REPORT

Stability and species richness in complex communities

Anthony R. Ives, Jennifer L. Klug and Kevin Gross
Department of Zoology, UW-Madison, 430 Lincoln Dr, Madison, WI 53706, U.S.A.
E-mail: arives@facstaff.wisc.edu

Abstract

Using both numerical simulations and analytical methods, we investigate how the stability of ecological communities depends on the number of species they contain. To investigate complex communities, we construct communities from modular "subcommunities" that can have arbitrary community structure; e.g. subcommunities could consist of pairs of predator and prey species, trios of prey, specialist predator and generalist predator, or any collection of interacting species. By building entire communities from subcommunities, we can change the number of species in the community without changing community structure. We further suppose that species sharing the same ecological role in different subcommunities act additively on the per capita population growth rates of other species. Under these assumptions, the interactions between species from different subcommunities have no effect on community-level stability, measured by the variability in the combined densities of species sharing the same ecological role in different subcommunities. Furthermore, increasing species richness (i.e. the number of subcommunities comprising the community) increases community-level stability only when it introduces species that respond differently to environmental fluctuations. Therefore, our results support the "insurance hypothesis" that species richness increases community-level stability by insuring that some species in a community are tolerant of different environmental fluctuations.

INTRODUCTION

The stability of an ecological community depends on the types of interactions among species in the community and the sensitivity of each species to different types of environmental fluctuations (MacArthur 1955; Elton 1958; Margalef 1969; May 1972, 1973; Pimm 1984). There is also a general belief that stability depends on the number of species in a community. However, isolating the effects of species number *per se* on stability is difficult. A natural community with many species is also likely to have many types of species with ecological roles not found in species-poor communities (Orians 1969; MacArthur 1972); e.g. species-rich communities may have a greater number of trophic levels than species-poor communities (e.g. Briand 1983). Similarly, communities with many species are more likely to have some species that are relatively insensitive to a particular environmental disturbance; e.g. a species-rich grassland community may be

more likely to have some species that are tolerant of fire or grazing (McNaughton 1977, 1985). Thus, species number may affect stability by introducing species that either interact with other species in novel ways or show novel responses to environmental fluctuations, and teasing apart these effects on stability is hard.

The stability of ecological communities may be measured in many different ways. Four commonly recognized properties associated with stability are resilience (measured by characteristic return times to equilibrium), resistance (measured by the displacement from equilibrium caused by an environmental disturbance), persistence of species and variability (Pimm 1984). Of these, resilience and resistance are often difficult to measure, because many communities do not possess a well-defined equilibrium. Although measuring stability by species persistence may be appropriate for communities that experience large fluctuations in species composition, persistence will not be informative for communities with

fairly constant composition which none the less show wide fluctuations in species abundances. Here, we have chosen to measure stability in terms of variability in abundances, which is the most frequently used measure of stability, although also the most poorly understood from a theoretical perspective (Pimm 1991).

Our goal is to determine the effect of species number on the stability of communities. We confine attention to variability in the densities of species persisting within communities, rather than address the question of how environmental variability itself may affect the persistence of species (Chesson 1985, 1994; Chesson & Huntly 1997). We first present our scheme for constructing communities that vary in the number of species they contain yet have the same structure (e.g. trophic levels, types of species interactions, etc.). This makes it possible to determine the consequences of species numbers *per se* on community stability. Second, we give a numerical example of communities with two trophic levels and use this to explore community stability measured both for individual species and for the aggregate of species in the same trophic level. Third, we generalize the results from the numerical example using multivariate autoregression, which provides a linear approximation of the dynamics of communities having arbitrary structure and arbitrarily large numbers of species.

CONSTRUCTING COMMUNITIES AND MEASURING STABILITY

We build model communities with different numbers of species but the same structure by combining modular "subcommunities" (Holt *et al.* 1994; Holt 1996). For example, to build communities with two trophic levels, we use subcommunities of predator–prey pairs (Fig. 1A). Thus, a community with four species consists of two predator–prey pairs linked together by predators attacking both prey species, and prey species competing for shared resources. A community with six species consists of three predator–prey pairs linked by predation and competition. The critical point here is that with the addition of subcommunities, no new ecological roles (e.g. a third trophic level) are added. This method of constructing communities can be performed with any configuration of subcommunity. For example, communities including prey, specialist predators (that only attack the prey) and generalist predators (that attack both prey and specialist predators) can be constructed from three-species subcommunities consisting of prey, specialist predator and generalist predator (Fig. 1B). Previously, we theoretically explored the relationship between species richness and stability for competitive communities consisting of a single trophic level (Ives *et al.* 1999). Our
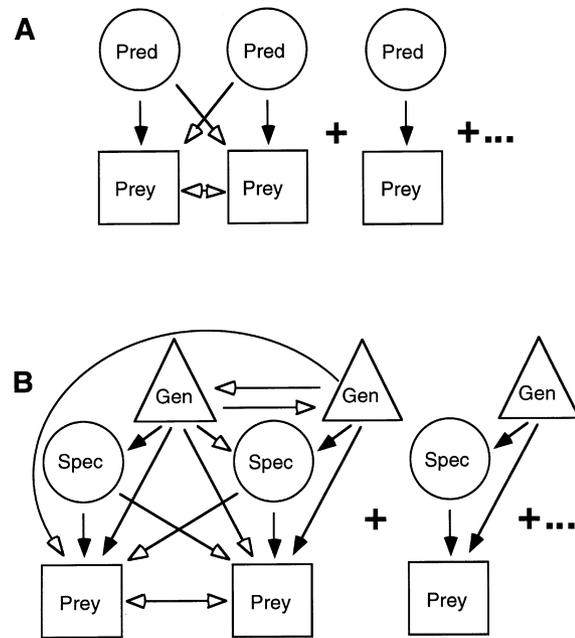
Figure 1 Construction of hypothetical communities from subcommunities with the same structure. In (A), subcommunities consist of predator–prey pairs, while in (B) subcommunities contain a prey, a specialist predator that consumes only the prey, and a generalist predator that consumes prey, specialist predators and members of its own species. Interactions within subcommunities are denoted with black arrows, and interactions between subcommunities are shown with white arrows. In (A), intraspecific competition for prey is not shown but is assumed to have the same form as competition between prey species in different subcommunities. In (B), intraspecific interactions for prey and generalist predators are similarly not shown.

