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## Path Modeling Methods and Ecological Interactions: A Response to Grace and Pugsek

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Grace and Pugsek (1998) comment on our cautions regarding the use of path analysis to detect direct and indirect interactions in nonexperimental systems. They discuss the limitations of path analysis and then use more sophisticated structural equation models (SEM) to reanalyze the data from our Portal long-term study site (Smith et al. 1997). For the most part their conclusions do not differ substantially from ours, and so we interpret the general thrust of their note as a further exploration of the strengths and weaknesses of path modeling methods. While we agree with many of the results and interpretations obtained by Grace and Pugsek, we would like to address several issues that arise from their analysis.

First, Grace and Pugsek's application of SEM to our complete data set does identify the indirect interactions between kangaroo rats, mice, and grass detected in our path analysis (Smith et al. 1997; treatment C). However, neither path analysis nor SEM multigroup analysis were able to detect this indirect interaction without incorporating data from the long-term manipulation. The strength of the indirect interaction was also consistently underestimated when Grace and Pugsek used unstandardized coefficients from the unmanipulated control plots to predict results from the short- and long-term manipulations. This underscores the main point of our note: the necessity of long-term experimental manipulations to detect certain kinds of indirect interactions. Grace and Pugsek state that "in order to predict the re-

sults of manipulations from unmanipulated plots, either . . . the unmanipulated plots must span a wide range of natural variation . . . or they must accurately estimate the slope of a linear relationship" (p. 152). At the time we conducted our analysis, the 10 control plots had been studied for over 17 yr, yet the indirect effect between kangaroo rats, grass, and mice still could not be detected based solely on measurements from these plots. Experimental manipulation of selected variables allows assessment of the effect of a wider range of variation than occurs under most natural conditions. For example, we were able to maintain the density of kangaroo rats on removal plots to very near zero, a condition never observed on unmanipulated control plots in the 17 yr and not likely to be observed in a habitat where kangaroo rats are the dominant small mammals. Further, long-term press experiments may be essential to detect indirect pathways of interactions with long time lags. Since many applications of path modeling methods in both biology and the social sciences have been to systems where no experimental perturbations have been performed, we remain skeptical of results from unmanipulated studies.

Second, Grace and Pugsek point out that our experimental design was not chosen a priori for application of path modeling methods. Consequently, the data are less than ideal for these types of analyses. However, our study has provided some of the best data available on the structure and dynamics of direct and indirect interactions in ecological communities (e.g., Brown et al. 1986; Brown, in press). Most other field experiments share a number of empirical limitations with our work, including the four that follow. First, only a small number of the potentially important variables are measured, consequently the species and interactions chosen for investigation are only a subset of a much larger network of interacting components. Second, because of practical considerations, samples sizes and replicates are severely limited. Third, typically more potentially important variables are measured than are experimentally manipulated. Fourth, there is considerable variation among control plots. Rather than being "selected so as to minimize variance among plots" (Grace and Pugsek, p. 152), in our study control plots were assigned at random so as to reflect the magnitude

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of background spatial and temporal variation. Given these and other constraints of manipulative field studies, experimental community ecology can be expected to continue to press the limits of statistical inference.

Finally, our goal in applying path modeling methods to the Portal data seems to differ from that of Grace and Pugesek. Our goal was to identify the mechanisms of direct and indirect interaction and to quantify their dynamic consequences for community organization. Only by understanding the mechanisms can we hope to predict how the system may respond to variation (e.g., global climate change) that exceeds the levels thus far observed. The primary objective of our article was to assess whether path analysis could identify such mechanisms based only on short-term experiments or unmanipulated systems. If so, the technique would offer a low cost alternative to long-term experimentation. Grace and Pugesek (p. 155) emphasize that “whether a model can be used for prediction of new situations is separate from the question of validity for that data set.” They go on to discuss four limitations of SEM that constrain its ability to identify mechanisms and thus to make predictions based on extrapolation beyond the observed range of variation.

Grace and Pugesek (p. 156) conclude that “path modeling methods such as SEM, while far from perfect, represent one of the most powerful approaches available for analyzing complex multivariate relationships.” We agree, but add an important qualification. Structural equation modeling and other statistical techniques will be inadequate when multivariate relationships are the consequence of direct and indirect interactions occurring on varying temporal and spatial scales and often exhibiting nonlinear behaviors. Although techniques such as SEM may be useful when applied to the appropriate data set,

they cannot extract information that is not present in the underlying data. Unfortunately, to understand the structure and dynamics of complex ecological systems, there is no substitute for well-designed long-term experiments.

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