

The effects of interaction compartments on stability for competitive systems

Ian D. Rozdilsky^{a,*}, Lewi Stone^a, Andrew Solow^b

^a *Department of Zoology and The Porter Super-Center for Ecological and Environmental Studies, Tel Aviv University, Ramat Aviv, Tel Aviv 69978, Israel*

^b *Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, MA 02543, USA*

Received 22 October 2002; received in revised form 3 October 2003; accepted 5 November 2003

Abstract

The interactions between species are unlikely to be randomly arranged, and there is increasing evidence that most interactions occur within small species sub-groups, or compartments, that do not strongly interact with one another. We examine whether arranging the interactions of a competitive system into compartments influences the system properties of linear stability, feasibility, reactivity, and biomass stability, thereby altering the likelihood of species persistence. Model Lotka-Volterra systems of diffuse competition were analysed with interactions arranged randomly and in compartments. It was found, using a variety of dynamical measures, that arranging interactions into compartments enhances the likelihood of species persistence. Since many natural competitive systems appear to have interactions arranged within compartments, this may be an outcome of the positive attributes that this form of organization offers.

© 2003 Elsevier Ltd. All rights reserved.

Keywords: Compartments; Lotka–Volterra; Competition; Stability; Biomass variability; Reactivity

1. Introduction

It has been known for some time that feeding links in predator–prey systems are not random, although the specific nature of their arrangement is still a matter of speculation. There is increasing evidence that arrangements of feeding links are composed of compartments, such that the feeding links are dense within compartments (sub-groups of species), and between compartments there are relatively few links (Solow and Beet, 1998). The implications of such a structure within predator–prey systems has been studied by many including: DeAngelis (1975), King and Pimm (1983), McMurtrie (1975), McNaughton (1977), May (1974), and reviewed by Pimm (1984). May's (1972) classic result that increasing model complexity can lead to dynamical instability was supported in many cases, but

other relationships were demonstrated using alternative model assumptions and alternative measures for assessing dynamical properties.

Competitive systems also appear to be compartmentalized (Simberloff and Dayan, 1991; Fox and Brown, 1993), but to our knowledge the implications on dynamics has not been addressed. Following the theoretical result of Rozdilsky and Stone (2001) that showed competitive systems with dense feeding linkages can be quite stable, we address the question of whether arranging interactions within a competitive systems into compartments (each having higher linkage densities) affects dynamical properties related to stability measures. Our results show that arranging the interactions of competitive Lotka-Volterra system into compartments significantly enhances a wide variety of dynamical measures typically used to assess stability. Qualitative dynamics can be characterized in different ways and instead of confining ourselves to the standard measure of local linear stability, we will also consider feasibility, resilience (Neubert and Caswell, 1997), and biomass variability.

*Corresponding author. Department of Ecology and Evolutionary Biology, Princeton University, Princeton, Guyot Hall, NJ, USA. Tel.: +1-609-258-7915; fax: +1-609-258-1712.

E-mail addresses: ian@eno.princeton.edu (I.D. Rozdilsky), lewi521@yahoo.com (L. Stone), asolow@whoi.edu (A. Solow).

2. Models

Consider a competition system consisting of m species and let $N_j(t)$ be the abundance or biomass of species j at time t . Suppose that the dynamics of this system are governed by the density-dependent Lotka-Volterra model:

$$\frac{dN_j(t)}{dt} = r_j N_j(t) (1 - \alpha_{jj} N_j(t) - \sum_{i=1, i \neq j}^m \alpha_{ij} N_i(t)), \tag{1}$$

where r_j is the intrinsic growth rate for species j , α_{jj} represents self-interaction of species j , and α_{ij} represents the direct competitive effect of species i on species j . This model has a long history in the ecological literature (e.g. May, 1972; Smith, 1974; Stone, 1988; Stone and Roberts 1991; Hughes and Roughgarden, 2000). Let $\alpha = [\alpha_{ij}]$ be the m -by- m matrix of interaction parameters. Following Hughes and Roughgarden (2000), we will consider the simplified system with $r_j = r$ and $\alpha_{jj} = 1$ for all j , and we will assume that all direct competitive effects have the same strength, so that $\alpha_{ij} = 0$ or γ with $0 < \gamma < 1$.