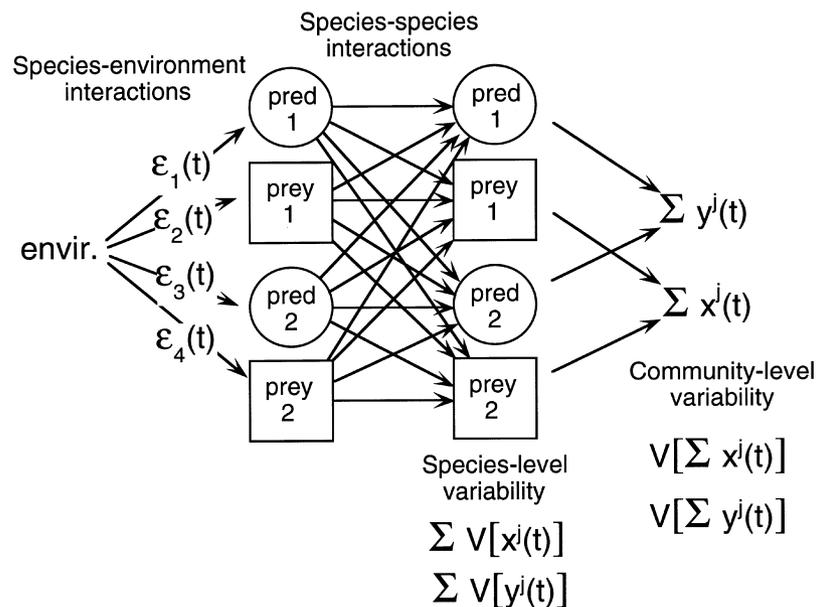analyses here extend these results to complex community structures.

It has been demonstrated both empirically (Tilman 1996) and theoretically (King & Pimm 1983) that the stability properties of a community may differ depending on the level of organization at which stability is measured. For example, if species exhibit compensatory responses to environmental fluctuations, in which decreases in some species are compensated by increases in other species, then the variability of the aggregate group of species will be less than that of the species taken separately (Frost *et al.* 1994; Klug *et al.* 2000). We measure variability at two different levels of organization within a community: at the level of individual species (species-level variability) and at the level of species that share the same ecological role (community-level variability). For example, in the predator–prey community (Fig. 1A) community-level variability is measured by the variability in density of all predators combined or the variability in density of all prey

combined. As we show below, it does not matter which species role is selected for measuring community-level variability; in the predator–prey community, the results are the same whether prey or predator are used.

The processes affecting variability in a community are illustrated heuristically in Fig. 2. Species–environment interactions are depicted by the species-specific random variables $\varepsilon_i(t)$, which give the environmentally driven changes in species population growth rates between times t and $t + 1$. If species i and j experience environmental fluctuations in a similar way, then $\varepsilon_i(t)$ and $\varepsilon_j(t)$ will be positively correlated. In addition to the direct effects of species–environment interactions, environmental fluctuations may affect species indirectly through species–species interactions. For example, environmentally driven variability in the density of a predator may drive variability in the density of its prey. These species–species interactions can be viewed as a filter which propagates environmentally driven fluctuations in species densities throughout the rest of the community. The community-level variability is given by the variability in the combined prey densities, $\Sigma\text{prey}_i(t)$, and combined predator densities, $\Sigma\text{pred}_i(t)$, which depend not only on the variability of the individual species but also the correlations between them. Although this illustration is heuristic, it can be made mathematically precise, as we do below (see Autoregressive approximation).

The number of species in a community can potentially influence stability by changing either the net effect of species–environment interactions or the net effect of species–species interactions. Increasing the number of species may introduce new species that respond differently to environmental fluctuations, such that $\varepsilon_i(t)$ for a new species is not strongly correlated with those of existing species in the community. This leads to the "insurance hypothesis" that species richness makes it more likely that the community contains species tolerant to numerous types of environmental fluctuations (McNaughton 1977; Yachi & Loreau 1999). Increasing species number may also influence stability by increasing the number of species–species interactions (Gardner & Ashby 1970; May 1972; Pimm 1982; McCann et al. 1998; Hughes & Roughgarden, 1998, 2000). Our analyses show that adding species affects both species-level and community-level variability by introducing new species–environment interactions. In contrast, although adding species may affect species-level variability by introducing more species–species interactions, this is not the case for community-level variability. Thus, in the framework of Fig. 2, variability in the sum of prey or predator densities ($\Sigma\text{prey}_i(t)$ or $\Sigma\text{pred}_i(t)$) depends primarily on the species–environment interactions encapsulated by values of $\varepsilon_i(t)$, rather than species–species interactions.

Figure 2 Heuristic illustration of processes affecting the stability of stochastic systems. The effects of environmental fluctuations on individuals species (species–environment interactions) are summarized by the random variables $\varepsilon_i(t)$. The resulting variability in the population densities of species are propagated through the community through species–species interactions. Thus, the net effect of environmental fluctuations on species-level variability (the sum of the variability in individual species densities, $\Sigma V[x^i(t)]$ and $\Sigma V[y^i(t)]$ for prey and predator, respectively) depends on both the direct effects of species–environment interactions and the indirect effects of species–species interactions. The community-level variability depends on the variability in the combined densities of species sharing the same ecological role ($V[\Sigma x^i(t)]$ and $V[\Sigma y^i(t)]$ for prey and predator, respectively). Thus, the community-level variability depends on both the magnitude and the correlation in variability of individual species densities.

EXPLICIT NUMERICAL EXAMPLE

For a community with two trophic levels consisting of n subcommunities (i.e. n prey and n predator species), we use the discrete-time version of the Lotka–Volterra predator–prey model (Lotka 1925) with competition among prey species and stochasticity added to the per capita population growth rates of both prey and predator. Letting $x^j(t)$ and $y^j(t)$ be the densities of prey and predator in subcommunity j,

$$x^j(t+1) = x^j(t)\exp\left[\varepsilon_1^j(t) + r^j\left(1 - \frac{X^j(t)}{K^j}\right) - aY^j(t)\right]$$

$$y^j(t+1) = y^j(t)\exp[\varepsilon_2^j(t) + c^j aX^j(t) + d^j] \quad (1)$$

where r^j is the prey intrinsic rate of increase, K^j is the prey carrying capacity, a is the predator attack rate, c^j is the scaling factor that translates predation into predator reproduction and d^j is the predator death rate. We assume that the net effect of competition and predation on the prey depend on $X^j(t)$ and $Y^j(t)$, respectively, where

$$X^j(t) = x^j(t) + \alpha \sum_{h=1, h\neq j}^{n} x^h(t)$$

$$Y^j(t) = y^j(t) + \alpha \sum_{h=1, h\neq j}^{n} y^h(t) \quad (2)$$

are the weighted averages of prey and predator densities in which prey and predators from different subcommunities are discounted by α. Thus, α gives the relative strength of interactions between subcommunities; when $\alpha = 0$ there are no interactions between species in different subcommunities, while when $\alpha = 1$ interactions between subcommunities are as strong as those within subcommunities.

