

Structural instability of food webs and food-web models and their implications for management

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Introduction

By *structural instability* we mean a sensitivity of the structure of ecological communities to changes in biological or ecological parameters—including external pressures—that is so high that small pressures or changes in the environment can have such large effects on the community that they lead to species extinctions (Rossberg, 2013; Rohr *et al.*, 2014). Since sensitivity increases with species richness in complex communities (Novak *et al.*, 2011), structural instability imposes, at least in principle, a limit to local species richness. There is good evidence, discussed below, that structural instability does indeed determine local species richness: the number of species in a community increases through invasions to the point where it becomes structurally unstable, and then cannot increase much more because the invasion of any further species leads to the extinction of another species on average. Structural instability unifies, among others, observations of high sensitivity of complex food-web models, made prominent by Yodzis (1988), with observations of difficulties in getting species to co-exist with reasonable abundances in empirically parameterized food webs, perhaps first reported by Andersen and Ursin (1977). We shall briefly review these lines of thought below.

The ecological concept of structural instability describes a phenomenon that is, in principle, just an

instance of particularly high sensitivity. Indeed, Flora et al. (2011) coined the term structural sensitivity for a closely related but different concept (small changes in the functional representation of processes in a model lead to large changes in attractors). Ecological structural instability is closely related to but different from the mathematical concept known as “structural instability” in dynamical systems theory (infinitesimal changes in flow fields lead to large changes in flow trajectories). Indeed, this mathematical concept (Pugh and Peixoto, 2008), which is narrower than the ecological understanding, has also been employed in the context of community ecology (Meszéna et al., 2006; Vandermeer and Goldberg, 2013)

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Despite this ambiguity, the established laxer understanding of “structural instability” in ecology (Rossberg, 2013; Rohr *et al.*, 2014) is adequate, because it captures the important role the phenomenon plays among many other forms of instability in the diversity-stability debate (Ives and Carpenter, 2007). While a good mathematical understanding of structural instability and of the reasons why it is common in Ecology is now emerging (Rossberg, 2013; Rohr *et al.*, 2014), we consider it too early to decide which specific, rigorous mathematical definition is the most useful for ecology.

This chapter will first discuss two simple models that illustrate the concept of structural stability in ecology and its implications, especially for management. Next, the relationship of structural stability to other notions of stability commonly used in Ecology is discussed. It is argued that some of the other kinds of “instability” considered in community ecology (Ives and Carpenter, 2007) naturally co-occur with structural instability, that some tend to be stronger when structural instability is weak, and that some others are causally unrelated to structural instability. On this basis, evidence from the empirical and modeling literature is then presented which suggests that structural instability is ubiquitous in ecology, especially in food webs.

Structural instability in two-species competition

A minimal model for structural instability, useful for building intuition, is a community consisting of exactly two species that are ecologically nearly identical and compete, but co-exist in a stable equilibrium. If one modifies the system by relatively small changes in population-dynamical parameters or by applying a weak pressure on one of the species, this is likely to tip the delicate balance between the two, leading to competitive exclusion of one species by the other. While the two species could originally co-exist over indefinite time, the modification leads to the inevitable extinction of one of the species. One also says that the two-species community, which was feasible before, has become unfeasible.

In this transition, gradual changes in pressures or parameters lead to a gradual decline of the equilibrium abundance of one of the species to zero, hence to its extinction. Once the abundance has reached zero, further-going changes in pressures or parameters do not change its abundance further (as ecologically obvious, the abundance cannot become negative). In dynamical systems theory, this kind of transition is called a transcritical bifurcation. Occurrence of such transcritical bifurcations differentiates structural instability from other kinds of instability of ecological communities. Among the few alternative types of bifurcations common in Ecology are the saddle-node (or fold) bifurcation, where an equilibrium disappears as parameters are changed, resulting in sudden, discontinuous transitions (and often bistability) as parameters or pressures change, and Hopf-bifurcations, where the system state begins to oscillate around a then unstable equilibrium configuration (as typical for predator-prey oscillations), either gradually as parameters or pressures change, or abruptly. The classification of bifurcations is a useful tool for discussing ecological stability, because each bifurcation type is associated with its own characteristic ecological phenomenology (Rossberg, 2013, sec.14.3) and dynamic systems theory reveals that the number of generic types of bifurcations is very limited (Guckenheimer, 2007).

