e.g., continuous vs. categorical variables), logistical considerations of costs and efficiency are also important. Inouye (2005) asserts that the goal of a regression-based design is to characterize the relationship between the predictor and the response variables and that this can be achieved by allocating fewer replicates to a greater number of experimental levels of the manipu-



lated factor, compared to what would be done in an ANOVA-based design. On this basis, Inouye (2005) contends that the two alternative designs would not differ in terms of total effort.

Replication plays a central role also in regression-based designs, especially when these are used as an indirect method to investigating previously unexplored relationships between the variance of predictor variables and the mean response of dependent variables. The purpose of a regression analysis is to model expected values of the dependent variable as a function of one or more predictor variables (Neter et al. 1996). That is, the fitted values obtained from a regression model are estimates of the mean values of  $Y$  for corresponding values of  $X$ . If few replicates are allocated to each experimental treatment, then the precision and accuracy with which these means are estimated may be low. Depending on the degree of natural variability, lack of precision and accuracy may result in a misidentification of the relationship between  $Y$  and  $X$ , impairing the ability of the regression model to adequately assess the effects of intensity and variance of the predictor variable. Because estimation of parameters and associated levels of uncertainty are the foundations of statistical inference regardless of the specific experimental design adopted (Hilborn and Mangel 1997, Burnham and Anderson 1998), adequate replication is necessary both in regression- and ANOVA-based designs.

Armed with these insights, a graphical representation of the relationship between predictor and response variables should include measures of uncertainty around estimates of mean values of  $Y$ . For example, the relationship between density of predator and density of prey from Fig. 1A in Inouye (2005) should incorporate standard errors around mean values of the dependent variable. In addition, because the mean and the variance are usually positively correlated for measures of density, a realistic representation of the dependence of  $Y$  on  $X$  should also depict a decrease in standard error as the mean density of prey decreases (assuming that the number of replicates is the same across treatments; Fig. 1A). Keeping in mind that empirical studies provide estimates of unknown parameters and that as such these estimates incorporate sampling error, the basic question is now how does Jensen's inequality perform in the presence of natural variability? Furthermore, what is the effect of a positive correlation between the mean and the variance in  $Y$  on the ability of nonlinear functions to predict the effects of variance in  $X$ ?

In order to answer these questions, I simulated experiments on interactions between predator and prey to estimate the effect of Jensen's inequality using the nonlinear function from Fig. 1A in Inouye (2005) as the true underlying model and adding sampling error

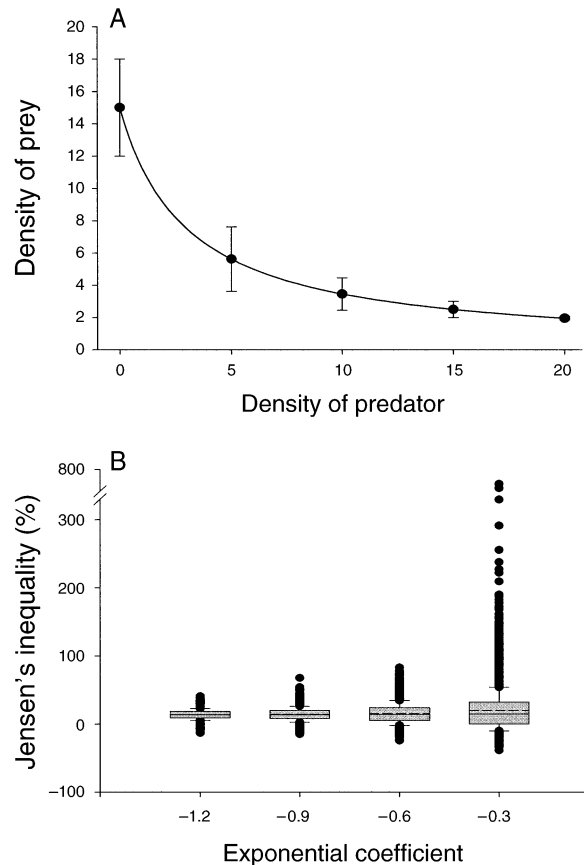


FIG. 1. (A) A representation of the relationship between density of predator and density of prey from Fig. 1A in Inouye (2005) that incorporates variation around estimates of mean density of prey. The figure depicts a positive relationship between the mean and the variance of the response variable (the size of error bars is arbitrary). (B) Box plots illustrating the effect of stochastic variation around estimates of mean density of prey on Jensen's inequality. Data are from simulated experiments in which the variance of the response variable decreases exponentially with the mean. The specific form of this relationship is defined by the exponential coefficient, with large negative values allocating most of the variation to the treatment with no predators and less negative values producing a more gradual decrease in variance across treatments (as in Fig. 1A). There are 5000 repetitions of the experiment for each level of heterogeneity of variances. Each experiment uses the nonlinear function from Fig. 1A in Inouye (2005) as the true underlying model and explores the specific condition of a mean density of two predators per experimental unit and a variance in density of 3.82 (see Table 1 in Inouye [2005]). Box plots show the median (dotted lines), the mean (dashed lines) and the 10th, 25th, 75th, and 90th percentiles of the distributions.

to estimates of mean density of prey. Variability was introduced by sampling normal distributions with mean zero and specified variance. I assumed that the variance in density of prey decreased exponentially with the mean. For simplicity, this effect was modeled as an

exponential decrease in variance with increasing density of predator. Different levels of heterogeneity of variances were obtained by repeating the simulations with exponential coefficients between  $-1.2$  and  $-0.3$ . Large negative values of these coefficients placed most of the variation around the largest mean value of the response variable, corresponding to the treatment with no predators. Less negative coefficients, in contrast, resulted in a more gradual decrease in variance with increasing density of predator (as in Fig. 1A). I examined the effects of a mean density of two predators per experimental unit and a variance in density of predators of either 3.82 or 8.73 (see Table 1 in Inouye [2004]). These values were obtained from two series of densities of predator, 4, 0, 5, 1, 0, 1, 0, 1, 5, 1, 4, 2 and 3, 1, 1, 0, 8, 0, 0, 1, 0, 8, 0, 2, corresponding to the low and large variance, respectively. The variance for the treatment with no predators was set to 20. The effect of Jensen's inequality was calculated as the percentage change between  $f(x)$  (the average density of prey given the variability in density of predator) and  $f(\bar{x})$  (the average density of prey in the absence of variation in density of predator). I ran 5000 simulations for each level of heterogeneity of variances in density of prey and each level of variance in density of predator.