Within this model system, the pattern of species interactions is determined by the arrangement of competitive interactions. A competitive interaction occurs between two species i and j when the element $\alpha_{ij} = \gamma$ and does not occur when $\alpha_{ij} = 0$. We will consider two structural arrangements for competitive species interactions. Under the random model, the elements $\alpha_{ij} (i \neq j)$ of α are independent and identically distributed with $prob(\alpha_{ij} = \gamma) = C$ and $prob(\alpha_{ij} = 0) = 1 - C$. The expected number of competitive interactions under this model is $Cm(m - 1)$ and the probability C represents the connectance of the system. Under the compartmental model, the m species are divided into k compartments each of size m/k (k being a positive integer), as shown in Fig. 1. There are no interactions

between species in different compartments. Within each compartment, the random model applies but with connectance C' . In the next section, we will compare the dynamical properties of random and compartmental systems with the same values of m , C , and γ . To ensure that the overall connectance of a compartmental system is C , it is sufficient to take $C' = Ck(m - 1)/(m - k)$ when $C' \leq 1$ (Solow et al., 1999). Note that in order to maintain equal values of overall connectance, some larger values of the connectance for a randomly arranged system could not be used, as they would require compartments to have an internal connectance greater than one, which is impossible.

3. Dynamical properties

We will consider three types of dynamical properties: feasibility and stability, reactivity, and variability of total abundance or biomass. Let N_j^* be the equilibrium abundance of species j . The m -vector $N^* = (N_1^*, N_2^*, \dots, N_m^*)'$ is given by

$$N^* = \alpha^{-1} e, \tag{2}$$

where e is an m -vector of ones. The m -by- m community matrix is given by

$$A = -rD\alpha, \tag{3}$$

where $D = diag(N_j^*)$. It is straightforward to show that, when the system is fully connected (i.e. $C = 1$):

$$N_j^* = n^* = (1 + (m - 1)\gamma)^{-1} \tag{4}$$

for all j and

$$A = -rn^*\alpha. \tag{5}$$

We will use these results later. It is important to note that the model used to derive the community matrix defined in Eq. (3) is different from the model used in many previous studies such as May (1972), in that it is a function of the equilibrium abundances.

The stability properties of the dynamical system (1) are dependent upon the characteristics of the linearized system in the neighborhood of the equilibrium. As we are considering the system (1) in the context of abundances, equilibrium abundances must be positive to be of interest for further analysis (negative abundances are not feasible). Formally, the system is said to be feasible if $N_j^* > 0$ for all j ; and Stone (1988) showed that, for the model assumptions used here, almost all feasible systems are locally stable. The system exhibits linear local stability if all of the eigenvalues of the community matrix A have negative real parts. As the growth rate r does not appear in N^* and appears only as a multiplicative factor in A , feasibility and stability do not depend on r . Let $p(m, c, \gamma)$ be the probability under the random model that a system with m species,

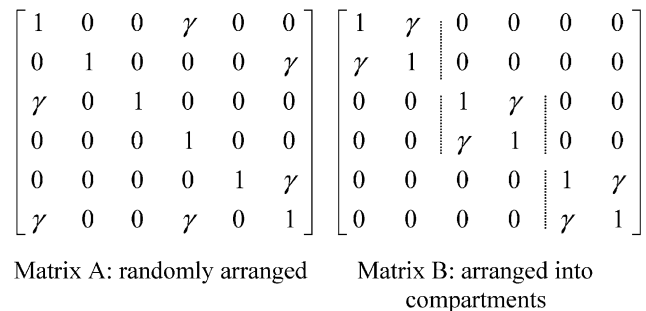


Fig. 1. Two interaction matrices are shown with the same overall: number of species $m = 6$, interaction strength, γ , and connectance $C = 6/30$ ($C' = 1$ for $k = 3$ compartments). The non-zero elements, $\alpha_{ij} (i \neq j)$ in matrix A , were chosen to be independently and identically distributed and therefore randomly arranged, and the non-zero elements, $\alpha_{ij} (i \neq j)$, in matrix B are assigned in the same manner within 3 compartments set along the diagonal while maintaining the overall connectance.

connectance C , and competitive interaction strength γ is both feasible and stable. A compartmental model of the same size, overall connectance, and interaction strength is feasible and stable if and only if all of its compartments are feasible and stable. The probability that one compartment will be feasible and stable is $p_c(m/k, Ck(m-1)/(m-k), \gamma)$ and the probability that the system will be feasible and stable (i.e. every compartment) is p_c^k .