A toy community model exhibiting structural instability

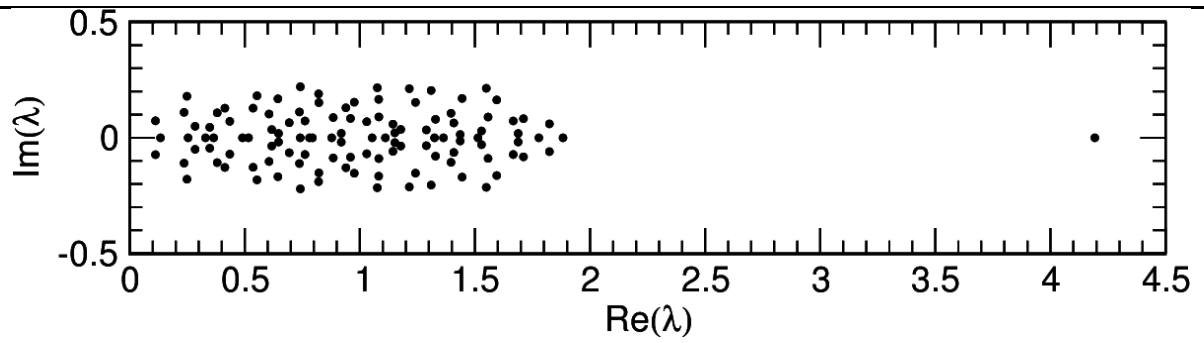


Figure 1: Locations in the complex plane of the eigenvalues of the competition matrix G for a community sampled from the satiated steady state of the toy community model described here.

We shall now discuss another structurally unstable community model, which is slightly more complex than the two-species model, to illustrate how structural instability can naturally arise in ecological communities and what its implications are for management.

The model discussed here is a member of a family of community assembly models with varying degrees of competition symmetry introduced by Rossberg (2013). Population dynamics in the model are given by a simple Lotka-Volterra competition model with S species. Starting with an empty community ($S = 0$), model communities are constructed through gradual assembly with only one species invading at a time. Species with biomasses decaying to zero as a result of another species' invasion are removed as extinct.

The model makes the simplifying assumption that in isolation all species would have identical, positive population growth rates at low abundance and reach identical population biomass at their carrying capacity. Population biomasses are measured as proportions of this carrying capacity, and time in units of the inverse population growth rate. Denoting the biomass of species i by B_i and the elements of the competition matrix by G_{ij} , this leads to the Lotka-Volterra system

$$\frac{dB_i}{dt} = \left(1 - \sum_{j=1}^S G_{ij}B_j\right)B_i.$$

For each newly invading species j , the entries of the j th row and column of the competition matrix are chosen at random by the following rule: when there are $S - 1$ species in the community before

the invasion, sample independently two S -component vectors $\boldsymbol{\psi}$ and $\boldsymbol{\psi}'$, such that each entry of the vectors is set to 0.2 with probability 0.2 and to zero otherwise. Then set $G_{jj} = 1$ and, for all $i \neq j$, $G_{ij} = 0.75 \psi_i + 0.25 \psi'_i$ and $G_{ji} = 0.75 \psi'_i + 0.25 \psi_i$. This leads to competition matrices with a moderate degree of symmetry.

After about 1000 successful invasions of species so sampled, the model community satiates.

Species richness S begins to fluctuate around a value of about 119 (S.D. 5.6) as species turnover continues. As illustrated in Fig. 1, the eigenvalues λ_i of the competition matrix \mathbf{G} in these satiated communities cover an ellipsis in the complex plane (Sommers *et al.*, 1988), centered near $\lambda = 1$ and extending such that it closely approaches or, in rare cases, slightly straddles the complex plane's origin, corresponding to $\lambda = 0$ (Rossberg, 2013, sec.18.3). In addition, the competition matrix has a single, real eigenvalue of around 4, corresponding to the average row sum of off-diagonal entries of \mathbf{G} .

