

used to characterize the structure of interaction networks and to choose among alternative models (e.g., Mitchell, 1992, 1994; Wootton, 1994; Grace and Pugsek, 1997; Siemann, 1998). These techniques are of some utility in identifying important pathways of direct and indirect interaction (but see Smith, Brown, and Valone, 1997, 1998; Grace and Pugsek, 1998). When SEM is used to estimate the relative strengths of particular processes or interactions, such inference can be limited by the problem of negative correlations. Both of the above classes of multivariate techniques have variations that utilize either correlation or covariance matrices. The PSD condition also applies to covariance matrices, but the constraints are not as clearly understood because they depend on the variances of the individual characteristics.

To the extent that ecology endeavors to infer process from pattern, this effort is complicated by the inherent complexity of ecological systems. Populations, communities, and ecosystems are all composed of multiple units that interact with each other and with their abiotic environment. These interactions are both positive and negative. Consequently, both the structure and dynamics of these systems exhibit complex correlation structures. The PSD constraint on correlation matrices is only one, but an important one, of the factors that makes the ecologist's exercise of inferring causation from correlation particularly challenging.

## 10.1

## Commentary

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A fundamental axiom of scientific inference is that correlation need not imply causation. One message of the interesting contribution by Brown et al. is that "the observation of weak (or no) correlation need not imply no causation" (with apologies for the triple negation), particularly when multiple factors interact in a causal nexus. We agree with essentially all the points raised by the authors. We have a few specific thoughts about the content of their paper, but will mainly focus our remarks on the more general issue of "constraints" in the pursuit of scientific knowledge.

## A SPECIFIC COMMENT

Some readers may have the impression that the authors are advocating the use of partial correlations. Though this technique has its uses, one should be

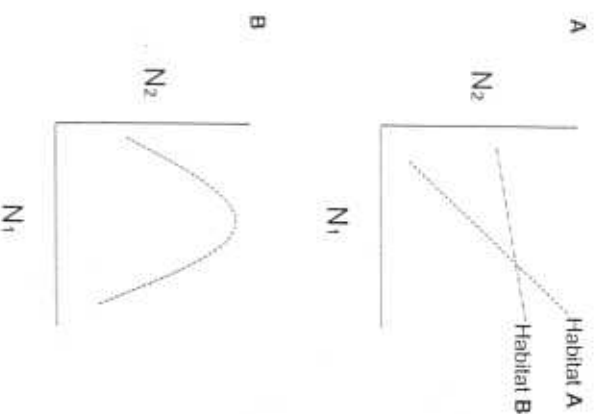


FIGURE 10.1.1 Misleading aspects of correlation as a measure of the strength of association. A: Perfect correlation, but different strength of effect. B: No correlation, but strong nonlinear association.

aware of its limitations. If one measures a correlation between variables  $X$  and  $Y$ , with no measurement error, and later discovers data about the correlation between those two variables and a third variable,  $Z$ , then this discovery does not change the initial estimate of a correlation between  $X$  and  $Y$ . This structural independence is not true for partial correlations; adding variables to a data set can often change the magnitude and even direction of partial correlation between two variables (for a concrete example in community ecology, see Carnes and Slade, 1988). Thus, there is a kind of robustness in correlations as descriptors of pattern, which is absent for partial correlations.

If the goal of scientific investigation is to go beyond pattern to discern generative processes, it is important to recognize that simple correlations are constrained along the lines sketched by the authors, and moreover that any given correlation can arise from a multitude of underlying causes, leading to the potential for error in causal interpretation. Using correlations as measures of strengths of association between variables can be misleading in any case, for reasons other than those discussed in Brown et al. Figure 10.1.1 shows several simple examples. In Figure 10.1.1a, we show the relationship

between the abundances of two species in each of two locations. At each location, the correlation is identically unity. Yet if it is actually the case that the abundance of species 1 impacts the abundance of species 2, clearly the strength of the effect is stronger at location A than at location B. In Figure 10.1.1b, there is no overall correlation between the two variables, yet they clearly have a strong nonlinear relationship. We suspect that most ecologists are interested in the functional relationships between variables, which cannot be assessed with a purely correlational approach. Correlational techniques are almost inescapable, particularly in exploring new areas of inquiry, but they should probably be viewed largely as tools for generating hypotheses, which will then be addressed in other ways.

