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Simplification of structured population dynamics in complex ecological communities

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Abstract Goldstone's idea of slow dynamics resulting from spontaneously broken symmetries is applied to Hubbell's neutral hypothesis of community dynamics, to efficiently simplify stage-structured multi-species models—introducing the quasi-neutral approximation (QNA). Rather than assuming population-dynamical neutrality in the QNA, deviations from ideal neutrality, thought to be small, drive dynamics. The QNA is systematically derived to first and second order in a two-scale singular perturbation expansion. The total reproductive value of species, as computed from the effective life-history parameters resulting from the non-linear interactions with the surrounding community, emerges as the new dynamic variables in this aggregated description. Using a simple stage-structured community-assembly model, the QNA is demonstrated to accurately reproduce population dynamics in large, complex communities. Further, the utility of the QNA in building intuition for management problems is illustrated by estimating the responses of a fish stock to harvesting and variations in fecundity.

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Introduction

Describing the dynamics of communities of interacting structured populations poses high demands on parametrisation and computation, especially when modelling realistic levels of species richness. Simpler, more intuitive and computationally less expensive are unstructured community models characterizing each population by a single variable only, or models distinguishing only a few life-history stages. Recently, corresponding aggregation methods that seek to minimise the loss of functional information have therefore been developed (De Roos et al. 2008b) and demonstrated in several applications (De Roos et al. 2008a, b; Van Leeuwen et al. 2008).

De Roos et al. (2008b) base their approach on ideas by Auger (1983) and Auger and Poggiale (1998), who stressed the practical importance of a separation of time scales for a successful aggregation: fast dynamics within aggregates and slow dynamics of the aggregated variables. Such separations of time scales naturally arise in the presence of conserved or nearly conserved quantities. For example, in spatially resolved (patch) models, individuals may rapidly migrate amongst patches, whilst populations summed over all patches (the aggregated variables) change relatively slowly. Several application of this principle are reviewed by Auger et al. (2008).

Here, we make use of a different mechanism generating slow dynamics, the slow *Goldstone modes* (Goldstone 1961) emerging in systems with broken symmetries, commonly studied in physics (see, e.g. Sethna 2006). The symmetry we invoke is related to the population-dynamic neutrality postulated by Hubbell (2001), in which populations can attain equilibria at

arbitrary population sizes (constrained is only population summed over all species). However, our proposed aggregation method does not require population-dynamical neutrality. Rather, it takes neutrality as a first approximation to study the effects and implications of deviations from it in a community of multi-stage populations. For this reason, we name the approach *quasi-neutral approximation* (QNA).

Specifically, we assume that the parameters determining transition rates between life stages of a species (e.g. growth rates, maturation rates etc.) are, to a first approximation, independent of the species' abundance and also independent of the specific state of the surrounding community. The resulting symmetry is invariance of dynamics under scaling of abundances at all life stages by a constant factor. This amounts to an assumption of density independence, which is often made in ecology (Caswell 2000) and proved to be useful in many practical applications.

The new aggregated variable can be interpreted as the sum of reproductive values over all individuals of this population. Reproductive value was first defined by Fisher (1930) as the expected contribution of an individual "to the ancestry of future generations". Intuitively, the central role of reproductive value in this context is not unexpected. Only those components of a structured population are of interest in a simplified description that determine the long-term abundance after several reproductive cycles; other components can, to a first approximation, be ignored. Whilst it is conventional to consider reproductive values for the Malthusian growth of small populations, we calculate them here for those environmental conditions that give rise to (approximate) neutrality, including non-linear feedbacks through community interaction. Whilst this broadened view of reproductive value has found applications in evolution (Metz et al. 1992; Metz 2008) and competition theory (Szilágyi and Meszéna 2009), its usefulness for the simplification of non-linear population-dynamical models appears largely unexploited. The special role of total reproductive value as a robust state variable recommends its use as a replacement for numerical abundance or biomass when characterizing or managing ecosystems.

In the following, we first introduce our formalism and motivate the QNA. It is then applied to a simple community model representing, as a coarse caricature, over 100 stage-structured populations of fish. The accuracy of the QNA in reproducing community dynamics for this model is compared to that of other conceivable approximations. Having verified the numerical viability of QNA, we then demonstrate applications investigat-ing analytically the sensitivity of dynamics to parametrisation and external perturbations.

Developing the QNA

Reproductive value in structured populations with linear dynamics

We develop the QNA by first considering Malthusian population growth of a structured population, thereby drawing attention to the fundamental relation between the concept of reproductive value and the left eigenvector of the population matrix (Goodman 1968). For an in-depth introduction to the theory, see, e.g. the excellent textbook by Caswell (2000) and Grafen (2006) for broader generalizations of the concepts.

Consider the population of a single, focal species and resolve it into P different stages that individuals of that species can potentially attain. These stages may be characterized, e.g. by the individuals' age, size, ontogenetic stage, location or genotype. Denote the number of individuals in stage i ($i = 1, \ldots, P$) by n_i and define the population vector $\mathbf{n} = (n_1, \ldots, n_P)^{\mathrm{T}}$. We assume that females direct population dynamics, so only females are counted, and further assume populations at all stages large enough to ignore demographic stochasticity and to described all populations n_i by real numbers.

The linear formulation of population dynamics implies the additional assumption that populations are sufficiently small that their effect on the environment (including other populations) can be ignored. Finally, we restrict analyses here to the case of a constant physical environment.[1] The linear problem can then be described by an equation of the form

$$\frac{d\mathbf{n}(t)}{dt} = \mathbf{A}\,\mathbf{n}(t), \tag{1}$$

where the population matrix $\mathbf{A}$ is a constant $P \times P$ matrix with entries given by the transition rates between stages and the rates for the generation of offspring. As for any linear dynamical system, the long-term dynamics is dominated by its fastest-growing linear mode (which is here an eigenvector of $\mathbf{A}$). Whilst the aggregate dynamics of the total population $N = \sum_{i=1}^{P} n_i$

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[1] Periodic environmental variations, e.g. daily or yearly cycles, can be incorporated into the formalism through a Floquet analysis, by which the population at each stage is formally split into a series of 'stages' corresponding to its Fourier modes (see, e.g. Bodenschatz et al. 1988).

initially depends on the details of the population structure, after a transient it will follow (see, e.g. Caswell 2000)

$$\frac{dN}{dt} \approx \lambda_{\max} N, \tag{2}$$

where $\lambda_{\max}$ is the eigenvalue of $\mathbf{A}$ with the largest real part. For ecologically meaningful problems, the imaginary part of $\lambda_{\max}$ is zero.[2] The population vector in this phase of exponential growth is $\mathbf{n} \approx \mathbf{w}N$, where $\mathbf{w}$ is the (familiar) right eigenvector of $\mathbf{A}$ corresponding to $\lambda_{\max}$, i.e.

$$\mathbf{A}\mathbf{w} = \lambda_{\max}\mathbf{w}, \tag{3}$$

normalized such that

$$\sum_{i=1}^{P} w_i = 1. \tag{4}$$

Another way of aggregating the structured population allows an even stronger prediction. Let $\mathbf{v}$ be the left eigenvector of $\mathbf{A}$ corresponding to $\lambda_{\max}$, i.e.

$$\mathbf{v}^{\mathrm{T}}\mathbf{A} = \lambda_{\max}\mathbf{v}. \tag{5}$$

Rather than looking for a prediction for N, we now seek to predict the dynamics of the aggregated variable

$$V = \mathbf{v}^{\mathrm{T}}\mathbf{n}. \tag{6}$$

In fact, this quantity satisfies an equation similar to Eq. 2, but now exactly and at all times:

$$\frac{dV}{dt} = \lambda_{\max}V. \tag{7}$$

This result follows from

$$\frac{dV}{dt} = \frac{d(\mathbf{v}^{\mathrm{T}}\mathbf{n})}{dt} = \mathbf{v}^{\mathrm{T}}\frac{d\mathbf{n}}{dt} = \mathbf{v}^{\mathrm{T}}\mathbf{A}\mathbf{n} = \lambda_{\max}\mathbf{v}^{\mathrm{T}}\mathbf{n} = \lambda_{\max}V, \tag{8}$$

which is verified by applying, in this order, Eqs. 6, 1 and 5 and then again Eq. 6. When normalizing $\mathbf{v}$ according to the convention

$$\mathbf{v}^{\mathrm{T}}\mathbf{w} = 1, \tag{9}$$

the structured population can be recovered from $V(t)$ as $\mathbf{n}(t) \approx \mathbf{w}V(t)$ after a transient. Furthermore, Eq. 7

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[2]This is the case, for example, when the off-diagonal elements of $\mathbf{A}$ are non-negative and $\mathbf{A}$ is irreducible, since then $\exp(\mathbf{A})$ is positive (Berman and Plemmons 1994) and the Perron–Frobenius theorem applies. General aspects of community dynamics for structured populations satisfying these conditions were recently studied by Hofbauer and Schreiber (2010).

implies immediately that $V(t) = V(0)\exp(\lambda_{\max}t)$. The value $V(0)$ of V at time $t = 0$ therefore determines the population structure and size in the future. Since

$$V = \mathbf{v}^{\mathrm{T}}\mathbf{n} = v_1 n_1 + v_2 n_2 + ... + v_k n_k, \tag{10}$$

the contribution to V from the n_1 individuals at stage 1 is $v_1 n_1$, and the contribution from a single individual at stage 1 is v_1. Therefore, v_1 is called the *reproductive value* of individuals at stage 1. Correspondingly, $\mathbf{v}$ assigns to each stage a reproductive value, and V is the sum of the reproductive values of all individuals in a population, that is, the *total reproductive value* (Fisher 1930; Goodman 1968, note: historically, other normalizations of $\mathbf{v}$ than Eq. 9 are preferred).