It is clear from (5) that a fully connected system must be feasible and stable. This follows from the fact that, when $C = 1$, the matrix A is negative definite, so that all of its eigenvalues have negative real parts. In fact, for this case the largest eigenvalue of the community matrix A is $-m^*(1 - \gamma)$.

When the system connectance C (or C' for a compartment) is less than 1, analytical solutions cannot in general be found and, to assess the feasibility and stability of such systems, we resorted to the following simulation procedure. For a given structural model (random or compartmental) and fixed values of m , k , and C , an interaction matrix α was simulated. All non-zero interactions were assigned a fixed value of γ . The corresponding community matrix A was formed and its dynamical properties were determined. The procedure was repeated a total of 5000 times for each structural model and selected combinations of m , k , C , and γ . The probability that the model was feasible and stable was estimated from the proportion of these 5000 simulated systems that were feasible and stable.

The fraction of feasible and stable systems, whose competitive interactions are arranged randomly and in compartments (but with the same overall connectance), are shown in Fig. 2 for a collection of parameters. The randomly arranged system was found, in general, to have a lower probability of being feasible and stable than the system arranged into compartments.

Given that a system is feasible and stable, it is often of interest to understand its transient response to perturbation and its ability to return to equilibrium after such a perturbation. This is commonly referred to as resilience. Let λ_{\max} be the eigenvalue of A with largest real part. A common measure of resilience is $-Re(\lambda_{\max})$, which, as $t \rightarrow \infty$, is the so-called e-folding time (Holling, 1973). Recently, Neubert and Caswell (1997) proposed an alternative measure of the instantaneous response of a stable system to perturbation. This measure, which is called reactivity, is defined as the maximum instantaneous growth rate of a perturbation, and is given by the largest eigenvalue of $(A + A')/2$. The system is said to be reactive if the largest eigenvalue of $(A + A')/2$ is positive and non-reactive otherwise. Here, we will focus on the probability that the system is reactive. Let $q(m, c, \gamma)$ be the probability that a system of m species with connectance C and interaction strength γ is reactive. The corresponding compartmental system is reactive if

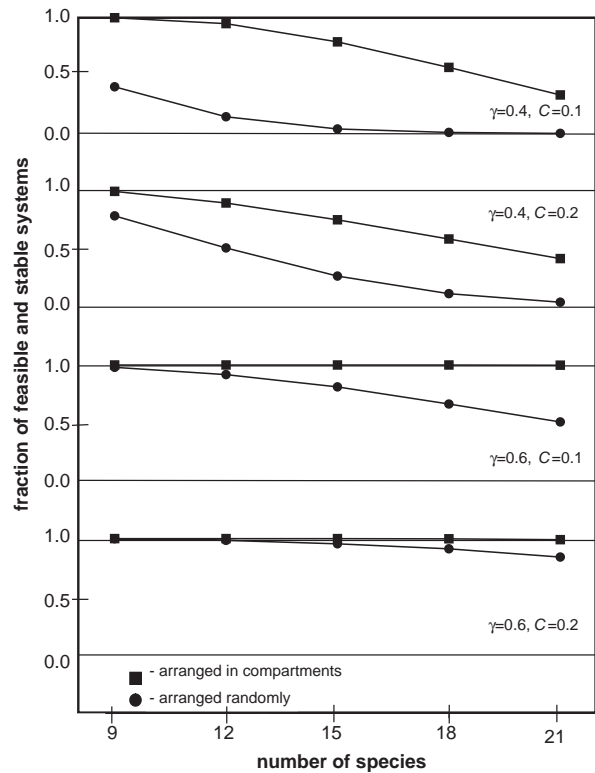


Fig. 2. The fraction of feasible and stable systems for interaction matrices that are arranged randomly and arranged into 3 compartments for parameter values $\gamma = 0.4, 0.6$ and $C = 0.1, 0.2$. For each data point 5000 interaction matrices were analysed resulting in a standard error of less than 3.5%.

any of its compartments are reactive. The probability that one compartment will be reactive is $q_c(m/k, Ck(m-1)/(m-k), \gamma)$ and the probability that the system will be reactive (i.e. at least one compartment) is $1 - (1 - q_c)^k$.