#### GENERAL REMARKS

The effects discussed by Brown et al. have to do with constraints, in sets of correlational measures of association. Constraints arise in science in various ways. All of science comprises a web of belief, and some philosophers (e.g., Quine and Ullian, 1978) detect a whiff of empirical contingency even in the austere domain of abstract mathematical truths. Nonetheless, to make any headway in any particular scientific investigation one takes certain aspects of the world as given in order to examine other aspects. We find it useful to distinguish three grades of constraints, in decreasing order of universality, stringency, and durability: necessity; hard contingency; and soft contingency. The Brown et al. paper is concerned with the first of these, but we feel a broader consideration of the nature of constraints in inferential reasoning is useful to this volume, and more broadly to the effective pursuit of the scientific enterprise.

#### NECESSARY CONSTRAINTS

Consider first necessary relationships among factors. Philosophically, "necessity" refers to definitions or to mathematical, deductive relationships. The authors show that because a matrix composed of correlation coefficients has a mathematical property known as "positive semidefinite" there can be constraints bounding the magnitudes of correlation coefficients in multivariate settings, particularly when all or most of the correlation coefficients are negative. So, knowing the values of certain matrix elements pre-determines (at least to a degree) the possible magnitudes of other matrix el-

ements. This follows not from facts about the natural world, but from the meaning and mathematical definition of "correlation coefficient".

Similar necessary constraints arise throughout science. For instance, in dynamical systems whose properties are described by a system of differential equations, if there are physical or biological units involved (e.g., mass, time, species), the physical units on the left side of the equations must match the physical units on the right side of the equations. So, in the basic equation of Newtonian mechanics,  $F = ma$ , "force" has the units  $[\text{mass}][\text{distance}]/[\text{time}]^2$ , and in the basic equation of population dynamics,  $dN/dt = rN$ , where  $N$  is population size, the intrinsic growth rate  $r$  has units  $1/[\text{time}]$ . Dimensional analysis can be used to reach surprisingly robust conclusions about natural phenomena. Okubo (1980) for instance used dimensional analysis to show in a few lines of reasoning that the speed of the wavefront of an invasive species moving into homogeneous terrain must be proportional to  $\sqrt{rD}$ , where  $r$  is intrinsic growth rate and  $D$  is a diffusion coefficient. Brute-force analysis of reaction-diffusion dynamical models leads to the same qualitative result, but only after much more difficult analyses (though such analyses are necessary to derive the proportionality constant).

At Princeton University, according to an apocryphal (one hopes) story circulating among the students in the physics department, a brilliant graduate student convinced himself that he had the key to the unified "theory of everything" and buried himself in the library for several years of hard analysis. One day he decided to show his work to his advisor and emerged into the light of day with reams of paper covered with symbols. His advisor's first comment was "This can't be right." After staring at the equations for a while, the advisor then sadly said, "This can't even be wrong." The student had set up equations that were dimensionally incorrect, and so were not just incorrect, but nonsensical from the get-go. Ignoring necessary constraints can lead to completely invalid inferences about the world.

The phenomenon discussed by Brown et al. is similar to this but more insidious. One could doubtless find examples in the ecological literature of the use of correlation matrices where interpretations of each pairwise interaction or relationship were made without due recognition of the necessary interdependence that arises in multivariate correlation analyses.

#### HARD CONSTRAINTS

Many important constraints are not necessary but can be viewed as similarly rigid and unquestioned, at least in a given domain of inquiry. In par-

ticular, the nature of physical laws and the values of physical parameters are discovered, not defined. Some physical laws (e.g., conservation of mass) are accurate only in certain domains. To an ecologist, however, such facts about the world can be treated as absolute constraints, within which biological processes occur.