Environmentally driven fluctuations in per capita population growth rates are given by $\varepsilon_1^j(t)$ and $\varepsilon_2^j(t)$ for prey and predator, respectively, where we have introduced the convention of using superscripts to identify the subcommunity and subscripts to identify the ecological role (prey *versus* predator). We assume $\varepsilon_1^j(t)$ and $\varepsilon_2^j(t)$ are normally distributed with mean zero and standard deviations σ_1 and σ_2, which are assumed to be the same for all subcommunities. Furthermore, we assume that $\varepsilon_1^j(t)$ and $\varepsilon_2^j(t)$ are independent of each other, but prey and predators in different subcommunities may experience environmental fluctuations in a correlated fashion. The correlation between $\varepsilon_i^j(t)$ ($j = 1, \ldots, n$) in different subcommunities is given by ρ, which for simplicity we have assumed to be the same for all subcommunities. Finally, we assume there is no serial (temporal) correlation in environmental fluctuations, although our general results also apply when there is serial autocorrelation (Ives 1995a).

All parameters in the model are different among subcommunities with the exception of a, the predator attack rate. This does not restrict the generality of the model, however, because differences in attack rates may be incorporated by rescaling predator densities. Specifically, if attack rates a^j differ among subcommunities, predator densities $y^j(t)$ can be scaled using $y^{j\prime}(t) = (a/a^j)y^j(t)$, and the conversion factor c^j can be rescaled as $c^{j\prime} = (a^j/a)c^j$. This rescaling leads back to equation (1).

It is easiest to analyse this model by assuming that the combined predator and combined prey densities are independent of the number of subcommunities, n, and the strength of linkage between subcommunities, α. This assumption is not necessary, as we show later. However, it simplifies the analysis, because it removes the effect of changing mean total densities on the variance in species densities, thereby making it possible to compare the variances among communities with different species richness n and linkage strength α. To make mean total densities constant, let K^j and a be scaled according to

$$\frac{1}{n}\sum_{j=1}^{n} K^j = \frac{1 + (n-1)\alpha}{n}\hat{K}$$

$$a = \frac{n}{1 + (n-1)\alpha}\hat{a} \quad (3)$$

where $\hat{K}$ and $\hat{a}$ are values of K and a for the case in which there is only one predator–prey subcommunity; it is easily confirmed that this scaling of K and a makes mean total prey and predator densities independent of n and α. To combine subcommunities that differ in the strengths of species interactions, for each subcommunity we selected values of r^j, K^j, c^j and d^j from normal distributions using a random number generator. In randomly selecting parameter values, it is possible to select values that are nonsensical (negative) or prohibit the coexistence of species. Because we are interested in variability of species densities rather than persistence of species, we set the standard deviations of the normal distributions small enough to insure sensible values and to allow coexistence.

Figure 3 illustrates the population dynamics produced by the model with successively added subcommunities when the environmentally driven fluctuations of species population growth rates in different subcommunities are uncorrelated ($\rho = 0$, Fig. 3A–C) and highly correlated ($\rho = 0.9$, Fig. 3D–F). The top panels (Fig. 3A, D) give the community-level variance in predator density, defined as the variance in the combined predator densities from all subcommunities,

$$V_{\text{com}} = V\left[\sum_{j=1}^{n} y^j(t)\right].$$

Figure 3 The effects of subcommunity number n on community-level variance, V_{com}, species-level variance, V_{sp}, and mean density for the predator species in a community consisting of predator–prey pairs (Fig. 1A). In each panel, communities without linkage among subcommunities ($\alpha = 0$) are shown with dashed lines, and solid lines correspond to the case of $\alpha = 0.5$. Means and variances were calculated from data sets generated by iterating equation (1) 500 times. Values of r^j, K^j, c^j and d^j were selected using a random number generator from normal distributions with means 0.8, 1000, 0.004 and 0.02, and standard deviations 0.05, 10, 0.0001 and 0.001, respectively. Greater variability in these parameters often leads to species extinctions. Environmental variance was added by letting $\varepsilon_1^j(t)$ and $\varepsilon_2^j(t)$ be normal random variables with mean zero and variance 0.001. The correlations between $\varepsilon_1^j(t)$ and $\varepsilon_2^j(t)$ within subcommunities were zero, and the correlations between $\varepsilon_i^j(t)$ ($i = 1, 2; j = 1, \ldots, n$) among subcommunities were $\rho = 0$ (A–C) and $\rho = 0.9$ (D–F).
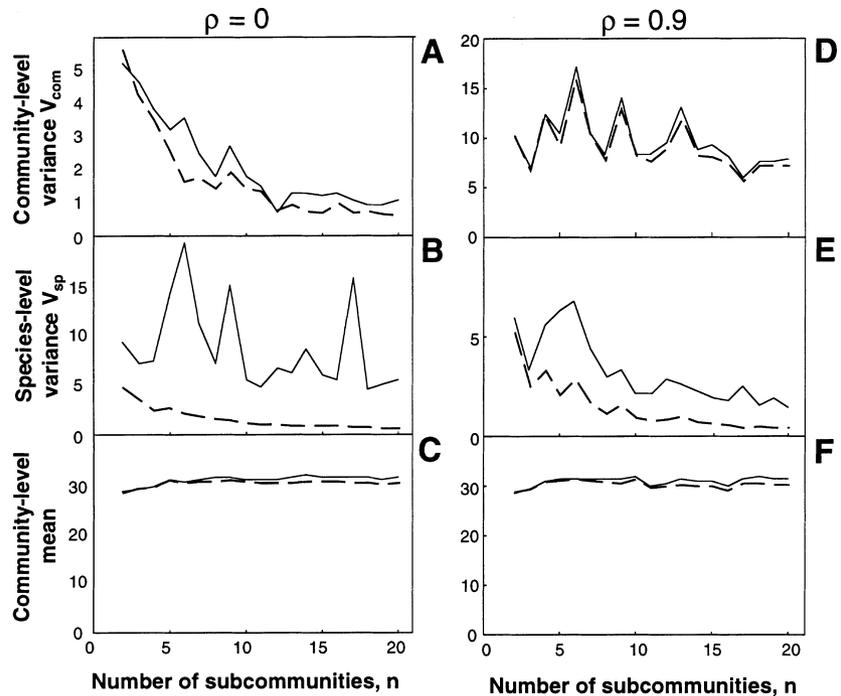
The middle panels (Fig. 3B, E) give species-level variances in predator densities, defined as the sum of variances of individual species densities,

