

Table 2 Acute Toxicity of Di-*n*-butyl Phthalate to Four Species of Fish

Species	Temperature (°C)	TL ₅₀ * (µg/l.)		
		24 h	48 h	96 h
Fathead minnow (<i>Pimephales promelas</i>)	17	—	1,490	1,300
Bluegill (<i>Lepomis macrochirus</i>)	17	1,230	731	731
Channel catfish (<i>Ictalurus punctatus</i>)	17	3,720	2,910	2,910

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Toxicity was measured by standard static bioassay.

*The tolerance limit is the concentration in which 50% of fish survive for a specified time.

from some statistical distribution. That is, each of these matrix elements is assigned from a distribution of random numbers, and this distribution has mean value zero and mean square value α . (For a fuller account of such a formulation, see refs. 2 and 3.) α may be thought of as expressing the average interaction "strength", which average is for simplicity common to all interactions. In short,

$$\mathbf{A} = \mathbf{B} - \mathbf{I} \quad (2)$$

where \mathbf{B} is a random matrix, and \mathbf{I} the unit matrix. Thus we have an unbounded ensemble of models, one for each specific choice of the interaction matrix elements drawn individually from the random number distribution.

It is important to note that randomness only enters in the initial choice of the coefficients a_{jk} , which then define a particular model. Once the dice have been rolled to get a specific system, the subsequent analysis is purely deterministic.

The system (1) is stable if, and only if, all the eigenvalues of \mathbf{A} have negative real parts. For a specified system size n and average interaction strength α , it may be asked what is the probability $P(n, \alpha)$ that a particular matrix drawn from the ensemble will correspond to a stable system. For large n , analytic techniques developed for treating large random matrices may be used to show* that such a matrix will be almost certainly stable ($P \rightarrow 1$) if

$$\alpha < (n)^{-1/2} \quad (3)$$

and almost certainly unstable ($P \rightarrow 0$) if

$$\alpha > (n)^{-1/2} \quad (4)$$

The transition from stability to instability as α increases from the regime (3) into the regime (4) is very sharp for $n \gg 1$; indeed the relative width of the transition region scales as $n^{-2/3}$.

Such a precise answer for any model in the ensemble in the limit $n \gg 1$ is a consequence of the familiar statistical fact that, although individual matrix elements are liable to have any value, by the time one has an $n \times n$ matrix with n^2 such statistical elements, the total system has relatively well defined properties.

Next we introduce Gardner and Ashby's connectance, C , which expresses the probability that any pair of species will interact. It is measured as the percentage of non-zero elements in the matrix, or as the ratio of actual links to topologically possible links in the trophic web. The matrix elements in \mathbf{B} now either, with probability C , are drawn from the previous random number distribution, or, with probability $1 - C$, are zero. Thus each member of the ensemble of matrices \mathbf{A} corresponds to a system of individually stable parts, connected so that each part is affected directly by a fraction C of the other parts. For large n , $\alpha^2 C$ plays the role previously played by α^2 , and we find the system (1) is almost certainly stable ($P(n, \alpha, C) \rightarrow 1$) if

$$\alpha < (nC)^{-1/2} \quad (5)$$

and almost certainly unstable ($P \rightarrow 0$) if

$$\alpha > (nC)^{-1/2} \quad (6)$$

* From equation (2) it is obvious that the eigenvalues of \mathbf{A} are $\lambda - 1$, where λ are those of \mathbf{B} . The "semi-circle law" distribution for the eigenvalues of a particular random matrix ensemble was first obtained by Wigner⁴, and subsequently generalized by him to a very wide class of random matrices whose elements all have the same mean square value⁵. Although the matrix \mathbf{B} does not in general possess the hermiticity property required for most of these results to be directly applicable, the present results for the largest eigenvalue and its neighbourhood can be obtained by using Wigner's⁴ original style of argument on $(\mathbf{B}^N)(\mathbf{B}^N)^*$ where N is very large. Indirectly relevant is Mehta⁵ and Ginibre⁶.

It is interesting to compare the analytical results with Gardner and Ashby's computer results for smallish n . (Their choice of \mathbf{A} differs slightly from ours, but in essence they have the fixed value $\alpha^2 = 1/3$, and diagonal elements intrinsically -0.55 rather than -1 .) Although our methods are based on the assumption that n is large, and are therefore only approximations when applied to $n=4, 7, 10$, the two approaches in fact agree well when compared, being not more than 30% discrepant even for $n=4$.

The central feature of the above results for large systems is the very sharp transition from stable to unstable behaviour as the complexity (as measured by the connectance and the average interaction strength) exceeds a critical value. This accords with Gardner and Ashby's conjecture.

Applied in an ecological context, this ensemble of very general mathematical models of multi-species communities, in which the population of each species would by itself be stable, displays the property that too rich a web connectance (too large a C) or too large an average interaction strength (too large an α) leads to instability. The larger the number of species, the more pronounced the effect.

Two corollaries are worth noting, although they should not be taken to have more than qualitative significance.

First, notice that two different systems of this kind, with average interaction strengths and connectances α_1, C_1 and α_2, C_2 respectively, have similar stability character if

$$\alpha_1^2 C_1 \approx \alpha_2^2 C_2 \quad (7)$$

Roughly speaking, this suggests that within a web species which interact with many others (large C) should do so weakly (small α), and conversely those which interact strongly should do so with but a few species. This is indeed a tendency in many natural ecosystems, as noted, for example, by Margalef⁷: "From empirical evidence it seems that species that interact feebly with others do so with a great number of other species. Conversely, species with strong interactions are often part of a system with a small number of species. . . ."

A second feature of the models may be illustrated by using Gardner and Ashby's computations (which are for a particular α) to see, for example, that 12-species communities with 15% connectance have probability essentially zero of being stable, whereas if the interactions be organized into three separate 4×4 blocks of 4-species communities, each with a consequent 45% connectance, the "organized" 12-species models will be stable with probability 35%. That is, of the infinite ensemble of these particular 12-species models, essentially none of the general ones are stable, whereas 35% of those arranged into three "blocks" are stable. Such examples suggest that our model multi-species communities, for given average interaction strength and web connectance, will do better if the interactions tend to be arranged in "blocks"—again a feature observed in many natural ecosystems.

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