Because the matrix \mathbf{G} has both eigenvalues that are close to zero and eigenvalues further away, it is, by definition, *ill conditioned* (Golub and Van Loan, 1996). The matrix inverse of ill-conditioned matrices is known to be dominated by large contributions corresponding to the eigenvalues near zero and to depend sensitively on the precise values of the matrix entries (Golub and Van Loan, 1996). Since in our model population biomasses are given through the inverse \mathbf{G}^{-1} of \mathbf{G} as $B_i = \sum_{j=1}^S G_{ij}^{-1}$ (recall that the linear growth rate is one for all species), population biomasses depend sensitively on the entries of \mathbf{G} .

Responses of the model community to pressures are also given by \mathbf{G}^{-1} . Specifically, if \mathbf{F} denotes a vector of the exploitation rates (dimension 1/Time) by which the biomasses of the S species in the model are hypothetically removed, then the corresponding changes in the equilibrium abundances of species are given as $-\mathbf{G}^{-1}\mathbf{F}$ (assuming pressures are small enough not to lead to extinctions).

When \mathbf{G} has eigenvalues near zero, the community's response to pressures is therefore sensitive in two ways: it depends sensitively on the entries of \mathbf{G} because the matrix is ill-conditioned, and the

large contributions to \mathbf{G}^{-1} related to small eigenvalues make $-\mathbf{G}^{-1}\mathbf{F}$ sensitive to small changes in \mathbf{F} . Because each invasion leads to new pressures on the residents, the invasion of one species into such a community often leads to the extinction of other species (Rossberg, 2013, Chapter 17). That is, the model community has self-organized to be structurally unstable.

How has this self-organized state been reached? The theory of Sommers *et al.* (1988) allows us to approximately compute the area covered by the distribution of the eigenvalues of \mathbf{G} in the complex plane. Fundamentally, it depends on mean size of the off-diagonal entries of \mathbf{G} , their variance, entry-wise correlations between \mathbf{G} and its transpose \mathbf{G}^T , and species richness. Independent of how off-diagonal elements are sampled, the area always increases with increasing species richness S in such a way that it reaches and then covers the origin of the complex plane for values of S that exceed some threshold (Rossberg, 2013, sec.18.3). For smaller S , all eigenvalues remain separated from zero, implying the community is less sensitive to perturbation. When simulating the process of gradual assembly in this model, S gradually increases until structural instability sets in (i.e. some eigenvalues get close to zero) at which point extinctions resulting from structural instability prevents further increases in species richness S . Community satiation therefore always coincides with the onset of structural instability.