$$V_{sp} = \sum_{j=1}^{n} V[y^j(t)].$$

The bottom panels (Fig. 3C, F) give the mean combined density of all predators. Finally, in each panel we have graphed the results for communities with linked subcommunities ($\alpha = 0.5$, solid lines) and unlinked subcommunities ($\alpha = 0$, dashed lines). The jitter in the lines is caused by differences among parameters in the subcommunities and the stochasticity of the simulated population dynamics. Although we show only the results for predator species, the prey show similar patterns.

This numerical example leads to two conclusions. First, linkage between subcommunities, α, has little effect on community-level variances. Specifically, V_{com} when there is no linkage ($\alpha = 0$, dashed lines) is similar to V_{com} when there is linkage ($\alpha = 0.5$, solid lines). Second, increasing the number of subcommunities, n, decreases community-level variability by adding species that respond differently to environmental fluctuations. Thus,

V_{com} declines with n when species responses to environmental fluctuations are uncorrelated ($\rho = 0$, Fig. 3A), but this decline is small when they are correlated ($\rho = 0.9$, Fig. 3D). These are the same conclusions derived for models of communities with only a single trophic level (Ives *et al.* 1999).

In contrast to community-level variance, species-level variance, V_{sp}, depends on both n and α. Linkage between subcommunities ($\alpha > 0$) strongly increases V_{sp} when species responses to environmental fluctuations are uncorrelated ($\rho = 0$, Fig. 3B), while this effect is reduced by correlated responses to environmental fluctuations ($\rho = 0.9$, Fig. 3E). Furthermore, the effect of linkage between subcommunities is greater when there are more subcommunities, n, because environmental fluctuations experienced in one subcommunity drive variability in the densities of species in other subcommunities.

To demonstrate that community-level variability is insensitive to the number of subcommunities making up the community even when total species densities change with n and α, we analysed the predator-prey model (equation (1)) with constant values of K^j and a (in contrast to equation (3)). Figure 4 presents simulation results analogous to Fig. 3. The mean density of predators in the

absence of linkage between communities (Fig. 4C, F, dashed lines) increases rapidly with n, resulting in a similarly large increase in community variance, V_{com} (Fig. 4B, E, dashed lines). In contrast, the mean density of predators in the presence of linkage (Fig. 4C, F, solid lines) increases slowly from 38 when $n = 2$ to 57 when $n = 20$, and V_{com} decreases from 8.7 to 3.0 (Fig. 4B, E, solid lines). However, if we account for changes in mean densities by employing the coefficient of variation in combined predator density, CV_{com} (Fig. 4A, D), the patterns are similar to those in Fig. 3. In particular, linkage between subcommunities has little effect on community-level variability measured by CV_{com}, and the reduction in CV_{com} with increasing n is greatest when species responses to environmental fluctuations are uncorrelated ($\rho = 0$, Fig. 4A *versus* $\rho = 0.9$, Fig. 4D). Thus, the effect of α on V_{com} is caused by differences in mean total species densities. Removing the effect of means by using CV_{com} shows that stability is not affected strongly by linkage between subcommunities.

AUTOREGRESSIVE APPROXIMATION

The predator–prey model above shows that linkage between subcommunities ($\alpha > 0$) has little effect on community-level stability. In contrast, communities composed of larger numbers of subcommunities, n, may have higher community-level stability if species responses to environmental fluctuations are not strongly positively correlated. Here, we use a general analytical model to

show that the same conclusions hold regardless of the structure of the subcommunities.

An analytical model can be constructed by approximating population dynamics as a multispecies linear autoregressive process (Judge *et al.* 1985). The population dynamics of a single subpopulation containing s species are given by

$$\boldsymbol{W}^j(t + 1) = \boldsymbol{A}^j + (\boldsymbol{I} + \boldsymbol{B}^j)\boldsymbol{W}^j(t) + \boldsymbol{E}^j(t) \qquad (4)$$

where $\boldsymbol{W}^j$ is a $s \times 1$ vector of densities $x_i^j(t)$ of species in ecological role i within subcommunity j at time t, $\boldsymbol{A}^j$ is a $s \times 1$ vector of constants, $\boldsymbol{B}^j$ is a $s \times s$ matrix whose elements b_{ik}^j give the per capita effect of species with ecological role k on the population growth rate of species with role i in subcommunity j, $\boldsymbol{I}$ is the identity matrix, and $\boldsymbol{E}^j(t)$ is a $s \times 1$ vector of random variables $e_i^j(t)$ expressing the effects of environmental fluctuations on the population growth rate of species with role i in subcommunity j. Although this autoregressive model is linear, it can nonetheless provide useful approximations to nonlinear processes (Ives 1995a, b; Solow & Sherman 1997; Ives & Jansen 1998; Ripa *et al.* 1998; Hansen *et al.* 1999).

The population dynamics of the entire community can similarly be modelled as the autoregressive process

$$\boldsymbol{W}(t + 1) = \boldsymbol{A} + (\boldsymbol{I} + \boldsymbol{B})\boldsymbol{W}(t) + \boldsymbol{E}(t) \qquad (5)$$