From the results given above, when $C = 1$, resilience is given by $(m^*(1 - \gamma))$. Also, in this case, $(A + A')/2 = A$, so the system is both locally stable and non-reactive. Similarly, systems arranged into compartments are both locally stable and non-reactive when $C' = 1$. Simulations were performed to determine the probability that a system is reactive when $C < 1$. Fig. 3 compares the reactivity of systems whose competitive interactions are arranged randomly with the reactivity of a system arranged into compartments maintaining the same overall connectance. The randomly arranged system was found, in general, to have a higher probability of being reactive than the system arranged into compartments.

Often the change in total biomass of a system is turned to for understanding the dynamical properties of a system. Following Hughes and Roughgarden (2000), we will analyse the variability of total abundance under a discrete time model that is homologous, in the sense of

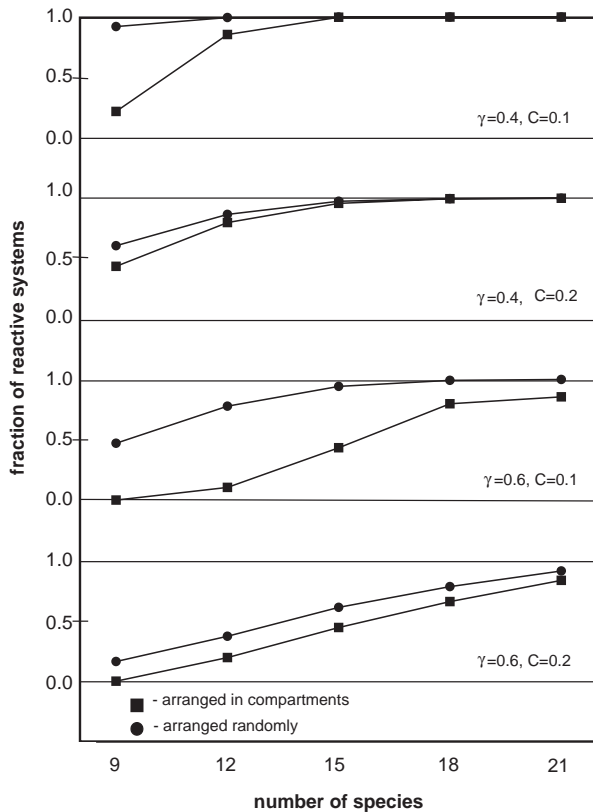


Fig. 3. The fraction of reactive systems for interaction matrices that are arranged randomly and arranged into 3 compartments for parameter values $\gamma = 0.4, 0.6$ and $C = 0.1, 0.2$. For each data point 5000 interaction matrices were analysed resulting in a standard error of less than 3.5%.

May (1974), to (1):

$$N_j(t) = N_j(t - 1) + rN_j(t - 1)(1 - N_j(t - 1) - \sum_{i=1, i \neq j}^m \alpha_{ij}N_i(t - 1)) + \varepsilon_j(t), \tag{6}$$

where $\varepsilon_j(t)$ is a normal process error with mean 0 and variance σ^2 . We will assume that the process errors are independent both in time and between species. Let $X_j(t) = N_j(t) - N_j(t - 1)$ and $X(t) = (X_1(t) X_2(t) \dots X_m(t))'$. In the neighborhood of the steady state N^* :

$$X(t) = BX(t - 1) + \varepsilon(t), \tag{7}$$

where $B = I + A$ with A given in (3) and where $\varepsilon(t) = (\varepsilon_1(t) \varepsilon_2(t) \dots \varepsilon_m(t))'$ is an m -variate normal process error with mean vector $(0, 0, \dots, 0)'$ and m -by- m variance matrix $\sigma^2 I$. In statistical terminology (7) is a first-order vector autoregressive (VAR(1)) process. This process is stationary if and only if the homologous continuous time model is locally stable.

Total abundance or biomass in period t is given by $T(t) = e'X(t)$. The variance of $T(t)$ is

$$VarT(t) = e'\Sigma e, \tag{8}$$

where Σ is the m -by- m variance matrix of $X(t)$ which satisfies:

$$\sigma^2 I = \Sigma - B\Sigma B'. \tag{9}$$

Although this expression is linear in the elements of Σ , in general there is no closed form expression for Σ .

Let $V(m, C, r, \gamma)$ be the variance of total abundance or biomass under the random model for a system of m species with connectance C , growth rate r , and interaction strength γ . The variance of total abundance or biomass for one compartment is $V_c(m/k, Ck(m - 1)/(m - k), r, \gamma)$, and the variance of the system is therefore kV_c .