Similar arguments can be made when stage-structured population dynamics are expressed for discrete time steps $\mathbf{n}(t+1) = \mathbf{L}\mathbf{n}(t)$ with an appropriate transition matrix $\mathbf{L}$ (Leslie 1945; Lefkovitch 1965). When $\mathbf{L}$ has the form of a Leslie matrix, definition Eq. 5 for the reproductive value is equivalent to the well-known formula for reproductive value in terms of fecundities and survivorships (Fisher 1930; Goodman 1968).

The quasi-neutral approximation

It was already clear to Fisher (1930) that linear models of structured population growth such as Eq. 1 break down when the focal population is large enough to change its biotic or abiotic environment, thereby altering the conditions of its own growth, especially as the focal population approaches its carrying capacity. But exactly this is the situation of general interest in ecology. Interactions with the environment are often accounted for by introducing density dependencies into the population matrix $\mathbf{A}$. For example, in a system of S interacting species, the dynamics of species i ($1 \leq i \leq S$) can be described by an equation analogous to Eq. 1:

$$\frac{d\mathbf{n}_i}{dt} = \mathbf{A}_i(\{\mathbf{n}_k\})\,\mathbf{n}_i, \tag{11}$$

where $\{\mathbf{n}_k\}$ denotes the population vectors of all S species, all of which potentially affect the population matrix $\mathbf{A}_i$ of species i. Samuelson (1978) suggested several generalizations of the notion of reproductive value that extend, to the non-linear case, its property of characterizing the initial contributions of different stages to the population size as $t \to \infty$. The generalization of reproductive value used here extends its use as a robust aggregate characterization of structured populations to the non-linear setting.

This generalization depends on the assumption, discussed in the introduction, of largely density-independent life-history parameters for structured populations embedded in a community. Formally, this becomes the assumption that the population matrix of the focal population i can be split into two parts:

$$\mathbf{A}_i(\{\mathbf{n}_k\}) = \mathbf{A}_i^{(0)} + \mathbf{A}_i^{(1)}(\{\mathbf{n}_k\}), \qquad (12)$$

where $\mathbf{A}_i^{(0)}$ is a constant matrix and $\mathbf{A}_i^{(1)}(\{\mathbf{n}_k\})$ is, in a sense explained below, small compared to $\mathbf{A}_i^{(0)}$. Furthermore, we require that $\mathbf{A}_i^{(0)}$ has an eigenvalue $\lambda_{\max} = 0$ and that all other eigenvalues of $\mathbf{A}_i^{(0)}$ have negative real parts. This is justified since, in the long term, a population is sustainable only if its life-history parameters are such that it neither rapidly grows nor decays. Conceivable small deviations of $\lambda_{\max}$ from zero can be absorbed into the second term in Eq. 12 by a redefinition of the split.

As we explain now, these assumptions imply approximate neutrality for population i. If $\mathbf{A}_i^{(0)}$ is large compared to $\mathbf{A}_i^{(1)}(\{\mathbf{n}_k\})$ in Eq. 12, we can, to a first approximation, set $\mathbf{A}_i(\{\mathbf{n}_k\}) = \mathbf{A}_i^{(0)}$, which leads to the linear problem $d\mathbf{n}_i/dt = \mathbf{A}_i^{(0)}\mathbf{n}_i$. Defining the long-term population structure $\mathbf{w}_i$, reproductive value $\mathbf{v}_i$ and total reproductive value V_i by analogy to $\mathbf{w}$, $\mathbf{v}$ and V from the previous section, the population vector, after a transient, is given by $\mathbf{n}_i(t) \approx \mathbf{w}_i V_i(t)$, with a neutrally stable equilibrium in reproductive value: $dV_i/dt = \lambda_{\max} V_i = 0$. Thus, species i has neutral population dynamics in this approximation: It remains constant, independent of population size.

The remaining small density-dependent contribution $\mathbf{A}_i^{(1)}(\{\mathbf{n}_k\})$ accounts for deviations from neutrality and leads to slow changes in V_i. To evaluate these slow dynamics, we approximate $\mathbf{n}_i \approx \mathbf{w}_i V_i$. Estimates for the other $S-1$ populations $\mathbf{n}_k$ can be obtained either by other means (such as explicit simulations or empirical observations) or one proceeds as for species i, resulting in a set of approximations $\mathbf{n}_k(t) \approx \mathbf{w}_k V_k(t)$. To avoid formal clutter, we assume that the QNA is used for all S species in a community. The time dependencies of the total reproductive values V_i are then obtained by a calculation similar to Eq. 8:

$$\frac{dV_i}{dt} = \mathbf{v}_i^{\mathrm{T}}\frac{d\mathbf{n}_i}{dt} = \mathbf{v}_i^{\mathrm{T}}\mathbf{A}_i(\{\mathbf{n}_k\})\mathbf{n}_i \approx \mathbf{v}_i^{\mathrm{T}}\mathbf{A}_i(\{\mathbf{w}_k V_k\})\mathbf{w}_i V_i$$
$$= f_i(\{V_k\})V_i, \qquad (13)$$

with

$$f_i(\{V_k\}) = \mathbf{v}_i^{\mathrm{T}}\mathbf{A}_i(\{\mathbf{w}_k V_k\})\mathbf{w}_i = \mathbf{v}_i^{\mathrm{T}}\mathbf{A}_i^{(1)}(\{\mathbf{w}_k V_k\})\mathbf{w}_i \qquad (14)$$

for $i = 1, \ldots, S$.

Equation 13 we call the QNA of the stage-structured density-dependent population dynamics of a community of S species. It is based on the assumption that dynamics deviate only little from neutral dynamics and approximates community dynamics by aggregating each population $\mathbf{n}_i$ into a single variable V_i, interpreted as the populations' total reproductive value. The QNA reduces a problem with $P \times S$ dynamic variables to a problem with only S variables. The functions $f_i(\{V_k\})$ entering Eq. 13 can be understood as effective population growth rates (Greiner et al. 1994). According to Eq. 14, they are obtained as weighted sums of nonlinear forcings over all life stages of a species, with the weights given by the reproductive values of the stages, $\mathbf{v}_i$. A short recipe, summarizing the computation of the QNA, is given in Box 1.

A rigorous proof of Eq. 13 as an approximation of Eq. 11 for important model classes describing continua of stages has been given by Greiner et al. (1994). As they explain, the case of discrete stages is implied by the general perturbation theory of Hoppensteadt (1969). The approximation scheme, going back to J. A. J. Metz (van den Bosch et al. 1990), was so far understood without the assumption of approximate neutrality. It is

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Box 1 Steps required to compute the QNA

1. For each species $i = 1, \ldots, S$

   (a) Split the density-dependent population matrix $\mathbf{A}_i(\{\mathbf{n}_k\})$ into a large, constant part $\mathbf{A}_i^{(0)}$ with dominating eigenvalue 0 and a small, density-dependent part $\mathbf{A}_i^{(1)}(\{\mathbf{n}_k\})$ (this decomposition is not unique, see "Choices in setting up the QNA").

   (b) Calculate the left and right eigenvectors $\mathbf{v}_i$ and $\mathbf{w}_i$ of $\mathbf{A}_i^{(0)}$ that correspond to the eigenvalue zero, normalizing them such that the components of $\mathbf{w}_i$ add up to one[a] and that $\mathbf{v}_i^{\mathrm{T}}\mathbf{w}_i = 1$.

   (c) Compute the initial total reproductive values $V_i(0) = \mathbf{v}_i^{\mathrm{T}}\mathbf{n}_i(0)$ from the initial population vectors $\mathbf{n}_i$.

2. Integrate the system of S ordinary differential equations $dV_i/dt = f_i(\{V_k\})V_i$, with $f_i(\{V_k\}) = \mathbf{v}_i^{\mathrm{T}}\mathbf{A}_i(\{\mathbf{w}_k V_k\})\mathbf{w}_i$, over the time interval of interest.

3. Reconstruct the approximate stage-structured population dynamics as $\mathbf{n}_i(t) \approx \mathbf{w}_i V_i(t)$.

[a] Alternatively, one could, e.g. normalize such that $\mathbf{w}_i$ corresponds to 1 kg biomass. Then the components of $\mathbf{w}_i$ have dimensions 1/Mass, those of $\mathbf{v}_i$ dimensions of Mass, and V_i will measure reproductive value in units of kg biomass.

then valid only over time intervals short enough that changes in the population matrix $\mathbf{A}_i(\{\mathbf{n}_k\})$ remain small. Over longer times, it requires asymptotic matching of subsequent approximations. In computational practice, this would amount to calculating, at each times step, for all species i population structures $\mathbf{n}_i$, normalized to the given abundances $||\mathbf{n}_i||_1 = N_i$, such that they self-consistently become the respective fastest-growing eigenvectors of the population matrices $\mathbf{A}_i(\{\mathbf{n}_k\})$ (Metz et al. 2000, p. 506). Then, the corresponding left eigenvectors $\mathbf{v}_i$ of $\mathbf{A}_i(\{\mathbf{n}_k\})$ are computed (normalized to $|\mathbf{v}_i^{\mathrm{T}}\mathbf{n}_i| = ||\mathbf{n}_i||_1$) and the population changes are obtain as $dN_i/dt = \mathbf{v}_i^{\mathrm{T}}\mathbf{A}_i(\{\mathbf{n}_k\})\mathbf{n}_k$. By assuming near neutrality, the QNA avoids this re-computation of eigenvectors, thus dramatically improving computational efficiency and analytical tractability.

Approximation error and higher-order approximations

"Appendix 1" describes a systematic formal derivation of the QNA. The technique employed there is a two-scale singular perturbation expansion (Kevorkian and Cole 1996) in a small parameter ϵ that represents the order of magnitude of the factor by which $\mathbf{A}_i^{(1)}(\{\mathbf{n}_k\})$ in Eq. 12 is smaller than $\mathbf{A}_i^{(0)}$. It is shown that the approximation error of the QNA is of the order of ϵ^2. That is, in the hypothetical limit that ϵ approaches zero from above, the error of the QNA's prediction of future system states will asymptotically decline as ϵ^2. With other approximation schemes, the approximation error will generally be of order ϵ at least. In this sense, the QNA is an optimal solution of the aggregation problem for structured populations.