where $\boldsymbol{W}(t)$, $\boldsymbol{A}$ and $\boldsymbol{E}(t)$ are $(sn) \times 1$ vectors, and $\boldsymbol{B}$ is an $(sn) \times (sn)$ matrix created by combining the autoregressive models for subcommunities. To build $\boldsymbol{A}$ and $\boldsymbol{B}$ from
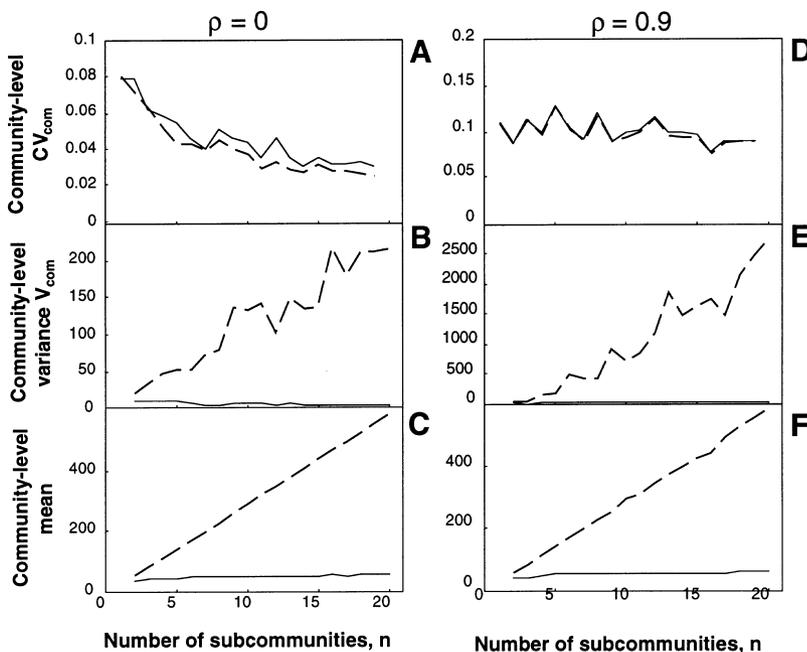

Figure 4 The effects of subcommunity number n on the community-level coefficient of variation, CV_{com}, community-level variance, V_{com}, and mean density for the predator species in a community consisting of predator–prey pairs (Fig. 1A). In each panel, communities without linkage among subcommunities ($\alpha = 0$) are shown with dashed lines, and solid lines correspond to the case of $\alpha = 0.5$. This figure was produced in the same way as Fig. 3 with the same parameters. The only difference is that values of a and K^j were held constant, rather than discounted according to equation (3). Because $CV_{com} = (V_{com})^{0.5}/$(community-level mean), a two-fold decline in CV_{com} in (A) is equivalent to a four-fold decline in V_{com} in Fig. 3(A).

subcommunity-specific A^j and B^j, we let

$$A = \begin{bmatrix} \frac{1}{n}A^1 \\ \frac{1}{n}A^2 \\ . \\ . \\ . \\ \frac{1}{n}A^n \end{bmatrix} \qquad (6)$$

and

$$B = \begin{bmatrix} \frac{1}{1+(n-1)\alpha}B^1 & \frac{\alpha}{1+(n-1)\alpha}B^1 & \cdots & \frac{\alpha}{1+(n-1)\alpha}B^1 \\ \frac{\alpha}{1+(n-1)\alpha}B^2 & \frac{1}{1+(n-1)\alpha}B^2 & \cdots & \frac{\alpha}{1+(n-1)\alpha}B^2 \\ & & \cdots & \\ & & \cdots & \\ & & \cdots & \\ \frac{\alpha}{1+(n-1)\alpha}B^n & \frac{\alpha}{1+(n-1)\alpha}B^n & \cdots & \frac{1}{1+(n-1)\alpha}B^n \end{bmatrix}. \qquad (7)$$

This formulation of A and B is comparable to the predator–prey model analysed in the previous section (equation (1)). Matrix A sets mean species densities, and so we let the total density of species in the community be independent of n by discounting elements of A by $1/n$. This assumption is made for convenience and does not affect any of our results, which depend solely on B. We construct B from the B^js so that the net strength of a given type of ecological interaction (competition, predation, etc.) on any given species is independent of n and α. Specifically, consider the species with role 1 in subcommunity 1 having density $x_1^1(t)$. From equation (7), the net strength of intra- and interspecific competition on the population growth rate of this species is

$$\frac{b_{11}}{1+(n-1)\alpha}\left(x_1^1(t) + \alpha \sum_{j=2}^{n} x_1^j(t)\right).$$

The strength of competitive interactions between species in different subcommunities is thus discounted by α, so α measures the linkage strength between subcommunities as in the numerical predator–prey model (equation (1)). Furthermore, the sum of per capita effects of competition on the species with role 1 in subcommunity 1 is independent of n and α;

$$\left(\frac{b_{11}}{1+(n-1)\alpha} + \alpha \sum_{j=2}^{n} \frac{b_{11}}{1+(n-1)\alpha}\right) = b_{11}.$$

The same arguments hold for other types of interactions. For example, the net effect of predators (role 2) on the prey (role 1) in subcommunity 1 depends on the sum

$$\frac{b_{12}}{1+(n-1)\alpha}\left(x_2^1(t) + \alpha \sum_{j=2}^{n} x_2^j(t)\right),$$

so interactions between subcommunities are discounted

by α, and the net effect of predation on the prey species in subcommunity 1 is independent of n and α.

To ground this construction of B in biological terms, consider a community in which each subcommunity contains a single plant species. How is the net effect of competition on a focal plant species likely to change with the number of plant species (subcommunities) in the community? With increasing numbers of plant species, n, the number of individual plants from any given subcommunity j within the neighbourhood surrounding a plant of the focal species should decrease, because the neighbourhood will be filled by individuals of other species. Therefore, the per capita effect of the plant species from subcommunity j on the focal species will decrease with increasing n. Making this decrease proportional to

$$\frac{1}{1+(n-1)\alpha}$$

makes the net per capita effect of competition independent of n and α. Although this particular assumption may not hold precisely in natural communities, many competition models have this property, including the deterministic Lotka–Volterra competition model (see the Appendix). A similar argument applies to predator–prey interactions. With increasing numbers of prey and predator species, n, the per capita effect of any one predator species on any one prey species should decrease, because predation is diluted among more prey species.

In the autoregressive model given by equation (5), we also assume that the variances in population growth rates, $e_i^j(t)$, are proportional to the square of mean species densities; $\sigma_i^{2\,j} = (x_i^{j*}/x_i^*)^2\,\hat{\sigma}_i^2$, where x_i^{j*} is the mean density of species with role i in subcommunity j, and x_i^* and $\hat{\sigma}_i^2$ are the mean and variance of the population growth rate of the species with role i when there is only a single subcommunity. This is equivalent to assuming that the coefficient of variation of the population growth rate is constant. Finally, we assume that the correlation ρ between $e_i^j(t)$ and $e_i^h(t)$ is the same between all species in different subcommunities sharing ecological role i.