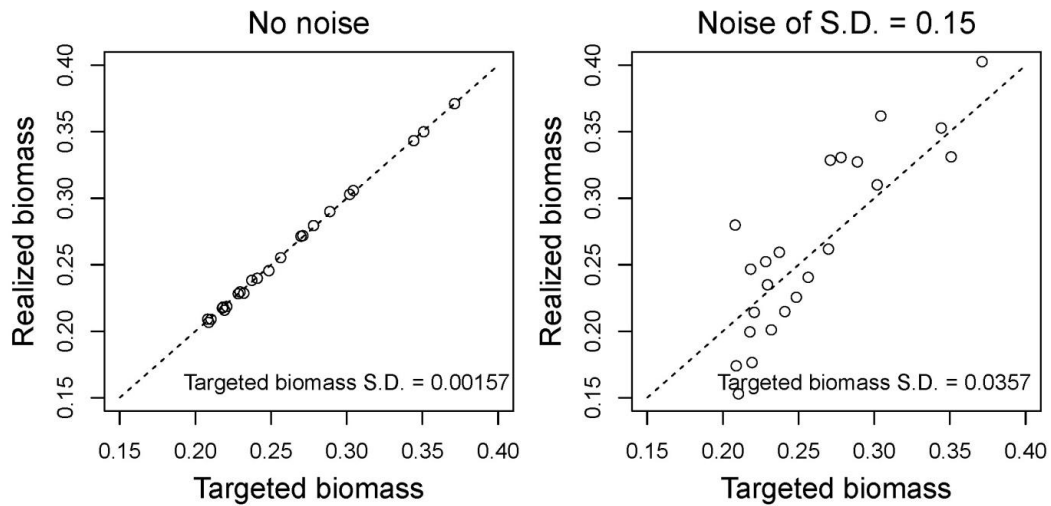


Figure 2: Simple illustration of the effect of parameter uncertainty on controllability in a structurally unstable model community. The management problem studied is that of exploiting the subset of most abundant species in the community at such rates that the biomasses of these species decline to 50% of their unexploited equilibrium biomass. For each abundant species, we represent the realized biomass as a function of the targeted biomass. In the left panel we assumed perfect knowledge of the competition matrix (i.e., no noise). In that case, the targets are met to high accuracy. In the right panel, we assumed that the competition matrix is known up to an observation error given by a log-normally distributed factor with median one and spread (S.D. of natural logarithm) equal to 0.15. As a result, the accuracy of meeting the targets is reduced. The absolute S.D. between targeted and realized biomasses is quoted in the insets.

In the absence of an effective mechanism to control abundances, the abundance distribution of resident species spreads out widely as structural instability sets in (Rossberg, 2013, Chapter 16). As a result, there will always be some species with abundances much lower than the average, and these are the ones most likely to go extinct when the next species invades (Rossberg, 2013, Section 14.6.3).

To illustrate the model's sensitivity to pressures, we shall now use this toy model to play fisheries managers. The studied fish communities are sampled from the steady state of the satiated toy model as species composition turns over. To avoid complications related to the extinction of rare species, we assume that fisheries target the most abundant species only, here taken to be all species with $B_i > 0.4$ in the unfished equilibrium. In the case illustrated in Fig. 2, these are 23 out of a total of 107 species. Management attempts to control the abundances of the targeted species by managing fishing effort, which is here expressed in terms of the corresponding exploitation rates F_i of the targeted species. The management objective is to fish such that all targeted species reach exactly half of their natural abundances. The correct choice of the exploitation rates F_i depends on the entire interaction matrix. In Fig. 2 we illustrate how miss-specifications of the off-diagonal entries of \mathbf{G} (while keeping ones on the diagonal) lead to deviations of the targeted species' abundances from the management goal. Absolute deviations are of similar magnitude for all species, so that relative deviations are larger for the less abundant species. As we demonstrate in Fig. 3, these errors are a consequence of structural instability. The ability of management to achieve its goal despite inaccurate knowledge of interactions changes dramatically depending on whether, for the particular model community sampled from the steady state, the community is more or less structurally unstable, i.e. the eigenvalue with the smallest real part is closer or further away from zero.

In Lotka-Volterra competition models, such as the one studied here, feasible equilibria are always linearly stable. However, the dynamical relaxation to these equilibria can be very slow, as we demonstrate in Fig. 4. Even though the linear growth rate of each species in isolation equals one, it lasts over 100 time units for the system to reach its new equilibrium state after fishing pressure has been applied to the targeted species. In principle, there are two reasons for this. The first is that eigenvalues of the competition matrix near zero always imply that, similar to the case of the two-species model, there are certain mixtures of one group of species that can gradually replaced an adequate mixture of another group of species without bringing the community much out of

equilibrium. Recovery from states where such a replacement has taken place to some degree therefore tends to be slow. The second reason is that in satiated, structurally unstable communities some species—those likely to go extinct soon—have population biomasses much smaller than the average. Because of these species, the community as a whole is always close to a transcritical bifurcation. Critical slowing down in the vicinity of this bifurcation contributes further to delaying community relaxation to equilibrium. The relative importance of these two mechanisms and conceivable interaction between them, however, do not appear to be fully understood, yet.