This seems obvious, but the conscious recognition of hard constraints can be rather useful. Consider for instance competition. Holt, Grover, and Tilman (1994) examined mechanistic models of competition between two consumer species for a single limiting resource (e.g., nitrogen), and attacked by a predator. This is a four-dimensional system, the analysis of which can be dauntingly complex. However, by assuming a closed system one can apply the principle of conservation of mass, so that all variables in the system (when measured in comparable units) must add up to a fixed nutrient mass. In effect, using the principle of conservation of mass permitted Holt, Grover, and Tilman (1994) to reduce the dimensions of the system from four to three. In the original four-dimensional phase space, the dynamics of the system were constrained to lie on a three-dimensional plane. Additional such constraints (e.g., one for each distinct nutrient) further reduce the possible dimensionality of the system's dynamics, with each fresh constraint reducing the potential "surface" of movement by one dimension. Recognizing the existence of such material constraints greatly facilitates analysis. Comparable insights with many important implications are currently emerging from the explicit incorporation of chemical stoichiometry into community ecology (Sternert and Hessen, 1994).

#### SOFT CONSTRAINTS

Finally, many constraints arise over short to long time scales from contingent facts of earth history and biological processes. One can find many different kinds of "soft constraints" in ecology and evolutionary biology. Part of the process of intellectual maturation in these disciplines has revolved around an increasing appreciation of the need to be explicit about constraints (e.g., in behavioral ecology, see Krebs and Davies, 1997, 10). We now briefly touch on several soft constraints that are in our opinion particularly important in ecology and evolution.

The results in Holt, Grover, and Tilman (1994) alluded to above were derived by assuming a closed arena for competition. But the inorganic nutrient pool may actually be influenced by spatial processes, coupling the pool with an external environment (e.g., nitrogen deposition, leaching). Does this

matter? Grover (1997) shows that this violation of assumptions need not vitiate the conclusions of Holt, Grover, and Tilman (1994), provided the system reaches equilibrium. Assuming equilibrium in effect imposes a constraint on a system, a constraint that arises because dynamical forces push the state of a system towards a particular configuration (e.g., a plane of potential equilibria). In like manner, Charnov (1995) assumed that populations are stationary (with births equaling deaths) in order to derive a startling variety of predictions about regularities in the life histories of vertebrates. Holt and Gomulkiewicz (1997) analyzed adaptive evolution in a stable "sink" population (one in a habitat where fitness is less than 1, but extinction is prevented by recurrent immigration). They showed that a demographic constraint could prevent adaptation by natural selection; specifically, to be retained by selection, mutants had to have absolute fitnesses greater than unity, regardless of the fitness of the immigrant (ancestral) type.

Assumptions of stationarity, stability, or equilibria are often not literally true; populations do go extinct, and explode, and in general vary through time in their abundance, and shift in genetic composition as well. But an assumption of "near-equilibrium" may nonetheless be close enough to the truth to be viewed as a "soft" contingent constraint, within which other dynamical processes (e.g., selection) may occur. For instance, consider the study of evolutionary dynamics. If ecological processes effectively equilibrate population size to a fixed carrying capacity, it simplifies analysis of evolutionary dynamics to assume a constant population size,  $N$ , and focus solely on changes in gene frequency. This is, in fact, the standard protocol in classical population genetics. Conversely, to understand short-term population dynamics, it is often reasonable to assume that the properties of organisms are fixed and concentrate on changes in numbers.

Abstractly, whenever one takes a dynamical system and reduces its dimensionality by taking particular entities that are potentially dependent variables, making them into constant or time-varying parameters, one has imposed a soft constraint upon system behavior. We contend that this is an essential intellectual maneuver for grappling with the behavior of complex systems and often does correspond reasonably well to reality. A clear understanding of system properties in the face of soft constraints provides yardsticks for understanding the consequences of breaking those constraints.