The autoregression model (equation (5)) describes mathematically the processes illustrated in Fig. 2. Species–environment interactions are summarized by the changes in population growth rates given by the random variables in $E(t)$, and species–species interactions are contained in B. The effect of environmental variability on variability in species densities, $W(t)$, depends both on the variability in $E(t)$ and how this variability is propagated by B. Thus, our analysis addresses whether increasing species richness affects stability through changes in B or E.

An important special case arises when the interaction strengths in all subcommunities are the same (i.e. $B^j = B^1$ and $A^j = A^1$ for all j). In this case, it can be shown easily

that increasing the size of the community, n, changes community-level variability not via species–species interactions, but instead by changing the net effects of species–environment interactions. With $\boldsymbol{B}^j = \boldsymbol{B}^1$ and $\boldsymbol{A}^j = \boldsymbol{A}^1$, equation (5) can be expressed in terms of the sum of densities of species sharing the same ecological role. Letting

$$z_i(t) = \sum_{j=1}^{n} x_i^j(t)$$

and $\boldsymbol{Z}(t)$ be the $s \times 1$ vector of values of $z_i(t)$,

$$\boldsymbol{Z}(t + 1) = \boldsymbol{A}^1 + (\boldsymbol{I} + \boldsymbol{B}^1)\boldsymbol{Z}(t) + \boldsymbol{U}(t) \tag{8}$$

where $\boldsymbol{U}(t)$ is the $s \times 1$ vector of random variables giving the aggregate response to environmental fluctuations of species sharing the same ecological role. Note that neither n nor α appear in this equation. Biologically, this means that the effects of species–species interactions in $\boldsymbol{B}$ on the dynamics of the combined densities of species sharing the same ecological role do not depend on the number of subcommunities nor the strength of linkage between them. Also, the expectations of $z_i(t)$ are independent of n and α, which implies that the expectation of species densities are proportional to $1/n$; specifically, $x_i^{j*} = x_i^*/n$.

In contrast to the species–species interactions, increasing n changes the net effect of the species–environment interactions in a way that may decrease community-level variability. The elements of the vector of random variables governing the aggregate responses of species to environmental fluctuations, $\boldsymbol{U}(t)$, are

$$u_i(t) = \sum_{j=1}^{n} e_i^j(t) \tag{9}$$

The variance in $u_i(t)$ is

$$V[u_i(t)] = \sum_{j=1}^{n} V[e_i^j(t)] + 2 \sum_{j=1}^{n} \sum_{k=j+1}^{n} cov[e_i^j(t), e_i^k(t)]$$

$$= \sum_{j=1}^{n} \left(\frac{x_i^{j*}}{x_i^*} \right)^2 \hat{\sigma}_i^2 + 2 \sum_{j=1}^{n} \sum_{k=j+1}^{n} \left(\frac{x_i^{j*} * x_i^{k*}}{(x_i^*)^2} \right) \rho \hat{\sigma}_i^2$$

$$= \sum_{j=1}^{n} \left(\frac{1}{n} \right) \hat{\sigma}_i^2 + 2 \sum_{j=1}^{n} \sum_{k=j+1}^{n} \left(\frac{1}{n} \right)^2 \rho \hat{\sigma}_i^2$$

$$= \left(\frac{1 + (n-1)\rho}{n} \right) \hat{\sigma}_i^2 \tag{10}$$

Thus, provided the environmental correlation between subcommunities is not perfect ($\rho < 1$), increasing n

decreases the variance in the combined population growth rates of all species sharing the same ecological role. This is the simple consequence of adding together random variables that are not exactly correlated; the same process is responsible for decreases in the standard error of an estimated quantity with increasing sample sizes. In an ecological context, this has been called "statistical averaging" (Doak *et al.* 1998) or the "portfolio effect" (Tilman *et al.* 1998). The reduction in variance, however, is eliminated when $\rho = 1$, because $e_i^j(t)$ vary synchronously among all subcommunities. Finally, note that these results are identical for all of the ecological roles i. Therefore, stability can be measured as the variance in combined species densities for any ecologically similar species.

This special case demonstrates two conclusions. First, community-level variability is independent of linkage between subcommunities, α, because equation (8) governing the population dynamics of the combined species densities $z_i(t)$ does not include α. Second, the effect of species number on community-level variability is to introduce species that experience environmental fluctuations differently from existing species. Equation (8) governing the dynamics of the combined densities among subcommunities, $z_i(t)$, is identical to equation (4) for the dynamics of a single subcommunity with densities $x_i(t)$. The dynamics only differ in the variance of the environmental fluctuations, $u_i(t)$ in equation (8) and $e_i(t)$ in equation (4). The decrease in the variance of $u_i(t)$ with increasing n is the consequence of adding species that experience environmental fluctuations differently ($\rho < 1$).

It is also possible to derive a general solution for the variance in individual species densities, V_{sp}. The autoregressive process given by equation (5) produces a joint stationary distribution of densities for all species in the community. The variance of this stationary distribution depends on the eigenvalues of the community matrix $\boldsymbol{C} = \boldsymbol{I} + \boldsymbol{B}$. In particular, the $(sn) \times (sn)$ matrix $\boldsymbol{C}$ has sn eigenvalues and sn corresponding eigenvectors. For each real eigenvalue, the variance in the stationary distribution is (Ives 1995a)

$$V_\lambda[W] = \frac{V_\lambda[E]}{1 - \lambda^2} \tag{11}$$

where $V_\lambda[W]$ and $V_\lambda[E]$ denote the variance in population densities and environmental fluctuations along the eigenvector corresponding to eigenvalue λ. Similarly, for each pair of complex conjugate eigenvalues, λ_+ and λ_-, in the plane defined by the corresponding eigenvectors (Ives 1995a),

$$V_{\lambda+}[W] + V_{\lambda-}[W] = \frac{V_{\lambda+}[E] + V_{\lambda-}[E]}{1 - ||\lambda_\pm||^2} \tag{12}$$

Thus, eigenvalues with magnitudes close to zero give rise to low variances in the stationary distribution, while magnitudes close to one give high variances (magnitudes greater than one are impossible for a stationary process). The eigenvalues of the community matrix C for the autoregressive model play a similar role as the eigenvalues of the community matrix used in the stability analysis of deterministic models (e.g. May 1973); eigenvalues with low magnitude correspond to greater stability.