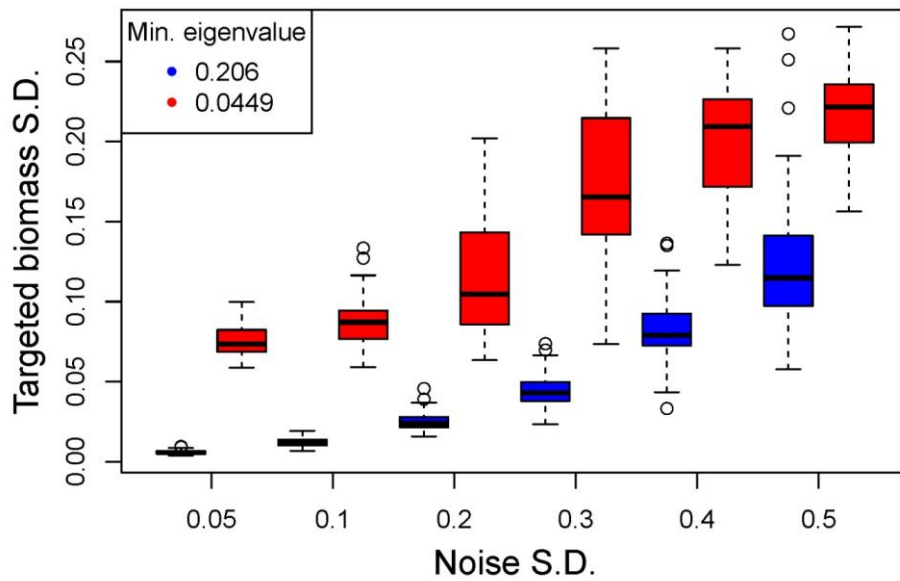


Figure 3: The effect of structural instability on community controllability. For two communities sampled from the steady state of the toy model (represented by blue boxes to the left and red boxes to the right, respectively), the accuracy of meeting the management goal (halving the populations of the most abundant species) was evaluated for varying degrees of imperfection of knowledge of the competition matrix. Imperfect knowledge was simulated by computing the exploitation rates meant to achieve the management target after multiplying the off-diagonal elements of the competition matrix with log-normally distributed random numbers with median one and a spread (S.D. of natural logarithm) given by Noise S.D (horizontal axis). Controllability was measured by the S.D. of the differences between targeted and realized biomasses, after simulating the relaxation of the community to its equilibrium under the calculated exploitation pressures. For each community and each level of Noise S.D., 50 independent replicates were evaluated. The competition matrices of the sample communities differ in the magnitude of the eigenvalue with the smallest real part. When this eigenvalue is close to zero, controllability is much worse than when it is further away. We find this to be a general pattern.

Relation of structural stability to other concepts for community stability

Ives and Carpenter (2007) discuss a useful selection of (in)stability measures for ecological communities, covering a range of different stability concepts. Here we discuss how these are related to structural (in)stability.

Going through the list of instability measures in Fig. 2 of Ives and Carpenter (2007), structural instability is only weakly related to the *number of alternative stable states* and the *rate at which intermediate, unstable equilibrium states destabilize* (assuming that, as conventional, extinctions are not counted among the “alternatives”); structural instability is also unrelated to the *probability of occurrence of periodic or chaotic oscillations* or the *amplitude of these oscillations*. The reason is

that the underlying bifurcations are different, as explained above: saddle-node bifurcations in the case of alternative stable states and Hopf bifurcations in the case of transitions to oscillations. The phenomenology of these kinds of destabilization is different, and so also the appropriate quantitative characterization.

On the other hand, structural instability tends to go along with a *slow rate of return of model communities to equilibrium* (Fig. 4) as discussed above, and so with *higher variability of population abundances* in response to environmental stochasticity (May, 1973), even though both are not the defining characteristics. Potentially indicative of structural instability is a low value of what Ives and Carpenter (2007) call Δr_{crit} , i.e. *the minimal rate of indiscriminate removal of individuals that destabilizes a community equilibrium and/or leads to an extinction*, because this represents