Further, a variant of the QNA is derived in "Appendix 1" for which the approximation error is of the order of ϵ^3. This *second-order QNA* is given by formulae similar to the lowest-order result

$$\mathbf{n}_i = \tilde{\mathbf{w}}_i V_i, \quad \frac{dV_i}{dt} = \tilde{f}_i(\{V_k\})V_i,$$

$$\tilde{f}_i(\{V_k\}) = \mathbf{v}_i^{\mathrm{T}}\mathbf{A}_i^{(1)}(\{\tilde{\mathbf{w}}_k V_k\})\tilde{\mathbf{w}}_i = \mathbf{v}_i^{\mathrm{T}}\mathbf{A}_i(\{\tilde{\mathbf{w}}_k V_k\})\tilde{\mathbf{w}}_i, \quad (15)$$

(the last identity follows from Eq. 5, where $\lambda_{\max} = 0$), however, now making use of more accurate population structures

$$\tilde{\mathbf{w}}_i = \tilde{\mathbf{w}}_i(\{V_k\}) = \mathbf{w}_i - \mathbf{A}_i^{\mathrm{D}}\mathbf{A}_i^{(1)}(\{\mathbf{w}_k V_k\})\mathbf{w}_i$$

$$= \mathbf{w}_i - \mathbf{A}_i^{\mathrm{D}}\mathbf{A}_i(\{\mathbf{w}_k V_k\})\mathbf{w}_i \quad (16)$$

(the last identity in Eq. 16 follows from Eq. 3). Equation 16 makes use of the Drazin inverse $\mathbf{A}_i^{(0)\mathrm{D}}$ of $\mathbf{A}_i^{(0)}$, which combines a projection onto the space orthogonal to the null space of $\mathbf{A}_i^{(0)}$ with an inversion of $\mathbf{A}_i^{(0)}$ restricted to this space. In most cases, it can be computed

as the matrix having the same eigenvectors as $\mathbf{A}_i^{(0)}$ but all non-zero eigenvalues replaced by their inverses. It appears that the formula of the time derivative for the second-order QNA is computationally more demanding than the solution of the original stage-structured model, yet the approximation may offer a computational advantage because it implicitly handles (just as the normal or *first-order* QNA) fast intra-specific population dynamics, thus admitting larger numerical integration time steps. The second-order QNA might also be of use for obtaining absolute estimates of the error in the time derivatives computed from the first-order QNA, by assuming that the exact error of the first-order QNA is similar to the difference between second-order QNA and first-order QNA.

Choices in setting up the QNA

Based on these perturbative results, we can now also discuss two questions related to freedom of choice in computing the QNA. The first choice to be made is, at least on the formal level, the way of splitting in Eq. 11 the non-linear functional dependence of the time derivative $d\mathbf{n}_i/dt$ for each species i into a density-dependent population matrix $\mathbf{A}_i(\{\mathbf{n}_k\})$ and the linear factor $\mathbf{n}_i$. The second choice is the way of splitting $\mathbf{A}_i(\{\mathbf{n}_k\})$ into a large constant and a small density-dependent part. In both cases, the approximate prediction of dynamics by the QNA depends on the way these splits are done, and different methods may be appropriate under different conditions (see discussion in "Two QNA variants" below). The approximation error is always of the order of ϵ^2, but the value of ϵ, given by the relative magnitudes of $\mathbf{A}_i^{(1)}(\{\mathbf{n}_k\})$ and $\mathbf{A}_i^{(0)}$, depends on the method used. All else equal, the method that yields the smallest value for ϵ will be preferred.

QNA for a multi-species two-stage-structured community model

Model

As a demonstration of the QNA, we apply it to a stage-structured community model. In order to keep calculations transparent, the model design favors simplicity over realism. In the model, the population (n_{Ji}, n_{Ai}) of each species i is represented by two life-history stages, which we interpret as juveniles (index J) and adults (index A). With the case of fish in mind, we assume inter- and intra-species competition amongst juveniles in the nursing grounds, described by competition coefficients G_{Jij}, and inter- and intra-species competition

amongst adults in the feeding grounds, described by G_{Aij}, but—for simplicity—no direct competition between the two stages. Competition leads to additional mortality at both stages. Species differ in their sets of competitors and the strengths of competition but are otherwise characterized by identical life-history parameters quantifying the rates of birth b, maturation m and death of juveniles d_J and adults d_A. The dynamics of a system composed of S species is given by

$$\frac{dn_{Ji}}{dt} = b\,n_{Ai} - d_J n_{Ji} - m\,n_{Ji} - \sum_{j=1}^{S} G_{Jij} n_{Jj} n_{Ji},$$

$$\frac{dn_{Ai}}{dt} = m\,n_{Ji} - d_A n_{Ai} - \sum_{j=1}^{S} G_{Aij} n_{Aj} n_{Ai} \qquad (17)$$

for $i = 1, ..., S$.

Intra-species competition strengths amongst juveniles $G_{Jii} = G_J$ and adults $G_{Aii} = G_A$ are identical for all species. The inter-specific competition coefficients are obtained by the algorithm below.

Starting with $S = 1$, communities are build up by stepwise assembly (Post and Pimm 1983; Drake 1990; Law and Morton 1996) from an infinite species pool (Post and Pimm 1983; Caldarelli et al. 1998). Each step starts with a community at a stable population-dynamical equilibrium. New species j are drawn at random as follows until one is found that can invade the community: For each extant species $i \neq j$, the two juvenile inter-specific competition coefficients G_{Jij}, G_{Jji} are set to zero with probability $1 - C_J$ and otherwise to random values between 0 and $2 I_J G_J$, drawn independently for both coefficients from an even distribution. Here, the competition probability C_J and the competition strength I_J are system parameters. Next, a corresponding rule is applied to determine adult interactions, using competition probability C_A and competition strength I_A. We set $C_A = C_J = C$ and $I_A = I_J = I$ for simplicity in what follows.

If the newly drawn species has a positive linear growth rate at low abundance, its invasion into the community is simulated until a new community equilibrium is reached, at the same time removing those species from the community that go extinct—as determined by their populations exponentially approaching zero. Thus, in each step, one species is added to the community and a dynamically determined number is lost. We measure the advance towards community buildup in terms of T, the number of species added (s.a.)—i.e. invasions.

Note that the asymmetric choice of competition strengths avoids dynamics that minimise a Lyapunov function, as would be the case if $G_{Jij} = G_{Jji}$, $G_{Aij} = G_{Aji}$

(MacArthur 1970). In this case, the community assembly process would never reach a stochastic steady state but would unceasingly seek lower values of the Lyapunov function. Our choice of competition coefficients nevertheless retains sufficient similarity to potential dynamics that, numerically, we find the system always to relax to a population-dynamical equilibrium, as was assumed above.

The parameter set used for simulations is listed in Table 1. Life-history parameters were defaulted to unity, but the fecundity b was set such as to obtain a positive linear growth rate in the case of an isolated species (i.e. $S = 1$).

Figure 1 documents an example time series of S in the course of community buildup. Species richness S saturated around 170. For comparison, the number of fish species in the North Sea is estimated to be somewhere between 100 (Kaschner et al. 2008) and 190 (Froese and Pauly 2009). During simulations, we regularly saved 'snapshots' of communities at their population-dynamical fixed points (i.e. equilibria) for analyses and tests of the QNA. The timing of snapshots was chosen to be approximately even on the log T scale.

Introducing QNA and other approximations of the model

Two QNA variants

We considered two variants of the QNA for the model defined above. The first requires knowledge of the competition matrices G_{Jik}, G_{Aik} and of the fixed point $\mathbf{n}_i^*$ ($i = 1, ..., S$) of community dynamics. It is defined by choosing $\mathbf{A}_i^{(0)} = \mathbf{A}_i(\{\mathbf{n}_k^*\})$. Since this variant is related to a particular point in state space, we call it the *local QNA*. It corresponds to situations where a specific ecosystem in a known state is to be modelled and the population matrices of all species can be estimated from field data.

Table 1 Model parameters

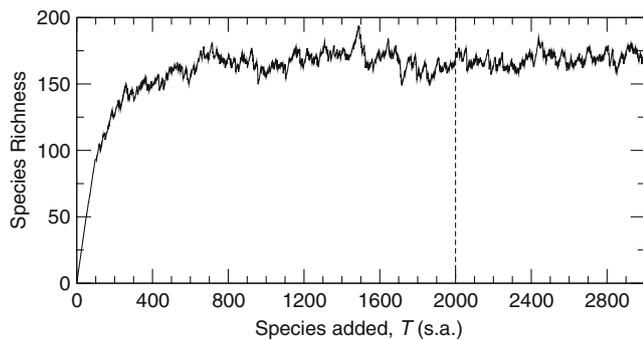| Model parameter	Interpretation	Default value
b	Fecundity	6
d_J	Juvenile mortality	1
d_A	Adult mortality	1
m	Maturation rate	1
G_J	Juvenile competition strength	1
G_A	Adult competition strength	1
C	Probability of competing	0.5
I	Ratio of inter- to intra-specific competition	0.1

Fig. 1 Saturation of species richness in our model community as more and more random species are added (invade). *Dashed line* marks the state used for Figs. 3, 4, 5 and 6

The second variant of the QNA corresponds to situations where it is to be derived prior to determining the specific interaction matrices. It can be used to study generic properties of structured communities from ab initio considerations. The magnitude of the interaction terms in Eq. 17 therefore must be estimated independently of the specific community structure. We do this by approximating the interaction coefficients G_{Jij} and G_{Aij} by their expectation values, assuming all population structures $\mathbf{w}_i$ at the fixed point to be equal. The problem can then be solved analytically, yielding $\mathbf{A}_i^{(0)}$ identical for all i and, consequently, identical $\mathbf{v}_i$ for all species. We call this the *mean-field QNA*, referring to a term often used for similar approximation techniques. In "Appendix 2", the mean-field QNA is derived step by step, thus providing a worked example for analytically computing the QNA for a given model.