It might be noted that the simulated conditions violated the assumption of homogeneity of variances and that in real studies action would be taken to mitigate this problem, usually by transforming the original data to a new scale. This option, however, may not be appropriate when trying to use Jensen's inequality to predict the effects of variance in predictor variables. First, heterogeneity of variances is a necessary condition for obtaining unbiased estimates of confidence intervals and for hypothesis testing, but it is not required for estimating regression parameters correctly (Neter et al. 1996). Second, transforming the original data may remove the non-linearity in the relationship between the predictor and response variables, preventing the use of Jensen's inequality. Finally, heterogeneity of variances might go undetected if the regression-based design is poorly replicated. For these reasons, the analyses shown here assume that the hypothetical experimenter would do nothing to mitigate the heterogeneity of variances and that he/she would use the regression-based design only for the purpose of estimation.

The results of the simulations are presented as box plots (Fig. 1B). Only results for variance in density of predator of 3.82 are illustrated, as those for variance of 8.73 showed the same pattern. The simulated experiments consistently estimated the effect of Jensen's inequality for large negative values of the exponential coefficient, with estimates centered on the true value of the parameter. In contrast, for less negative values of the exponential coefficient, the distribution of effects

was skewed towards positive values overestimating the true value of the parameter. These results show that the ability of nonlinear monotonic functions to predict the effect of the variance of ecological processes may be impaired by natural variation in the response variable. Jensen's inequality is likely to overestimate the effect of variance in the predictor variable if the variance in the response variable decreases exponentially, though not abruptly, with the mean.

Should these results deter us from conducting regression-based experiments and applying the potentially useful properties of nonlinear monotonic functions to investigate effects of variance (and intensity) of predictor variables? My answer is no. This is not what the results of the simulated experiments suggest. Rather, they indicate that the indirect approach, like the more direct one of manipulating variances explicitly, should be viewed as a problem of estimation and not as a deterministic application of a property of nonlinear functions. Hence, the predictions generated by Jensen's inequality should be interpreted as empirical estimates of parameters and not as true effects. Consequently, regression-based experiments should be designed with due attention to the needs of replication and optimal allocation of resources with respect to the amount and form of variability in the response variable. It is not by neglecting the importance of undesired variation that we will progress in understanding the effects of variance in ecological processes. Regression-based designs can be a powerful tool to address this issue, but their use cannot be advocated at the expenses of the precision and accuracy with which effects are estimated.

It should be noted that inferring effects of variance from nonlinear functions is not the same as examining these effects by direct experimentation. Inouye (2005) correctly noted this and discussed how indirect interactions mediated by behavioral responses of prey could impair the ability of Jensen's inequality to correctly predict the effect of variance in density of predator. Because most natural systems are variable and unpredictable, it seems premature to rely solely on Jensen's inequality to anticipate effects of variance of ecological processes. Hence, regression- and ANOVA-based designs should be viewed as complementary rather than as alternative approaches. Regression-based designs could be used to investigate the form of the relationship between predictor and response variables in order to assist the design of subsequent experiments, including choice of appropriate levels of intensity and variance of manipulated processes (Inouye 2005). It is the repetition of these experiments in space and time, however, that ultimately will establish whether or not the variance of ecological processes, either in isolation or concomitantly to changes in mean intensity, is generally

important regardless of the complexity and unpredictability of natural systems (Benedetti-Cecchi 2003).

As a final consideration, it should be noted that there may be cases where a regression-based design is not appropriate to investigate relationships between predictor and response variables because this is not consistent with the ecology of the system under study. For example, there may be cases where the density of a predator changes abruptly in space or time due to episodic events of recruitment and mortality. In these circumstances it may not be appropriate to establish an experimental gradient of densities of the predator simply because such a gradient does not occur under natural conditions. More generally, the choice of the experimental levels of fixed effects, like those considered in the present discussion, is dictated by the particular hypothesis under investigation. The nature of the experimental design should reflect the specific question of interest (Underwood 1997).

Recognizing the importance of the variance around the mean effect-size of predictor variables and the possibility that effects of variance change with mean intensity provide new avenues for investigating cause-and-effect relationships in ecology (Benedetti-Cecchi 2003). A limited, albeit growing body of literature indicates that spatial or temporal variance of predictor variables such as density of consumers (Butler 1989, Ruel and Ayers 1999, Benedetti-Cecchi 2000), irradiance (Ruel and Ayers 1999), heterogeneity of the substratum (Cardinale et al. 2002) and concentration of nutrients (Hutchings et al. 2003), can elicit strong responses in dependent variables. The extent to which these effects can be predicted by Jensen's inequality and whether they are specific to a narrow range of ecological processes or reflect a pervasive feature of ecological systems is far from clear. As it is commonly

the case in science, progress in understanding will require the judicious combination of existing techniques with novel methodologies that are specifically designed to address the problem of concern.

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