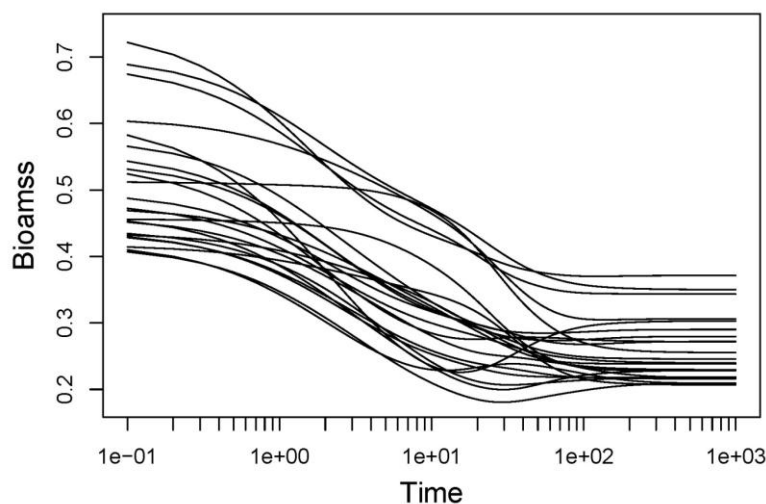


Figure 4: Typical trajectories of population biomasses in response to exploitation. Only the trajectories of the most abundant species, subject to exploitation, are shown. A logarithmic time axis is used to visualize the broad range of relevant time scales.

sensitivity to a particular kind of pressure. Note, however, that in the special case of our toy-model pressure applied evenly to all species, which Ives and Carpenter (2007) choose for their definition, is exactly the perturbation that leaves all relative abundances unchanged; sensitivity to other pressures is more relevant. In satiated communities *the average number of secondary extinctions following an invasion* will always be one, provided the community can be invaded at all.

Characteristic for structural instability is that, because each invasion acts essentially as a random perturbation and has an effect of similar magnitude as forced removal of a random species, the *number of secondary extinctions following removal of a random species* will be close to one as well. As exemplified by the minimal two-species example we gave, a high degree of *compensation after species loss* is typical for structurally unstable communities [for an example with larger communities, see Fig. 14.5 of Rossberg (2013)]. Along with structural instability comes also enhanced *invasion resistance*. Typically, only around 50% of randomly sampled species will succeed at invading a community that is satiated *via* structural instability (Rossberg, 2013, Section 14.6.2).

Summarizing, structural instability naturally goes along with a range of other phenomena, some of which can be interpreted as declines in stability (e.g. fluctuating population sizes), others as manifestations of increased stability (e.g. resistance to invasion).

Evidence for structural instability from models

Yodzis (1988) was probably the first to systematically describe the high sensitivity to misspecifications of food-web models constructed from detailed observation data:

When the sizes of direct interactions [in an ecosystem] are determined to within an order of magnitude, the long-term outcomes of press perturbations are highly indeterminate, in terms both of whether species density increases or decreases, and of which interactions have the largest effects.

This line of thinking was later followed up, among others, again by Yodzis (1998), who highlighted

the consequences of this indeterminacy for ecosystem management, and Novak *et al.* (2011), who noted that this indeterminacy increases with increasing species richness and connectance (proportion of species pairs that directly interact). We reproduced a similar phenomenon above using our toy model.

Constraints imposed to the feasibility of model communities, implied by this high sensitivity, have been noted since the early days of fish-community modeling (Andersen and Ursin, 1977, Section 2.4). A common response by modelers to this problem is to increase the strength of intraspecific competition in some form (Andersen and Pedersen, 2010; Andersen and Ursin, 1977; Speirs *et al.*, 2010), e.g. through built-in limits to the number of recruits to a stock per year (Blanchard *et al.*, 2014). In the picture of the toy model discussed above, this corresponds to increasing the values of the entries on the diagonal of the competition matrix \mathbf{G} , thus shifting its eigenvalues to the right in the complex plane (Fig. 1), away from zero, and so reducing structural instability. This operation can be justified in some cases (Farcas and Rossberg, 2015), but generally carries a risk of systematic model misspecification.

Coexistence of species in model communities can often be enforced by appropriate choices of free model parameters. Structural instability then manifests itself through tight limits to the region in parameters space where communities are feasible (Meszéna *et al.*, 2006; Rohr *et al.*, 2014). Rohr *et al.* (2014) analyzed this phenomenon in detail for empirical mutualistic systems, and could show that these were structured so as to mitigate structural instability.