In both variants, the QNA reduces model 17 to a Lotka–Volterra competition system

$$\frac{dV_i}{dt} = \left(r_i - \sum_{j=1}^{S} G_{ij} V_j \right) V_i. \qquad (18)$$

In the mean-field QNA (see "Appendix 2"), all linear growth rates r_i are identical as a consequence of $\mathbf{w}_i$ and $\mathbf{v}_i$ being identical for all i. Competition coefficients G_{ij} ($i \neq j$) are of the form $c_J G_{Jij} + c_A G_{Aij}$ with constants $c_J, c_A > 0$ (independent of i), where the values of G_{Jij} and G_{Aij} are obtained from the snapshots of the stage-structured assembly model whose community dynamics is to be approximated. Specifically, the intra-specific competition coefficients are $G_{MF} = c_J G_J + c_A G_A$. In the local QNA, coefficients differ slightly form the mean-field values and vary between species because left and right null eigenvectors of the population matrices differ.

Two population-balance approximations

For comparison, two further approximations of the stage-structured model were evaluated. In both approximations, the aggregated description refers to the total populations $N_i = n_{Ji} + n_{Ai}$ rather than to total reproductive values. We therefore denote them as *population balance approximations* (PBA). Formally similar to the QNA, dynamics are approximated as:

$$\frac{dN_i}{dt} = g_i(\{N_k\}) N_i, \quad g_i(\{N_k\}) = \hat{\mathbf{v}}^T \mathbf{A}(\{\hat{\mathbf{w}}_k N_k\}) \hat{\mathbf{w}}_i N_i, \qquad (19)$$

but now with $\hat{\mathbf{v}}^T = (1, 1)$ to sum changes in populations over stages. The first variant (*local PBA*) again requires knowledge of the fixed point of the full model. It approximates the population structures $\hat{\mathbf{w}}_i$ by the population structures at the fixed point $\mathbf{n}_i^*/N_i^*$, just as the local QNA. The second variant approximates the population structures $\hat{\mathbf{w}}_i$ by those attained at linear population growth in the absence of competitors. For some parameter values, this can be quite different from the population structures actually realized. We therefore call this approximation the *naive PBA*.

Comparing accuracy amongst the four approximations

To test the accuracy of the four aggregation methods described above, the following numerical experiment was conducted for different combinations of community structure and approximation method: A model community at its population-dynamical fixed point, as saved during the simulated community buildup, was perturbed by reducing abundances at both stages to 1/3 of their equilibrium values for 1/3 of all species. The relaxation of the aggregated variables to the fixed point, as computed using each of the four approximation schemes, was then compared with the relaxation of the corresponding aggregated variables when these were directly computed from the numerical solution of the stage-structured model as $V_i(t) = \mathbf{v}_i^T \mathbf{n}_i(t)$ (QNA) or $N_i(t) = \hat{\mathbf{v}}^T \mathbf{n}_i(t)$ (PBA).

In Fig. 2, the trajectories of the abundances $N_i = n_{Ji} + n_{Ai}$ of ten randomly selected species are shown for a community snapshot of the size-structured model taken after 2,000 s.a. (marked in Fig. 1). The community contains a total of 170 species. The trajectories exhibit a characteristic combination of fast dynamics on the order of a few unit times and slow dynamics continuing over 200 unit times and more. We therefore go over to a logarithmic time scale in the following comparisons of the approximate solutions with the original.
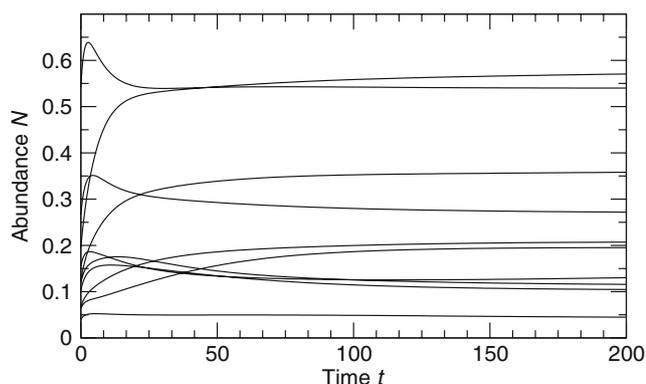
Fig. 2 Sample population dynamical trajectories of ten species out of 170 present after 2,000 s.a. (dashed line in Fig. 1). After reducing the abundance of 1/3 of species by 2/3, the populations relax back to the community fixed point. Characteristic is the combination of slow and fast dynamics

In a comparison of the ten trajectories obtained from the local QNA (solid lines) of the relaxation process with the trajectories obtained from the full, structured model (dashed lines) in Fig. 3, barely any difference is visible. The local PBA, by comparison, follows the original trajectories only over the first tens of time units (Fig. 4). Then deviations become large, in some cases leading to extinctions of species. As time proceeds, cascading extinctions of further species follow (for most of which trajectories are not shown). The system takes a long time to settle in at a new fixed point, which is reached after about 7,500 unit times and a total of 23 extinctions, and deviates considerably from the fixed point of the original system.

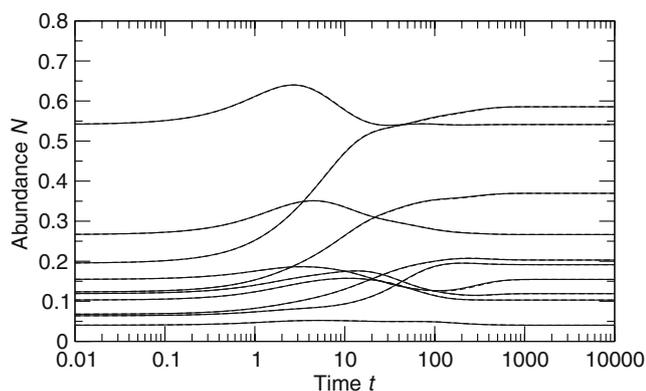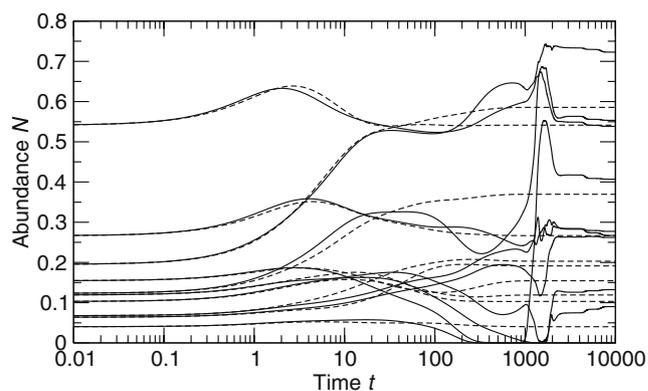For the two approximations that do not relate to a particular community state, the discrepancy between

Fig. 4 Same as Fig. 3, now comparing the original model with the local PBA

QNA and PBA is similar. The mean-field QNA closely follows the trajectories of the structured model (Fig. 5). In contrast to the local QNA and PBA, where the fixed points of original and approximation coincide by construction, the fixed point is slightly shifted in the mean-field QNA. Yet, it is stable: None of the 170 species in the community goes extinct. In the naive PBA (Fig. 6), some trajectories differ qualitatively already from the very beginning (e.g. the one starting at $N \approx 0.54$). Whilst of the local PBA, the original fixed point was preserved by construction but became unstable, a fixed point with positive abundance for all 170 species may not even exist for the naive PBA. Without the saddle point characteristic of the local PBA, dynamics here is less complex. Yet, it differs again drastically from the original system. When the naive PBA finally settles in, 43 species have gone extinct.

Next, we report quantitative comparisons of the quality of the four approximation methods across different stages of community buildup, using a suitable
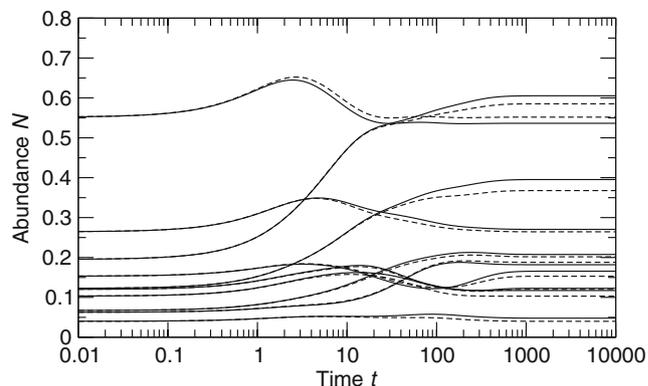

Fig. 3 Comparison of population dynamics in the original model 17 (*dashed lines*) and it the aggregated approximation using the local QNA (*solid lines*) for ten sample species of our 170 present in the simulation after 2,000 s.a.. Since the *lines* nearly perfectly overlap, the *dashed lines* are barely visible

Fig. 5 Same as Fig. 3, now comparing the original model with the mean-field QNA
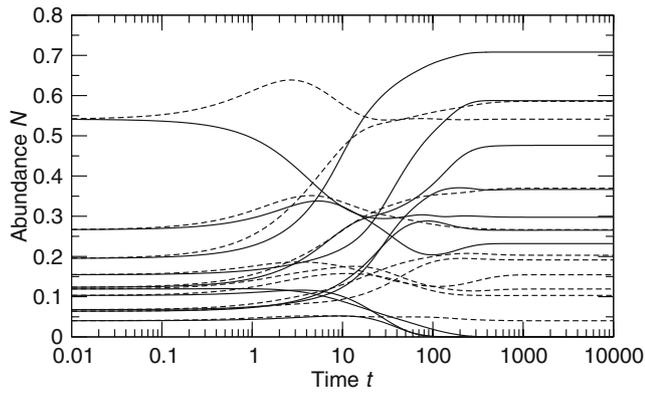
Fig. 6 Same as Fig. 3, now comparing the original model with the naive PBA

measure of accuracy. As discussed above, the QNA can be derived from a singular perturbation expansion of the original models for small deviation from neutrality. Characteristic for these techniques is that the convergence of the approximation to the exact solution, as the perturbation (ϵ) becomes smaller, is uniform over all times (up to unavoidable deviations due to non-negative Lyapunov exponents in the cases of periodic or chaotic attractors). An appropriate measure for the accuracy of the method is therefore the maximum error over all times in approximating the trajectories. Here, we compute the root mean square of this deviation over all species. We normalize this value to the mean reproductive value or abundance of species at the fixed point because this value decreases with increasing species richness. That is, as a quantitative measure, we characterize accuracy in terms of

$$\alpha = S^{1/2} \frac{\sqrt{\sum_{i=1}^{S} \max_t \left[V_i^{\text{approx}}(t) - V_i(t) \right]^2}}{\sum_{i=1}^{S} \lim_{t \to \infty} V_i(t)}, \tag{20}$$

where $V_i(t)$ denotes the actual total reproductive value of species i computed as $V_i(t) = \mathbf{v}_i^{\text{T}} \mathbf{n}(t)$ from the original system (with $\mathbf{v}_i$ depending on the approximation used) and $V_i^{\text{approx}}(t)$ is the prediction of $V(t)$ from the aggregated approximation. For the two PBA, all V in Eq. 20 need to be replaced by N. Species that went extinct are naturally included in this index by setting $V_i(t)^{\text{approx}} = 0$ or $N_i(t)^{\text{approx}} = 0$.