For the special case of identical subcommunities, the sn eigenvalues of C can be grouped into s sets of n eigenvalues. Each of these sets consists of one of the eigenvalues λ_i ($i = 1, \ldots, s$) of the subcommunity matrix $I + B^1$, and ($n - 1$) identical eigenvalues of the form

$$\lambda_{ik} = 1 - \frac{(1 - \alpha)}{1 + (n - 1)\alpha}(1 - \lambda_i) \qquad (13)$$

From this expression, increasing the strength of linkage between subcommunities, α, increases the eigenvalues λ_{ik} of the entire community, and this increase is greater when n is larger. Provided λ_{ik} is real and positive, or complex with the real component of $\lambda_{ik} > \| \lambda_{ik} \|^2$, increases in α increase the magnitude of λ_{ik}. Thus, the variance of population densities $V_\lambda[W]$ increases relative to the variance of environmental fluctuations $V_\lambda[E]$. Biologically, this means that increasing the strength of linkage between subcommunities increases the variance in species densities, with this effect more pronounced when the number of subcommunities n is large. Equation (13) is similar to equation (4) in Ives *et al.* (1999) for the case of competitive communities, but in the latter case we assumed that α decreased with n in order to preserve the relative strengths of intra- and interspecific competition.

Increasing n not only changes the magnitudes of the eigenvalues of community matrix C, it also decreases the variances in species population growth rates caused by environmental fluctuations, $e_i^j(t)$, by reducing the mean densities of individual species. These factors may work in opposition, with increases in the magnitudes of eigenvalues promoting higher V_{sp}, and decreases in the variance of $e_i^j(t)$ promoting lower V_{sp}. This opposition is seen in the simulated example in Fig. 3(B). Increasing n decreases V_{sp} when subcommunities are not linked ($\alpha = 0$, dashed line), because it decreases the mean density of individual species. The addition of linkage among subcommunities ($\alpha = 0.5$, solid line) then increases V_{sp} by increasing the magnitudes of the eigenvalues of the community matrix. By combining equation (13) with equations (11) or (12) under the assumption that the variances of $e_i^j(t)$ decrease with the square of mean densities, it is possible to show that V_{sp} always decreases with n.

So far we have only considered the case in which subcommunities are governed by the same matrices $B^j = B^1$. None the less, the results obtained for identical subcommunities approximately hold when the B^js are not identical. To demonstrate this, we constructed a linear autoregressive model for subcommunities of prey, specialist predator and generalist predator (Fig. 1B) by randomly selecting elements of B^j for different subcommunities. The results of the simulation are predicted by the analysis of the case of identical subcommunities. With increasing n, the variance in combined specialist predator densities, V_{com}, decreases when $\rho = 0$ (Fig. 5A). The absence of an effect of linkage between subcommunities, α, is demonstrated by the similar values of V_{com} obtained with linkage ($\alpha = 0.5$, solid line) and without linkage ($\alpha = 0$, dashed line). The reduction in V_{com}, however, does not occur if species in different subcommunities respond to environmental fluctuations in a highly correlated way, since V_{com} changes little with increasing n when $\rho = 0.9$ (Fig. 5D). Finally, the species-level variability of the specialist predator, V_{sp}, is greater when there are interactions between subcommunities (Fig. 5B, E, solid lines) than when there is no linkage, with positive environmental correlations ($\rho = 0.9$) reducing this effect. All of these patterns were also found for the nonlinear predator–prey model (Fig. 3). Furthermore, although we have formulated the model such that the mean combined densities of all species sharing the same ecological role are independent of n and α, similar results can be obtained without this restriction provided coefficients of variation, CV_{com}, are used rather than variances, V_{com}, to measure community variability.

DISCUSSION

The conclusions from both numerical simulations and analytical models are that (i) species number increases community-level stability by adding species that respond differently to environmental fluctuations, thereby introducing new species–environment interactions, and (ii) linkage between subcommunities through species–species interactions has no effect on community-level stability. This supports the "insurance hypothesis" that increased numbers of species leads to greater diversity in species tolerances to different types of environmental fluctuations (McNaughton 1977, 1985; Walker 1992; Sankaran & McNaughton 1999; Yachi & Loreau 1999).

The generality of our results depend on the generality of the assumptions under which they were derived. By constraining communities to be composed of subcommunities with the same structure, we have intentionally excluded the question of how community structure affects stability. The complexity of community structure likely increases with species richness, with the introduction of species with new trophic roles. Although we do not
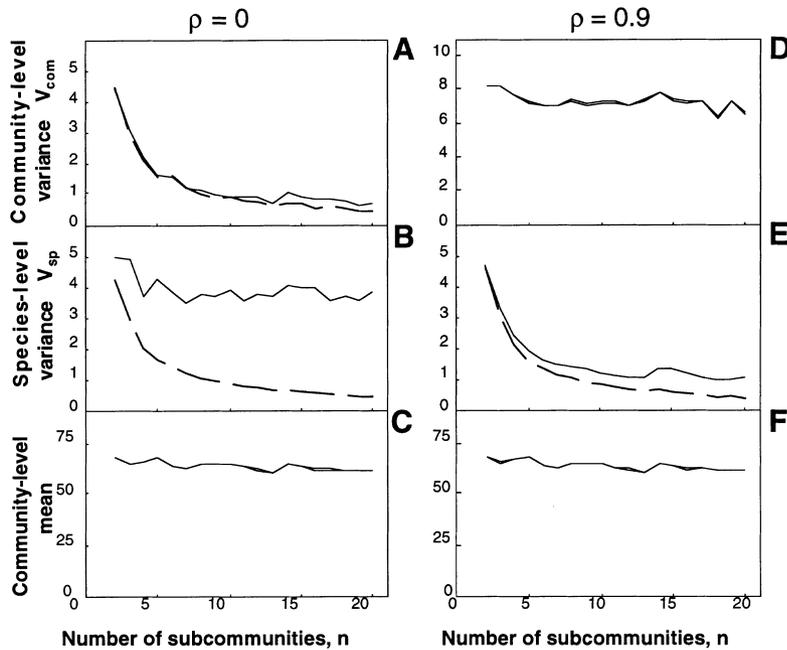
Figure 5 The effects of subcommunity number n on community-level variance, V_{com}, species-level variance, V_{sp}, and mean density for the specialist predator in a community consisting of prey, specialist predators and generalist predators (Fig. 1B). In each panel, communities without linkage among subcommunities ($\alpha = 0$) are shown with dashed lines, and solid lines correspond to the case of $\alpha = 0.5$. Means and variances were calculated from data sets generated by iterating equation (5) 2000 times. Species interactions within subcommunities were given by matrices $\boldsymbol{B}^j$ of the form