In some circumstances, different constraints lead to similar outcomes. Brown et al. show that with equivalent competition among  $n$  species, the magnitude of the correlation coefficient necessarily declines with increasing  $n$ . Similar effects can emerge from dynamical models of species interactions. For instance, consider a model of shared predation leading to indirect

competition among prey (from Holt, 1984). Assume that a predator feeds equivalently upon  $n$  prey species. Each prey in the absence of the predator exhibits logistic growth with equal  $r$  and  $K$ , and they do not directly compete. At equilibrium, the predator reduces total prey numbers to  $N$ . This is a "soft" constraint, because the system does not have to be at equilibrium (for the particular model in question [Holt, 1984], the equilibrium is globally stable, so it should be reasonable to assume that the system will "usually" be near equilibrium). Because of the assumed symmetry in prey growth, each prey species equilibrates at an abundance of  $N/n$ . If one prey species is removed, again the prey equilibrate, to  $N/(n-1)$ . The proportional change in a focal prey species abundance is  $[N/(n-1) - N/n]/(N/n) = 1/(n-1)$ . This quantity, which measures pairwise indirect competition, declines with increasing  $n$ . The conclusion that interspecific interactions will seem weaker when more species are simultaneously present thus seems to emerge from several different kinds of constraints.

Another example of a biological constraint was used by Ronald Fisher (1930) to examine the evolution of sex ratio: in sexual species all individuals must have a mother and a father. This fact, when used in evolutionary arguments, predicts the evolution of equal investment in the two sexes during reproduction if near relatives do not mate and compete. This again is a contingent constraint, because it depends upon the fact that there are just two sexes in the vast majority of living organisms. This particular constraint is embedded deeply enough in the organization of life that it has almost the "hard" status of a physical constraint.

The final, very broad class of soft constraints we wish to touch upon are those referred to loosely as "historical" or "phylogenetic" constraints. One reason introduced rabbits could wreak such havoc on the vegetation of Australia was that these plant species had evolved on a continent without a history of exposure to rabbits or rabbitlike herbivores. The constraint here reflects the contingent history of a place: the water barrier between Australia and Asia prevented species in the former continent from experiencing certain selective agents in their evolutionary history. Another very important class of constraints comes from considering the evolutionary dynamics of lineages themselves. Evolution depends upon variation, but variation always arises via mutation against the background of a phenotype and genotype generated by evolution. Not everything is possible. The range of potential variation is constrained by the kind of organism in question, and the developmental pathways it has inherited from its ancestors, along with its environment (e.g., historical factors of stabilizing selection, continuity in environments experienced by a given lineage). In general, small changes in

developmental pathways are more likely than large changes. This is a soft constraint on evolution because it is not impossible for mutants or large or unique effects to arise or for species to persist through episodes of environmental change that facilitate large evolutionary changes. One way to view the history of life is that it involves the interplay of constraint breaking (e.g., the development of flexible behaviors and learning) and constraint generation (e.g., metabolic dependence upon oxygen) (Rosenzweig, 1995; Joel S. Brown, personal communication).

Brown et al. convincingly show that necessary constraints arising from the PSD properties of correlation matrices may make it particularly difficult to infer causation from correlation, given the multivariate causal complexity of biological systems. We agree, and further suggest that the explicit recognition of constraints—including necessary constraints, hard constraints, and soft constraints—should be an essential part of the conceptual repertoire of scientists, both to avoid unwitting error (the main point of the Brown et al. paper) and to assist in the challenge of understanding the structure and dynamics of complex biological systems in general.

## 10.2

### Commentary

Stew Cherry

Brown et al. discuss how a mathematical property (positive semidefiniteness, or PSD) of covariance and correlation matrices imposes constraints on the scientific inferences one can make about complex ecological systems, particularly in the presence of negative relationships. They go much further and claim that the PSD property constrains "not only the relationships among variables, but also the operation and outcome of the mechanisms that produce these relationships." I found the discussion interesting but ultimately was unconvinced by their arguments.

Throughout their chapter, Brown et al. discuss the use of linear models and in particular the use of correlation analysis to identify important ecological relationships among pairs of variables in a multivariate setting. Correlation measures the strength of the linear relationship between two quantitative variables, and that is all it measures. It provides no information on causal mechanisms and, as is well known, can lead to incorrect conclusions

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