Computing α for different stages of community buildup, we found both variants of the QNA consistently about 30 times more accurate than the corresponding PBAs (Fig. 7). When the community fixed point lost stability in the local PBA, a process illustrated in Fig. 4 and indicated in Fig. 7 by pronounced spikes

towards larger α, the predictions of this approximation became much worse. Interestingly, such loss of stability is found only after about 500 s.a.. The effect therefore appears to be related to community saturation (or 'packing'): Saturated communities are more easily destabilized and therefore community dynamics more difficult to approximate by simplified models.

For the local QNA, on the other hand, such a destabilization was never observed. The deeper mathematical reasons of this surprising robustness are currently unclear. Overall, the local QNA is remarkably accurate in all phases of community buildup; only rarely do we get values of α larger than 0.004. For the mean-field QNA, we occasionally found that rare species go extinct, with little effect on the remaining community (in other words: by the small displacement of the community fixed point due to the mean-field approximation, it crosses the phase-space boundary). Again, genuine loss of community stability was never found. Similar results were obtained when parameter values in the stage-structured model were varied (not shown).

The naive PBA always gives the worst approximations. Yet, for communities much less diverse than the saturated state, its approximation error is less than 20%. For some applications, it could still be useful in such cases.

Reduced accuracy for hard competition

Since the QNA builds on a separation of the time scales of intra-specific and inter-specific population dynamics, one must expect the accuracy of the QNA to decline as these time scales become more similar. Whilst the intra-specific time scale follows directly from the second but largest real part of the eigenvalues of $\mathbf{A}_i^{(0)}$, the
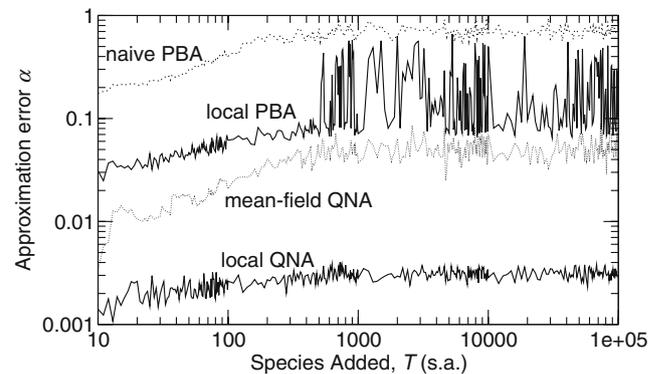

Fig. 7 Dependence of approximation error α on the degree of community packing and approximation method. Snapshots were taken and analyzed only when the number of species added was a number between 10 and 99 times a power of 10. For the definition of α, see Eq. 20

inter-specific time scale is more difficult to determine. Figures 2 and 3 illustrate that saturated communities can exhibit a broad range of characteristic times.

As long as our simple model can be approximated by a Lotka–Volterra competition model of the form Eq. 18 at all, the fact that, in both variants of the QNA, all linear population growth rates r_i have values similar or equal to the mean-field value r implies (when measuring abundances in terms of carrying capacity) that r^{-1} sets the overall time scale of inter-specific dynamics. As argued in "Appendix 3", r^{-1} is necessarily, by a factor of at least 2, larger than intra-specific relaxation time for model 17.

Inter-specific time scales can be stretched further when competition is diffuse (MacArthur 1972), that is, when a species typically competes weakly with many other species. In this case, effects from changes in the populations of other species largely average out, leading to small effective perturbations $\mathbf{A}_i^{(1)}$ (that is, small ϵ). For harder competition, that is, stronger competition between fewer species, this additional separation of time scales should be less pronounced.

We demonstrate this phenomenon by increasing the value of the parameter I which regulates the strength of competition in our model. Communities were assembled to saturation by the algorithm described above. In qualitative agreement with the prediction by May (1972), the number of co-existing species in saturated communities decreased with increasing I, and competition became harder.

Simulations were run until the number of successful invasions T reached 50 times the maximum species richness $S_{\max}$ hitherto attained in the run, and the mean steady-state approximation error α was evaluated from the steady-state samples taken between $T = 5\,S_{\max}$ and $50\,S_{\max}$ (for $I = 0.1$, this approximately corresponds to the range $T = 1{,}000$–$10{,}000$ s.a. in Fig. 7). The approximation error α with $I = 0.1, 0.2, 0.4$ and 1.0 is shown in Fig. 8 for all four approximation methods. As expected, the error increases with I for both variants of the QNA, but the increase is not dramatic (the data suggest $\alpha \sim I^{1/2}$). Apparently, diffuse competition contributes to improving the QNA. By contrast, for the PBA in both variants, the mean approximation error decreases as I increases and competition becomes harder. This result is in line with observations made above that the PBAs are limited by their ability to correctly reproduce the community fixed point and its stability. With harder competition, the balance of interactions at the community fixed point is less delicate and more easily reproduce by these coarser approximations.

Application to gauge effects of perturbations and parameter uncertainty

General theory

The QNA offers a simple and powerful means for estimating the impact of anthropogenic or natural perturbations on population dynamics: Above, we considered only the effects of perturbations $\mathbf{A}^{(1)}(\{\mathbf{n}_k\})$ of perfect neutrality that result from inter-specific interactions (throughout this section, the index i referring to the focal species is suppressed). But other kinds of perturbations can be treated by exactly the same analytic techniques. The method is easily applied once the population structure $\mathbf{w}$ and the reproductive value vector $\mathbf{v}$ are known for the focal species. Simply construct the matrix $\mathbf{B}$ describing the perturbations of the population matrix due to the effects considered (see examples below) and obtain the resulting correction to the density-depend growth rate $f(\{V_k\})$ as $\mathbf{v}^{\mathrm{T}}\mathbf{B}\mathbf{w}$. As for $\mathbf{A}^{(1)}(\{\mathbf{n}_k\})$ (cf. Eq. 14), this correction is accurate to the lowest order in the magnitude of $\mathbf{B}$.

Of course, any perturbation of the population matrix also leads to corrections $\delta\mathbf{w}$ and $\delta\mathbf{v}$ to population structures $\mathbf{w}$ and reproductive value vectors $\mathbf{v}$. But these corrections affect dynamics only at higher order in the magnitude of the perturbation and can therefore often be ignored. Analytically, this is implied by the fact that, since $\mathbf{v}^{\mathrm{T}}\mathbf{A}^{(0)} = 0$ and $\mathbf{A}^{(0)}\mathbf{w} = 0$, one has $(\mathbf{v} + \delta\mathbf{v})^{\mathrm{T}}\mathbf{A}^{(0)}(\mathbf{w} + \delta\mathbf{w}) = 0$ at linear order in the perturbations.
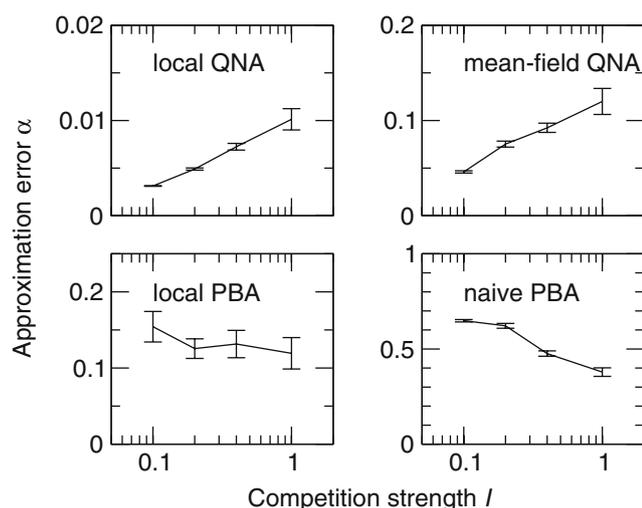

Fig. 8 Dependence of the error of the four approximation methods investigated on the relative strength I of inter-specific competition. *Error bars* indicate numerical sampling standard errors

Examples

As an example, the population-level effect of harvesting adult fish is estimated using the two-stage model Eq. 17. Let F be the fishing mortality of adults (dimension 1/Time). The corresponding perturbation of the population matrix is

$$\mathbf{B} = \begin{pmatrix} 0 & 0 \\ 0 & -F \end{pmatrix}, \tag{21}$$

where we associated the first row and column with juveniles and the second row and column with adults. The non-zero entry in $\mathbf{B}$ represents removal of adults at a rate proportional to the abundance of adults. By the rule given above, fishing leads to (negative) population growth at a rate $\mathbf{v}^{\mathrm{T}}\mathbf{B}\mathbf{w} = -Fv_A w_A$ until, potentially, a new equilibrium is reached through density-dependent effects. In this expression, the term $v_A w_A$ is the reproductive value of adults times their relative proportion in the population: It describes the relative contribution of adults to the total reproductive value of the population.