$$\boldsymbol{B}_j = \begin{bmatrix} -b_{11} & -b_{12} & -b_{12} \\ b_{21} & 0 & -b_{23} \\ b_{31} & b_{32} & b_{33} \end{bmatrix}$$

where values of the elements were assigned by selecting b_{ik} from normal distributions with standard deviation 0.2 such that the mean values of b_{11}, b_{12}, b_{13}, b_{21}, b_{23}, b_{31}, b_{32} and b_{33} were 0.8, 0.6, 0.3, 0.4, 0.7, 0.2, 0.4, and 0.7, respectively. Matrix $\boldsymbol{A}$ was constructed from subcommunity matrices $\boldsymbol{A}^j = [100, 10, 1]^t$. This manner of parameterizing the model produced subcommunities that varied roughly 2-fold in the mean density of specialist predators when $\alpha = 0.5$. Environmental variance was added by letting $e_i^j(t)$ be normal random variables with mean zero and standard deviation $0.02(x_i^*)^2$, where x_i^* is the mean density of species with role i in a single subcommunity. The correlations between $e_i^j(t)$ for different species within the same subcommunity were zero, and the correlations between $e_i^j(t)$ ($j = 1$, ..., n) among subcommunities for species sharing the same ecological roles were $\rho = 0$ (A–C) and $\rho = 0.9$ (D–F).

consider how community structure affects community stability, we none the less make addressing this problem easier. Once the stability properties of any subcommunity module (Holt 1996) are known, we have shown how the stability properties of a community constructed from these subcommunities can be derived.

Investigating the role of species–species interactions on community stability using α as the linkage strength between subcommunities is abstract; real communities do not compartmentalize into identical subcommunities.

None the less, many communities contain only a few strong interactions, with the majority of interactions between species being weak (Paine 1992; Polis & Strong 1996; Power *et al*. 1996). We found that α has little effect on community-level variability for the entire range of α from 0 to 1, and this summarizes a range of scenarios from complete compartmentalization to complete integration. Superficially, this result contrasts with that of McCann *et al*. (1998) that ''weak'' interactions can stabilize population dynamics. However, an important difference between our

studies is that McCann *et al.* investigate the dynamics of small communities that differ in structure, while we have built up large communities by linking subcommunities with the same structure. The communities of McCann *et al.* most appropriately correspond to our subcommunities.

When increasing species number by adding subcommunities, our models have the property that the combined effect of species sharing the same ecological role on any given species in the community remains the same. This property is difficult to test in real communities. Intuitively, one might expect that changes in the total density of species sharing the same ecological role should give information to either support or refute this property. There has been considerable interest in how total biomass of plant communities changes with increasing species number; typically, total plant biomass increases with species number but at a decelerating rate, such that above 10 species little biomass is added with increasing species number (Tilman *et al.* 1996; Hector *et al.* 1999; Tilman 1999). However, this need not reveal anything about the strength of species interactions. For example, in the simple Lotka–Volterra competition equations, the combined strength of competition on a species is independent of the carrying capacity K (see Appendix). Since K governs mean population densities, information about mean densities cannot be used to infer interaction strengths between species.

By confining attention to communities with the same structure, we have investigated only two components of the relationship between species diversity and community stability: species number and the interactions among many species. Increasing species diversity is likely associated with more complex community structure, as species with unique ecological roles are added. The introduction of new ecological roles may be stabilizing or destabilizing, depending on how species function within the community. For example, the addition of a third trophic level to an otherwise stable community with only prey and predators could potentially destabilize the system (Pimm & Lawton 1977; Hastings & Powell 1991; Ives & Jansen 1998). Unfortunately, we are only beginning to develop a synthetic understanding of how diverse community structures influence stability (Abrams 1987; Hastings *et al.* 1993; Holt & Lawton 1994; McCann *et al.* 1998). None the less, we hope to have simplified the investigation of the relationship between species diversity and community stability by showing that once the stability properties of a modular unit within a community (i.e. a subcommunity) are worked out, these properties can be extended easily to communities built up from these modules.

APPENDIX

Here we demonstrate for the deterministic Lotka–Volterra multispecies competition equations that at equilibrium the sum of per capita effects of competition on each species is independent of the number of species. This is true for both the continuous and the discrete-time versions of the equations; here we analyse the continuous-time equations given by

$$\frac{\partial x^i}{\partial t} = x^j(t)r^j\left(1 - \frac{x^j(t) + \alpha \sum_{h=1,h\neq j}^{n} x^h(t)}{K}\right) \quad \text{(A1)}$$

where $x^j(t)$ is the density of species j at time t, r^j is the intrinsic rate of increase of species j, α and K are the competition coefficient and carrying capacity assumed to be the same for all species. This model describes a community made up of n subcommunities, each containing a single species.

At equilibrium, the densities of all species satisfy the set of n equations

$$K = x^{i*} + \alpha \sum_{h=1,h\neq j}^{n} x^{b*} \quad \text{(A2)}$$

$$= \{1 + (n-1)\alpha\}x^*$$

where x^{j*} denotes the equilibrium density of species j and $x^{j*} = x^*$ for all j. The per capita effect of competition from species h on species j, b_{jh}, is given by the derivative of $\frac{\partial x^j}{\partial t}$ with respect to x^h evaluated at equilibrium. Thus,

$$b_{jh} = \frac{\partial(\partial x^j/\partial t)}{\partial x^h}\bigg|_{h\neq j,x*} = -\frac{\alpha r^j}{K}x^{j*} \quad \text{(A3)}$$

and

$$b_{ij} = r^j\left(1 - \frac{x^{j*} + \alpha \sum_{h=1,h\neq j}^{n} x^h}{K}\right) - \frac{r^j}{K}x^{j*} \quad \text{(A4)}$$

$$= -\frac{r^j}{K}x^{j*}$$

The sum of per capita effects of competition is

$$\sum_{h=1}^{n} b_{jh} = -\frac{r^j}{K} x^{j*} - \alpha \sum_{h=1, h\neq j}^{n} \frac{r^j}{K} x^{h*}$$

$$= -r^j$$

Thus, the combined per capita effects of all competitors on the population growth rate of any given species is independent of the number of species n and the strength of interspecific competition α, and the carrying capacity K.

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BIOSKETCH

Anthony R. Ives is a theoretical ecologist who studies multispecies population dynamics. He also conducts experimental research on the biological control of pea aphids.