It is again possible to derive a simple result when $C = 1$. By premultiplying (9) by e' and postmultiplying the product by e :

$$m\sigma^2 = e'\Sigma e - e'B\Sigma B'e. \tag{10}$$

Note that $e'B$ is the m -vector of column sums of B and $B'e = (e'B)'$. When $C = 1$, all of the column sums of B are equal to $1 - rn^* - (m - 1)rn^*\gamma$. It follows after some rearrangement that

$$VarT(t) = \frac{m\sigma^2}{1 - (1 - r)^2}. \tag{11}$$

This recovers, by a simpler method, a result of Hughes and Roughgarden (2000). It is more typical to examine the coefficient of variation of the biomass (or CV of biomass) which can be found using the following relationship.

$$CV(T(t)) = \frac{\sqrt{Var(T(t))}}{\langle T(t) \rangle} = \frac{(1 + [m - 1]\gamma)\sigma}{\sqrt{m(1 - (1 - r))^2}}. \tag{12}$$

The CV of biomass for systems arranged into compartments, where each compartment is fully connected (i.e. $C' = 1$ but $C < 1$), can also be solved analytically as the total system variance is the sum of the variance in each compartment.

For the case when $C < 1$ numerical simulations of (6) were performed to estimate $CV(T(t))$ (details of which can be found in the caption of Fig. 4). The results produced were very similar to the previous stability comparisons. The systems containing compartments exhibit a lower CV of biomass (and are therefore considered to be more stable) than the randomly arranged systems, as shown in Fig. 4.

At the suggestion of a reviewer, a variety of the modeling assumptions used were relaxed and comparisons were made between the stability properties of systems arranged into compartments and randomly arranged systems for these modifications. Assumptions which were relaxed include: (1) adding noise to the interactions strength terms, γ , and (2) including additional interactions outside of compartments to destroy their strict independence. The same qualitative result that systems arranged into compartments have favorable stability properties was found to generally hold

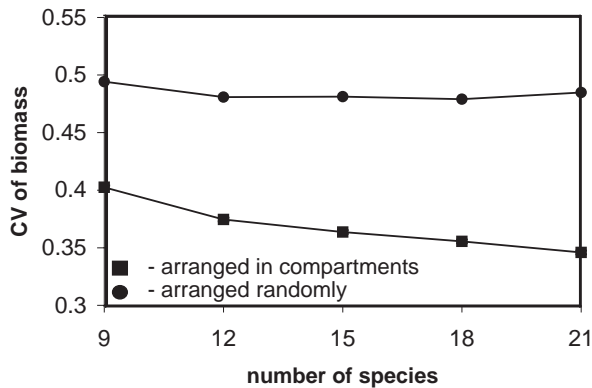


Fig. 4. The coefficient of variation (CV) of biomass for interaction matrices that are arranged randomly and arranged into 3 compartments. Parameter values used: $\gamma = 0.6$, $C = 0.1$, and for each data point 200 interaction matrices were analysed over 50 time steps. The resulting standard error is less than 0.4%.

true. It was additionally suggested by reviewers that stability properties can be changed by altering the number of compartments. In the results reported above, we compared the stability properties of systems with 1 compartment (i.e. randomly arranged) and 3 compartments. Increasing the number of compartments (for example from 2 compartments to 6 compartments) also acts to make stability properties more favorable, and the causal reasoning is similar to that found in the final paragraph of Section 4.

4. Discussion

May's (1974) publication explored the relationship between "stability" and "complexity" in ecosystems using a model which described interactions between species in the natural world as elements of a matrix which were randomly arranged. Within the model assumptions May used, greater complexity led to less stability. The competition model analysed here allows us to address Ecology's complexity/stability debate from the different context that the structural arrangement of interactions can significantly alter stability measures. It also has the advantage that the community matrix is a function of the populations' equilibrium abundances (see Eq. (3)), which is thought to be more realistic. The model is not intended to have a direct application to a specific natural system but to add another piece to the puzzle involving how the structural arrangement of interactions influences dynamic behavior.