The mean-field QNA of model 17, derived in "Appendices 2 and 3", gives

$$v_A w_A = \frac{M^{-1}}{T_m + M^{-1}}, \tag{22}$$

with T_m denoting the mean age at maturation and M the effective adult mortality ("Appendix 3"). Since M^{-1} is the mean duration of adulthood, Eq. 22 equates the fraction $v_A w_A$ of reproductive value allocated with adults with the mean proportion of lifetime that those individuals that do reach maturation spend after maturation. This fraction varies between species. For cod, for example, one finds $v_A w_A \approx 0.6$ for the commonly used values $M = 0.2$ year^{-1} and $T_m = 3$ years, whilst for salmon species that die in the year they mature $v_A w_A \approx 0.2$, assuming $T_m \approx 4$–5 years (Gilbert 1912). Thus, cod populations respond faster than salmon when fished at the same mortality F. Equation 22 explains this by the fact that, for salmon, there is a larger reservoir of yet-to-mature juveniles than for cod. We caution, however, that it is currently unclear if this simple reasoning remains valid for more detailed stage-structured models.

Using the same method, we can also estimate the impact of a change (or measurement error) Δb in the fecundity b on the population growth rate. By "Appendix 3", the relevant weight here is $v_J w_A = b^{-1}/(T_m + M^{-1})$. That is, the resulting change $v_J w_A \Delta b$ in the linear population growth rate r is the inverse of the generation time $(T_m + M^{-1})$ ("Appendix 3") times the relative change $\Delta b/b$ in fecundity.

Discussion

The need for the QNA

The ecosystem approach to natural resource management (CBD 1992) specifically requires us to build models that can explain how community interactions and higher ecosystem phenomena (especially population stability, ecosystem function and biodiversity) arise from dynamic processes (Plagány 2007). The size-based community-level indicators recently developed for the North Sea (ICES 2001) for an ecosystem approach to fisheries management highlight the importance of size structure especially in marine systems, where the body masses of many species span five orders of magnitude or more over their life time. There is therefore a need for more comprehensive models capable of predicting the effects of anthropogenic influences on community structure, resolved by population and body-size or growth stage. Whilst computer simulations may offer quick illustrations of hypotheses, they cannot provide the level of understanding needed to intelligently manage human influences on these communities; deeper analytical understanding is required. Since the systems of interest are complex, highly non-linear and remain opaque to intuition, an approximation is needed that maximises explanatory power at minimum complexity. The QNA achieves this by establishing a simple, yet in the perturbation theoretical sense optimal, link between structured populations and the common sense characterization of a population by its size.

The crucial innovation of the QNA as compared to earlier recipes (Metz et al. 2000) is the hypothesis that the effective life-history parameters of a species embedded in a complex community change only little when the populations of the surrounding species vary in a natural way, so that linear single-species population dynamics of the focal species is a good lowest-order approximation even over long times. For consistency with the nomenclature of "Approximation error and higher order approximation", we call this linear approximation the *zeroth-order* approximation. Such single-species matrix models are successfully employed in many management applications. Fisheries management offers some striking illustrations of this practice. Top predators such as cod are an influential component of many marine communities, inducing population effects that cascade through the system. Adult cod spawn millions of eggs per year, with predation accounting for the death of most offspring before maturation. In principle then, their populations could grow or shrink by several orders of magnitude each year. But through non-linear interactions with other species, the annual

variation is constrained to only a few percent (ICES 2008). Models currently employed in fisheries management largely ignore this density dependence, using constant values for natural mortality, and very simple models for recruitment (classically the Ricker curve, but see Andersen et al. 2009). The mutual balancing of non-linearities enables these simple models to be useful for single species management, up to a point. The QNA improves this zeroth-order approximation by including the first-order correction due to dynamic interactions with other species.

Scope and limitations of the QNA

Conceivable applications of the QNA go far beyond the simple model system we used to illustrate it, and the full scope over which it can usefully be applied will become clear only when testing it for a broader range of models. The formalism covers, for example, models with continuous size or age structures and models distinguishing individuals by their phenotype, genotype, behaviour or location. Whilst in our simple model, Eq. 17, all interacting species had essentially the same life histories, this is not a general requirement of the QNA. As made explicit by the general derivation in "Appendix 1", population structures and dynamics can differ substantially between species. Neither is the QNA restricted to systems in the vicinity of a fixed point.[3] Our examples using the mean-field QNA demonstrate applicability of the method without any reference to a particular community fixed point. Thus, we expect that systems characterized by oscillatory or chaotic dynamics can be described, as well. Future work needs to clarify how far the QNA's numerical strengths prevail for such systems. Since one can expect many natural communities to be in a saturated state (each invasion leading to an average of one extinction), it would be particularly important to understand why the QNA consistently preserved the stability of our model communities, even when these were saturated, and to derive the general conditions for the same to be found in other systems. Important will also be the question how the method performs when trophic dynamics is explicitly described rather than just implied by the resulting competitive interactions. Specific applications we have in mind are the reduction of food-web models, with size-resolved species, to their unresolved counterparts, the collapse of the empirically known three-dimensional structure

of the habitats of interacting fish stocks to its effective zero-dimensional counterpart and an optimization of fishery management strategies for highest yields at lowest impacts on stocks.

Some effects the QNA in its current form will be unable to capture. For example, since the QNA does not explicitly describe changes in intra-specific size structure, it is unlikely to reproduce community bi-stability mediated by changes in this size structure (Claessen and de Roos 2003; Van Leeuwen et al. 2008).

For other problems, the ratio between the time scales of system-level population dynamics and of intra-specific demographics will not be sufficiently large to obtain a desired accuracy using the QNA. As illustrated in "Reduced accuracy for hard competition", this ratio can be split into two factors: The first relates the intra-specific time scale to the Malthusian growth rate that a species would experience in a sparsely packed community ("farming"). In "Appendix 3", it is shown that this factor is at least 2 in our model and generally larger. For more detailed models of structured populations, smaller values for this factor can be expected: Matrix population models often exhibit oscillatory modes, representing strong cohorts and their offspring, that take several generation to decay (Caswell 2000). The second factor relates the 'farming' growth rate to the relaxation rate of saturated community states. In the examples in "Reduced accuracy for hard competition", the first factor was kept fixed and the second factor varied by simulating cases of more or less diffuse competition. Diffuse competition appears favorable for the QNA. But there may be other, currently unknown, aspects of community structure that affect the time scales of community relaxation as well. Currently, a characterization of the QNA's accuracy for complex communities is therefore difficult without actually simulating or observing complex community dynamics. From a practical point of view, one can expect time scales to be separated well if population dynamical trends change only on time scales long compared to the mean generation time of the focal species. Whilst, as explained above, the empirical success of simple single-species models indicates that near neutrality in complex communities is a common phenomenon and similar phenomena have emerged in simulated communities as well (Doncaster 2009), more research is required to pinpoint the precise conditions leading to near neutrality in ecological communities.

Neutrality and symmetry

To localize the QNA within the broader context of macroecological theories, it is useful to understand

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[3]Formally, this can be seen from the fact that the leading order term in the perturbative expansion of $\mathbf{n}_i(t)$ (Eq. 25), which is the only one taken into account in the first-order QNA, is of the order ϵ^0.

the relationship between the approximate neutrality underlying the QNA and the concept of neutrality at the core of the neutral theory of biodiversity (Hubbell 2001). Neutrality in the QNA sense means that, at zeroth order, the population of a species that has attained its equilibrium stage structure (**w**) will neither grow nor shrink, independent of its population size as measured by total reproductive value (V). As a result, populations at any value of V are neutrally stable in the mathematical sense: Small perturbations of V do neither grow nor decay. In nature, of course, such permanent changes of population size generally go at the expense of other, competing populations. This regulation is described at the next order, the (proper) first-order QNA. Neutrality in the sense of Hubbell (2001) is the ecological equivalence of all individuals, disregarding species identity and, to some degree, life-history stage. From this neutrality hypothesis, it follows immediately that any species can replace, fully or in part, the population of any other species. Disregarding demographic stochasticity and the resulting entropic forcing (Azaele et al. 2006), as well as immigration pressure, a species in the neutral theory can therefore also attain a neutrally stable equilibrium at any population size.

Thus, a community of S species has in both cases a large family of equilibrium states, parametrised by the S or $S − 1$ population sizes, depending on whether constraints on total population apply or not. This family of equilibria can be understood as being generated by a 'symmetry' of the community under replacement of parts of the population of one species by that of other species. Now, a general rule first exploited by Goldstone (1961) (see also Goldstone et al. 1962) states that a symmetry with continuous parameters (here the population sizes) leads to slow dynamics along axes identifiable with these parameters ("Goldstone modes") when perturbed (see, e.g. Sethna 2006). Applied to our case: Perturbations of the symmetry underlying population-dynamical neutrality lead to slow population dynamics. The resulting separation of time scales between individual and population dynamics is exploited in the formal calculations of "Appendix 1".

The neutral theory of biodiversity accounts for the slow dynamics resulting from demographic stochasticity and immigration pressure (Azaele et al. 2006). The QNA accounts for the slow dynamics resulting from deviations from neutrality by the simple fact that neutrality is just an ecological idealization. Demographic (and environmental) stochasticity could be included in the QNA by incorporating the approach Engen et al. (2009) developed for stochastic linear dynamics of

structured populations. This would lead to a unification of both kinds of neutral theories.