Evidence for structural instability from natural food webs

In the empirical literature, evidence for emergent high sensitivity of natural communities to perturbations is frequently found under the keyword “indirect effects”, as reviewed by Wootton (1994). A prominent example is the study of manipulations of rocky shore communities by Menge (1995), which revealed that indirect effects consistently accounted for about 40% of change in community structure after perturbations, independent of species richness. Analytic theory is

consistent with this observation, provided that the interactions among species in these communities are largely asymmetric (Rossberg, 2013, Section 17.2.6). Strong indirect effects manifest themselves, for example, through the idiosyncratic forms in which populations respond to climate change (Cahill *et al.*, 2013).

Consistent with structural instability are observations that large changes in communities of competing species can result from introduction or exclusion of a single predator species (Paine, 1980). Supportive of structural instability, in view of the associated long relaxation times exemplified in Fig. 4, is also the often strongly felt empirical intuition that natural ecological communities generally respond too slowly to ever reach the population-dynamical equilibria so central to ecological theory (Sousa, 1984). Further indirect support for structural instability comes from the observation that the establishment probability for species that invaded Europe from North America or vice versa, averaged over a wide range of species, is close to 50% (Jeschke and Strayer, 2005), in agreement with theoretical expectations mentioned above.

Less obvious but probably even stronger evidence comes from observations of approximately constant ratios between the species richness at one trophic level in a food web and the richness at the next higher level. For community food webs with several trophic levels, independent studies report that species richness at a given trophic level tends to be about three times as high as richness at the next higher level (Jeffries and Lawton, 1985; Jennings *et al.*, 2002), or, correspondingly¹, twice as high as the combined species richness at all higher trophic levels (Warren and Gaston, 1992). To relate these observations to structural instability, we recall first that, according to classical theory, the richness of a community of consumers competing for resources cannot be larger than the number of kinds of resources they compete for (MacArthur and Levins, 1964; Rescigno and Richardson, 1965). If the richness of consumers was larger than this limit, their (appropriately defined) competition matrix would have eigenvalues equal to zero, so rendering the consumer

¹ Recall that

$$\frac{1}{3} + \frac{1}{3^2} + \frac{1}{3^3} + \dots = \frac{1}{2}.$$

community structurally unstable (Meszéna *et al.*, 2006). In food webs, this limit is modified because for most conceivable consumer-resource pairings trophic interaction strength is so weak that it is effectively zero. The small number of relevant trophic interaction pairs leads to a competition matrix (precisely, a competitive overlap matrix, Rossberg, 2013) in which just a few off-diagonal entries have a magnitude comparable to that of the entries on the diagonal. Most off-diagonal entries are effectively zero. Such so-called “sparse” competition matrices can have eigenvalues very close to zero even when the number of resources clearly exceeds the number of competing consumers. For multi-level food webs, where complications due to competition among resources need to be taken into account, one finds numerically that accumulation of eigenvalues near zero and the resulting transition to structural instability set in when species richness declines by a factor three with each higher trophic level (Rossberg, 2013, Section 18.5). This is the empirically observed value.

This explanation of the observed fixed richness ratios as representing a limit to species richness due to structural instability is consistent with their interpretation by Arnold (1972) as manifestations of competitive exclusion among consumers sharing common resources. The consistent observations of richness ratios close to the numerical values where structural instability is predicted to set in (Warren and Gaston, 1992; Jennings *et al.*, 2002; Wright and Samways, 1998; Santos de Araújo, 2011; Rossberg, 2013) leaves little room for other explanations than the one that the observed communities are indeed structurally unstable.

Conclusions, especially for management

We have demonstrated convergence of a number of lines of reasoning leading to the conclusion that structural instability is a ubiquitous phenomenon in natural ecological communities. There is good evidence that structural instability is the mechanism limiting and controlling species richness in community food webs, at least for non-basal species, which implies that most natural communities are self-organized to be structurally unstable.

Modelers and managers of ecological communities should be conscious of structural instability in their work, as it imposes constraints on what can and what can not be achieved. Strategies to work around structural instability in management have recently been proposed (Rossberg, 2013, Sec. 24.3) and successfully tested (Farcas and Rossberg, 2015).

Acknowledgements

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