Despite the highly simplified structure of the model when compared to the complex competition communities found in the natural world, we nevertheless believe it provides what should be a useful first approximation. It is in fact a widely used competition model that has been widely discussed and analysed in the literature for decades from a theoretical perspective (Jansen and

Kokkoris, 2003; Hughes and Roughgarden, 2000; Stone and Roberts, 1991; Rejmanek et al., 1983; May, 1974). Further studies that examine the effects of alternative structural arrangements of interactions using other dynamical models (e.g. competitive communities with more complex resource dynamics), are needed to determine if the results of this study have wider applicability.

While May reported that complexity (measured in terms of connectance) reduces stability (measured in terms of the fraction of systems exhibiting local linear stability); one of the simplest ecological models, the competitive Lotka-Volterra system, reveals a more complex relationship (Rozdilsky and Stone, 2001). In agreement with May's general conclusion, competitive Lotka-Volterra systems with small values for the connectance (i.e. $C \rightarrow 0$) lead to a large fraction of systems exhibiting linear stability; but unlike May's result, large values for the connectance (i.e. $C \rightarrow 1$) also lead to a large fraction of systems exhibiting linear stability.

Consider a comparison between the feasibility of two systems with the same overall connectance, one arranged randomly and one arranged into k compartments. The probability that the randomly arranged system is feasible, P_{random} , can be found through direct simulation. Now a system arranged into independent compartments is only feasible if every compartment is feasible. Therefore the probability that the entire system is feasible is equal to the probability that an individual compartment is feasible, $P_{compartment}$, raised to the k th power. We are thus comparing P_{random} and $(P_{compartment})^k$. Each compartment has a smaller size and higher internal connectance than the system when arranged randomly, and we have found (numerically) that $P_{compartment} > P_{random}$ across a wide parameter range. Our simulation results have shown that generally $(P_{compartment})^k > P_{random}$ making systems arranged into compartments more feasible. When other measures of stability were tested, similar results were found which favored species persistence for systems with competitive interactions arranged into compartments when compared to randomly arranged systems.

Acknowledgements

This research would not have been possible without the support of the Fulbright foundation, Tel Aviv University, and the James S. McDonnell Foundation.

References

- DeAngelis, D.L., 1975. Model for trophic interaction. *Ecology* 56, 238.
- Fox, B.J., Brown, J.H., 1993. Assembly rules for functional-groups in North American desert rodent communities. *Oikos* 67, 358–370.

- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Hughes, J.B., Roughgarden, J., 2000. Species diversity and biomass stability. *Am. Nat.* 155, 618–627.
- Jansen, V.A.A., Kokkoris, G.D., 2003. Complexity and Stability revisited. *Ecol. Lett.* 6, 498–502.
- King, A.W., Pimm, S.L., 1983. Complexity, diversity, and stability—A reconciliation of theoretical and empirical results. *Am. Nat.* 122, 229–239.
- May, R.M., 1972. Will a large complex system be stable. *Nature* 238, 413–414.
- May, R.M., 1974. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.
- McMurtrie, R.E., 1975. Determinants of stability of large randomly connected systems. *J. Theor. Biol.* 50, 1–11.
- McNaughton, S.J., 1977. Diversity and stability of ecological communities—Comment on role on empiricism in ecology. *Am. Nat.* 111, 515–525.
- Neubert, M.G., Caswell, H., 1997. Alternatives to resilience for measuring the responses of ecological systems to perturbations. *Ecology* 78, 653–665.
- Pimm, S.L., 1984. The complexity and stability of ecosystems. *Nature* 307, 321–326.
- Rejmanek, M., Kindlmann, P., Leps, J., 1983. Increase of stability with connectance in model competition communities. *J. Theor. Biol.* 101, 649–656.
- Rozdilsky, I.D., Stone, L., 2001. Complexity can enhance stability in competitive systems. *Ecol. Lett.* 4, 397–400.
- Simberloff, D., Dayan, T., 1991. The guild concept and the structure of ecological communities. *Annu. Rev. Ecol. Syst.* 22, 115–143.
- Smith, J.M., 1974. *Models in Ecology*. Cambridge University Press, Cambridge, UK.
- Solow, A.R., Beet, A., 1998. On lumping species in food webs. *Ecology* 79, 2013–2018.
- Solow, A.R., Costello, C., Beet, A., 1999. On an early result on stability and complexity. *Am. Nat.* 154, 587–588.
- Stone, L., 1988. Ph.D. Thesis. Monash University, Australia.
- Stone, L., Roberts, A., 1991. Conditions for a species to gain advantage from the presence of competitors. *Ecology* 72 (6), 1964–1972.