Appendix 1: Systematic derivation of the QNA

In this appendix, which provides a systematic derivation of the QNA, we go over from matrix notation to tensor notation. Roman lowercase indices ($i, j, k, \ldots$) are used to refer to different species. Greek lowercase indices $\alpha, \beta, \gamma, \ldots$ refer to different stages individuals of such species may run through in the course of their lives. In principle, the number of stages can vary between species. However, in order not to unnecessarily inflate the formalism, this possibility is not explicitly referred to here. Instead, it can be handled implicitly by suitably adding formal 'ghost' stages to species which are unattainable from real stages, so that all species have the same formal number of stages P. Thus, in a community of S species, Roman indices always run from 1 to S and Greek indices always run from 1 to P and in the calculations below. With these conventions, the original problem 11 can be re-written as

$$0 = \frac{dn_{\alpha i}}{dt} - \sum_{\beta} A_{\alpha\beta i}(\{n_{\gamma k}\}) n_{\beta i}. \tag{23}$$

The QNA as given by Eq. 13 can be derived as the lowest-order contribution in a two-scale perturbation expansion (Kevorkian and Cole 1996; Chow 2007) of the solution of the general problem 23, under the assumption that the largest part of $A_{\alpha\beta i}$ is constant, singular and stable for all i. We introduce the small book-keeping parameter ϵ and rewrite Eq. 12 as

$$A_{\alpha\beta i}(\{n_{\gamma k}\}) = A^{(0)}_{\alpha\beta i} + \epsilon A^{(1)}_{\alpha\beta i}(\{n_{\gamma k}\}) \tag{24}$$

by rescaling $A^{(1)}_{\alpha\beta i}(\{n_{\gamma k}\})$ such that it becomes of similar size as $A^{(0)}_{\alpha\beta i}$ and choosing ϵ appropriately.

A two-scale expansion formally distinguishes the fast time scale t (corresponding to the relaxation of perturbations of the equilibrium population structures) and a second, slow time scale $\tau = \epsilon t$. The solution of Eq. 23 is then expanded in a power series in ϵ of the form

$$n_{\alpha i}(t) = n^{(0)}_{\alpha i}(t, \tau) + \epsilon n^{(1)}_{\alpha i}(t, \tau) + \epsilon^2 n^{(2)}_{\alpha i}(t, \tau) + \text{h.o.t.} \tag{25}$$

Here, h.o.t. denotes corrections due to terms of higher order in ϵ. Substituting this ansatz and Eq. 24 into Eq. 23, observing that $d/dt = \partial/\partial t + (\partial/\partial\tau)(\partial\tau/\partial t) = \partial/\partial t + \epsilon(\partial/\partial\tau)$ and sorting terms by powers of ϵ yield

$$
0 = \left[\frac{\partial n_{\alpha i}^{(0)}}{\partial t} - \sum_{\beta} A_{\alpha\beta i}^{(0)} n_{\beta i}^{(0)} \right]
$$
$$
+ \epsilon \left[\frac{\partial n_{\alpha i}^{(0)}}{\partial \tau} + \frac{\partial n_{\alpha i}^{(1)}}{\partial t} - \sum_{\beta} A_{\alpha\beta i}^{(0)} n_{\beta i}^{(1)} - \sum_{\beta} A_{\alpha\beta i}^{(1)}(\{n_{\gamma k}^{(0)}\}) n_{\beta i}^{(0)} \right]
$$
$$
+ \epsilon^2 \left[\frac{\partial n_{\alpha i}^{(1)}}{\partial \tau} + \frac{\partial n_{\alpha i}^{(2)}}{\partial t} - \sum_{\beta} A_{\alpha\beta i}^{(0)} n_{\beta i}^{(2)} \right.
$$
$$
\left. - \sum_{\beta} A_{\alpha\beta i}^{(1)}(\{n_{\gamma k}^{(0)}\}) n_{\beta i}^{(1)} - \sum_{\beta\nu l} A_{\alpha\beta i,\,\nu l}^{(1)}(\{n_{\gamma k}^{(0)}\}) n_{\nu l}^{(1)} n_{\beta i}^{(0)} \right]
$$
$$
+ \text{h.o.t.}. \tag{26}
$$

In the last bracket, $A_{\alpha\beta i,\,\nu l}^{(1)}(\cdot)$ denotes the derivative of $A_{\alpha\beta i}^{(1)}(\cdot)$ with respect to the abundance of stage ν of species l. These derivatives arise from a truncated Taylor expansion of $A_{\alpha\beta i}(\{n_{\gamma k}\})$ at the point $n_{\gamma k}(t) = n_{\gamma k}^{(0)}(t, \tau)$. If power series Eq. 26 is zero for arbitrary small ϵ, each coefficient of the expansion in ϵ must be zero.

At order ϵ^0, this requires

$$
0 = \frac{\partial n_{\alpha i}^{(0)}(t, \tau)}{\partial t} - \sum_{\beta} A_{\alpha\beta i}^{(0)} n_{\beta i}^{(0)}(t, \tau). \tag{27}
$$

This equation can be solved for each species i separately. We write the left and right eigenvectors of $\mathbf{A}_i$ defined in "The quasi-neutral approximation" as $v_{\alpha i}$ and $w_{\alpha i}$ in tensor notation. Apart from fast transients during which the population structures decay to $w_{\alpha i}$, which are here ignored for simplicity, the general solution of Eq. 27 is

$$
n_{\alpha i}^{(0)}(t, \tau) = w_{\alpha i} x_i^{(0)}(\tau). \tag{28}
$$

The functions $x_i^{(0)}(\tau)$ are determined in the following: Inserting Eq. 28 into the first-order term in expansion 26 gives

$$
0 = w_{\alpha i} \frac{\partial x_i^{(0)}}{\partial \tau} + \frac{\partial n_{\alpha i}^{(1)}}{\partial t} - \sum_{\beta} A_{\alpha\beta i}^{(0)} n_{\beta i}^{(1)}
$$
$$
- \sum_{\beta} A_{\alpha\beta i}^{(1)}(\{w_{\gamma k} x_k^{(0)}\}) w_{\beta i} x_i^{(0)}, \tag{29}
$$

an inhomogeneous system of linear differential equations for $n_{\alpha i}^{(1)}$. Since the inhomogeneity does not depend on t, we may set $\partial n_{\alpha i}^{(1)}/\partial t = 0$.

Equation 29 represents as system of $S \times P$ ordinary differential equations over τ, but contains the $S + S \times P$ undetermined τ-dependent variables $x_i^{(0)}$ and $n_{\alpha i}^{(1)}$. The system is therefore underdetermined. Yet, it admits only a single solution for the S variables $x_i^{(0)}$. This can be seen by solving Eq. 29 in two steps. First in the linear subspace spanned by the S left eigenvectors $v_{\alpha i}$ and then in its orthogonal complement. Multiplication of Eq. 29 with $v_{\alpha i}$ and summation over α yield

$$
0 = \frac{\partial x_i^{(0)}}{\partial \tau} - \sum_{\alpha\beta} v_{\alpha i} A_{\alpha\beta i}^{(1)}(\{w_{\gamma k} x_k^{(0)}\}) w_{\beta i} x_i^{(0)}. \tag{30}
$$

The term $\sum_{\beta} A_{\alpha\beta i}^{(0)} n_{\beta i}^{(1)}$ has dropped out here because $v_{\alpha i}$ is in the left null space of $A_{\alpha\beta i}$ for each i. The result are S equations for the S unknowns $x_i^{(0)}$.

Equation 30 must be satisfied, no matter how the remaining $S \times P$ variables $n_{\alpha i}^{(1)}$ are chosen; such an equation is therefore called a *solvability condition* in the mathematical literature. Such conditions arise at each order of the expansion in ϵ and are the reason why the projections of the basic equations Eq. 23 onto $v_{\alpha i}$ (for each i) are dominating community dynamics. These projections (summed over all orders in ϵ) determine the time derivatives of the projections of $n_{\alpha i}$ onto $v_{\alpha i}$ for each i,

$$
V_i = \sum_{\alpha} v_{\alpha i} n_{\alpha i}, \tag{31}
$$

that is, of the total reproductive values. Making use of Eqs. 25 and 28, it is seen that $V_i(t) = x_i^{(0)}(\epsilon t) + \text{h.o.t.}$. With the identification $V_i(t) = x_i^{(0)}(\epsilon t)$ in Eq. 30, the QNA defined by Eqs. 13 and 14 is recovered. But we are now in the position to improve this approximation by including higher-order corrections.

Denote by $A_{\alpha\beta i}^{\mathrm{D}}$ the Drazin inverse of $A_{\alpha\beta i}^{(0)}$ for species i, i.e. a projection onto the space orthogonal to $v_{\alpha i}$ followed by an inversion of $A_{\alpha\beta i}$ restricted to this space. The general solution of Eq. 29 in the subspace orthogonal to $v_{\alpha i}$ is then

$$
n_{\alpha i}^{(1)}(t, \tau) = w_{\alpha i} x_i^{(1)}(\tau)
$$
$$
- \sum_{\nu\beta} A_{\alpha\nu i}^{\mathrm{D}} A_{\nu\beta i}^{(1)}(\{w_{\gamma k} x_k^{(0)}(\tau)\}) w_{\beta i} x_i^{(0)}(\tau).
$$
$$
\tag{32}
$$

The term with the new unknowns $x_i^{(1)}(\tau)$ arises because $w_{\alpha i}$ is in the null space of $A_{\alpha\beta i}^{(0)}$ (for each i) and the size of its contribution to $n_{\alpha i}^{(1)}$ is therefore not constrained by Eq. 29.

Of the second-order term of condition 26, we consider here only the component parallel to $v_{\alpha i}$ since this is sufficient to determine the functions $x_i^{(1)}(\tau)$ entering

Eq. 32 above and thus the first-order correction to $n_{\alpha i}$ in Eq. 25. Putting Eq. 28 into the second-order term in Eq. 26, setting $\partial n^{(2)}_{\alpha i}/\partial t = 0$ as above, multiplying by $v_{\alpha i}$ and summing over α, we arrive at the condition

$$0 = \frac{\partial x^{(1)}_i}{\partial \tau} - \sum_{\alpha\beta} v_{\alpha i} A^{(1)}_{\alpha\beta i}(\{w_{\gamma k} x^{(0)}_k\}) n^{(1)}_{\beta i}$$
$$- \sum_{\alpha\beta vl} v_{\alpha i} A^{(1)}_{\alpha\beta i, vl}(\{w_{\gamma k} x^{(0)}_k\}) n^{(1)}_{vl} w_{\beta i} x^{(0)}_i. \quad (33)$$

By Eqs. 25, 28, 31 and 32,

$$V_i(t) = \sum_{\alpha} v_{\alpha i} n_{\alpha i}(t) = x^{(0)}_i(\epsilon t) + \epsilon x^{(1)}_i(\epsilon t) + \text{h.o.t.} \quad (34)$$

Thus, $dV_i/dt = \epsilon \partial x^{(0)}_i/\partial\tau + \epsilon^2 \partial x^{(1)}_i/\partial\tau + \text{h.o.t.}$ Using Eqs. 30 and 33, this becomes, up to errors of order ϵ^3,

$$\frac{dV_i}{dt} = \epsilon \sum_{\alpha\beta} v_{\alpha i} A^{(1)}_{\alpha\beta i}(\{w_{\gamma k} x^{(0)}_k + \epsilon n^{(1)}_{\gamma k}\})[w_{\gamma k} x^{(0)}_i + \epsilon n^{(1)}_{\gamma k}], \quad (35)$$

as can be verified by doing the same Taylor expansion of $A^{(1)}_{\alpha\beta i}(\cdot)$ as before. By Eqs. 32 and 34, the combination $w_{\alpha i} x^{(0)}_i + \epsilon n^{(1)}_{\alpha i}$ in which time-dependent variables enter Eq. 35 is, to first order in ϵ, equal to $\tilde{w}_{\alpha i} V_i$ with

$$\tilde{w}_{\alpha i} = \tilde{w}_{\alpha i}(\{V_k\}) = w_{\alpha i} - \epsilon \sum_{v\beta} A^{D}_{\alpha v i} A^{(1)}_{v\beta i}(\{w_{\gamma k} V_k\}) w_{\beta i}. \quad (36)$$

Absorbing ϵ into $A^{(1)}_{\alpha\beta i}$ and going back to matrix notation, the first-order correction to the QNA is therefore given by Eqs. 15 and 16.

Appendix 2: The mean-field QNA of the stage structured model

In this appendix, we compute the QNA for the stage structured model 17 by making use of a so-called mean-field approximation for the interaction terms in Eq. 17. The result is referred to as *mean-field QNA* in the main text. In this approximation, we assume that the equilibrium population structure $\mathbf{w} = (w_J, w_A)^{\mathrm{T}}$ of all species interacting with a focal species i is the same as that of the focal species itself and then approximate the interaction terms by their expectation values. This leads to a self-consistency condition specifying $\mathbf{w}$.

Introducing the abbreviations $q_i = G_J^{-1} \sum_{j=1}^{S} G_{Jij} n_{Jj}$ and $Q_i = G_A^{-1} \sum_{j=1}^{S} G_{Aij} n_{Aj}$ for the density dependencies and substituting $(n_{Ji}, n_{Ai}) = (w_J, w_A) N_i$, the equi-

librium condition for the focal species i by Eq. 17 becomes

$$0 = b\, w_A - d_J\, w_J - m\, w_J - G_J\, q_i\, w_J \quad (37\mathrm{a})$$
$$0 = m\, w_J - d_A\, w_A - G_A\, Q_i\, w_A. \quad (37\mathrm{b})$$

To implement the mean-field approximation, we approximate q_i and Q_i by their expectation values, denoted by q and Q. Further, we assume that the expectation value of $G_J^{-1} G_{Jij} n_{Jj}$ is by a factor w_J/w_A larger than that of $G_A^{-1} G_{Aij} n_{Aj}$, implying that $q = (w_J/w_A)\, Q$. This relation would be exact if invasion and extinction probabilities and abundances of species were independent of their competition coefficients. In reality, species with fewer competitors and smaller competition coefficients are, of course, more likely to invade and survive at high abundance. But the resulting bias on mean competition coefficients turns out to be weak and similar for both juveniles and adults, which justifies our approximation.

From $q = (w_J/w_A)\, Q$ and Eq. 37b, we get

$$w_J = \frac{d_A + G_A Q}{m}\, w_A. \quad (38)$$

Putting both into Eq. 37a and factoring out w_A yield the self-consistency condition

$$0 = -m^2\, b + (d_J\, m + m^2)\,(d_A + G_A\, Q) + G_J\, Q\,(d_A + G_A\, Q)^2. \quad (39)$$

Assuming all model coefficients to be positive, which is plausible for biological reasons, the right-hand side of this condition is a strictly increasing third-order polynomial in Q. The condition therefore uniquely determines Q. At $Q = 0$, the condition reduces to m times the determinant of Eq. 37 for $Q = q = 0$, in other words, the product of the two eigenvalues of the population matrix for linear growth. If populations grow linearly, that is, if at least a single species can establish itself in the model, we have one positive and one negative eigenvalue, and this product is negative. Together with the monotony of the right-hand side of Eq. 39, this implies that the value of Q satisfying Eq. 39 is positive. The equation is easily solved numerically.

Model 17 can be re-written in the matrix form (Eq. 11) with a density-dependent population matrix

$$\mathbf{A}_i(\{\mathbf{n}_k\})$$
$$= \begin{pmatrix} -d_J - m - \sum_{j=1}^{S} G_{Jij} n_{Jj} & b \\ m & -d_A - \sum_{j=1}^{S} G_{Aij} n_{Aj} \end{pmatrix}. \quad (40)$$

Using the self-consistent approximations for the density dependencies computed above, we can now predict that $\mathbf{A}_i(\{\mathbf{n}_k\})$ contains a large, constant contribution

$$\mathbf{A}_i^{(0)} = \begin{pmatrix} -d_J - m - G_J M m^{-1} Q & b \\ m & -M \end{pmatrix}, \qquad (41)$$

where the effective adult mortality $M = d_A + G_A Q$ has been introduced as an abbreviation. This matrix has an eigenvalue zero. The corresponding left and right eigenvectors, normalized according to conditions 4 and 9 are

$$\mathbf{w}_i = \frac{1}{m+M} \begin{pmatrix} M \\ m \end{pmatrix} \qquad (42)$$

and

$$\mathbf{v}_i = \frac{m+M}{bm+M^2} \begin{pmatrix} M \\ b \end{pmatrix}. \qquad (43)$$

The density-dependent growth rate $f_i(\{V_k\})$ given by Eq. 14 can now be computed. It is easily seen to have the general form $f_i(\{V_k\}) = r_i - \sum_j G_{ij} V_j$. Evaluating Eq. 14, we obtain

$$r_i = r = \frac{bm(2M - d_A) - M^2(d_J + m)}{bm + M^2}, \qquad (44)$$

and

$$G_{ij} = c_J G_{Jij} + c_A G_{Aij} \qquad (45)$$

with

$$\begin{pmatrix} c_J \\ c_A \end{pmatrix} = \frac{1}{(m+M)(bm+M^2)} \begin{pmatrix} M^3 \\ bm^2 \end{pmatrix}. \qquad (46)$$

Specifically, $G_{ii} = G_{\text{MF}} = c_J G_J + c_A G_A$. Equations 44 to 46 define the mean-field QNA of our stage-structured model.

Appendix 3: Ecological interpretation of the mean-field QNA and separation of time scales

The results of the previous section, whilst explicit in the model parameters, somewhat conceal the underlying ecology. To obtain a clearer picture, first abbreviate the effective mortality of juveniles as $D_J = d_J + G_J M m^{-1} Q$ (see Eq. 41). Since our model implies a Poisson process for events at which juveniles either die or mature, the mean age at maturation is $T_m = 1/(m + D_J)$. Equation 41 can be re-written as

$$\mathbf{A}_i^{(0)} = \begin{pmatrix} -T_m^{-1} & b \\ m & -M \end{pmatrix}. \qquad (47)$$

It follows from $\det \mathbf{A}_i^{(0)} = 0$ that $m = M T_m^{-1} b^{-1}$. With this substitution, we obtain

$$\mathbf{w}_i = \frac{1}{1 + b T_m} \begin{pmatrix} b T_m \\ 1 \end{pmatrix}, \qquad (48)$$

illustrating that the relative proportion of juveniles in a population increases the more are born and the longer they stay young and alive, and

$$\mathbf{v}_i = \frac{1 + b T_m}{M^{-1} + T_m} \begin{pmatrix} b^{-1} \\ M^{-1} \end{pmatrix}, \qquad (49)$$

illustrating that the reproductive value of juvenile individuals decreases with fecundity, whilst that of adults decreases with adult mortality. The expression for the effective linear growth rate r can then be re-written as

$$r = \frac{2 - M b^{-1} - M^{-1} d_A - T_m d_J}{M^{-1} + T_m}. \qquad (50)$$

Due to the Poisson nature of adult death, M^{-1} is the mean duration of adulthood, and the denominator is not only the mean age at which adults die but also the mean age of mothers at giving birth, that is, the generation time. The expression $2 - M b^{-1} \approx 2$ in the numerator can be traced back to the reproduction cycle (birth and maturation), whilst the subsequent two negative terms weight in the effects of non-competitive death.

It follows from Eq. 50 that the linear growth rate r, which sets the time scale underlying all community dynamics, is bounded from above as $r \leq 2(M^{-1} + T_m)^{-1}$. Since the trace of a matrix equals the sum of its eigenvalues and one of the two eigenvalues of $\mathbf{A}_i^{(0)}$ is zero, the other one, which determines the intra-specific relaxation rate is, using Eq. 47, $\lambda_2 = \text{Tr}\{\mathbf{A}_i^{(0)}\} = -(T_m^{-1} + M)$. The ratio of intra-specific to inter-specific relaxation rates is therefore bounded from below as $|\lambda_2|/r \geq (1 + T_m M)(1 + T_m^{-1} M^{-1})/2$, which has a minimum of 2 at $T_m M = 1$ and grows beyond all bounds as $T_m M$ either decreases or increases away from 1. Inter-specific time scales are therefore by a factor of at least 2 time longer than intra-specific time scales in this model. But the time-scale separation can be larger. For our choice of parameters (Table 1), for example, $|\lambda_2|/r = 5.2$.

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