
Does functional redundancy exist?

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Functional redundancy has often been assumed as an intuitive null hypothesis in biodiversity experiments, but theory based on the classical Lotka-Volterra competition model shows that functional redundancy *sensu stricto* is incompatible with stable coexistence. Stable coexistence requires differences between species which lead to functional complementarity and differences between the yields of mixtures and monocultures. Only a weaker version of functional redundancy, i.e. that mixture yields lie within the range of variation of monoculture yields, is compatible with stable coexistence in Lotka-Volterra systems. Spatial and temporal environmental variability may provide room for functional redundancy at small spatial and temporal scales, but is not expected to do so at the larger scales at which environmental variations help maintain coexistence. Neutral coexistence of equivalent competitors, non-linear per capita growth rates, and lack of correlation between functional impact and biomass may provide the basis for the existence of functional redundancy in natural ecosystems. Overall, there is a striking parallel between the conditions that allow stable coexistence and those that allow overyielding.

The potential consequences of biodiversity loss for ecosystem functioning and services have received considerable attention during the last decade (Loreau et al. 2001, 2002, Kinzig et al. 2002). The concept of functional redundancy was introduced to articulate hypotheses in this emerging area (Lawton and Brown 1993). Functional redundancy means that different species perform the same functional role in ecosystems so that changes in species diversity does not affect ecosystem functioning. Therefore, functional redundancy has implicitly served as a null hypothesis in recent studies on the potential consequences of biodiversity loss for ecosystem functioning. Several controlled experiments have now established that species diversity influences ecosystem-level processes such as primary production in grasslands (Tilman et al. 1997a, 2001, Hector et al. 1999, Loreau and Hector 2001), and heterotrophic consumption of suspended resources in streams (Cardinale et al. 2002). Furthermore, they have shown functional complementarity resulting from processes such as resource partitioning and facilitation among at least part of the species used in

these experiments, thereby explicitly rejecting the null hypothesis of functional redundancy. Not all experiments, however, have been able to reject this null hypothesis (reviewed by Loreau et al. 2002), and rejection of the null hypothesis does not necessarily imply that functional redundancy is not present among some of the species, e.g. within functional groups (Loreau et al. 2001).

How common is functional redundancy expected to be in natural ecosystems? There have been remarkably few theoretical efforts to answer this simple question and guide research in this area. Theoretical studies pertaining to the effects of biodiversity on ecosystem functioning have identified the conditions under which loss of species diversity is expected to impair ecosystem processes in controlled experiments (Tilman et al. 1997b, Loreau 1998a, 2000, Petchey 2000). They have, however, rarely addressed explicitly how species diversity itself is maintained in ecosystems (Chesson et al. 2002, Mouquet et al. 2002, Pacala and Tilman 2002), which limits their application to natural conditions. Furthermore, their focus was not on redundancy itself. Redundancy is a multifaceted concept that is difficult to define unambiguously because it can be assessed by either individual-level or population-level impacts, and potentially involves many different niche dimensions (Rosenfeld 2002). My goal in this contribution is to explore some implications of the classical Lotka-Volterra competition model for the existence of functional redundancy in natural ecosystems, and to discuss more broadly how functional redundancy is expected to be linked intimately to mechanisms of species coexistence. I focus on the equilibrium properties of the system, and thus I do not consider hypotheses about the potential impact of redundancy on ecosystem stability (Walker 1992, Naeem 1998), especially since in these hypotheses, it is really temporal niche complementarity, not redundancy, which generates the stabilising effect of diversity (Loreau 2000).

Functional redundancy in a Lotka-Volterra world

The Lotka-Volterra competition model has served historically as the basis both for the theory of inter-specific competition (Case 2000) and for methods to measure its effects in agricultural sciences (Vandermeer 1989). In the classical system with two species, its equations have the form:

$$\frac{dN_i}{dt} = \frac{r_i N_i}{K_i} (K_i - N_i - \alpha_{ij} N_j) \quad i, j = 1, 2 \quad (1)$$

where N_i is the biomass of species i , r_i is its intrinsic rate of natural increase, K_i is its carrying capacity, and α_{ij} is the competition coefficient, which measures the inter-specific competitive effect of species j on species i , relative to the intraspecific competitive effect of species i on itself.

Stable equilibrium coexistence is achieved between the two species if and only if (Case 2000):

$$\alpha_{21} < x < 1/\alpha_{12} \quad (2)$$

where

$$x = K_2/K_1 \quad (3)$$

The two populations then reach the following equilibrium biomasses:

$$N_1^* = \frac{K_1(1 - x\alpha_{12})}{1 - \alpha_{12}\alpha_{21}} \quad (4a)$$

$$N_2^* = \frac{K_1(x - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}} \quad (4b)$$

In what follows I assume, without any loss of generality, that species 2 has the highest carrying capacity, i.e.:

$$x \geq 1 \quad (5)$$

Complementarity vs redundancy

Functional complementarity is generally contrasted against functional redundancy because it involves differences in the functional attributes of species that result in mixtures performing better than expected based on monoculture performances (Loreau 2000, Loreau and Hector 2001). In niche theory, the mechanistic basis for functional complementarity is niche differentiation or resource partitioning, which allows different species to exploit partly different resources, whereas species that utilise identical resources can be regarded as redundant. In competition or biodiversity experiments, complementarity has usually been assessed by its effects at the population level, i.e. by non-transgressive overyielding as measured by the relative yield total (RYT, Harper 1977, Vandermeer 1989, Hector 1998, Hector et al. 2002) or some of its variants (Loreau and Hector 2001). The RYT is defined by:

$$RYT = \frac{N_1}{K_1} + \frac{N_2}{K_2} \quad (6)$$

where N_1 and N_2 are the respective yields of species 1 and 2 in mixture (here at the coexistence equilibrium) and K_1 and K_2 are their yields in monoculture. Functional complementarity is detected when $RYT > 1$.

When yield is simply measured by biomass, as is often done in annual plants, a graphical analysis shows easily that the equilibrium point which corresponds to stable coexistence in the system lies above the straight line $RYT = 1$ which connects the two monoculture equilibria ($K_1, 0$) and $(0, K_2)$ (Vandermeer 1989, Fig. 1). Thus, stable coexistence necessarily implies $RYT > 1$, and hence complementarity, in the Lotka-Volterra model. No functional redundancy is possible by this standard in any stable community.

Perfect redundancy

Although functional redundancy has usually been defined implicitly in terms of niche similarity, species with identical niches may still differ in their ability to exploit resources (Loreau 1998a), which amounts to differences in their carrying capacity in the Lotka-Volterra model. Perfect functional redundancy, however, means that species are exactly equivalent in functional terms, so that losing any species from a mixture does not alter function (Johnson 2000). In the Lotka-Volterra model this implies that $K_1 = K_2 = K$, and

$$N_1^* + N_2^* = K \quad (7)$$

Equation (7) is identical to $RYT = 1$, and thus requires that the isoclines of the two species be confounded with the line $RYT = 1$ so that the coexistence equilibrium

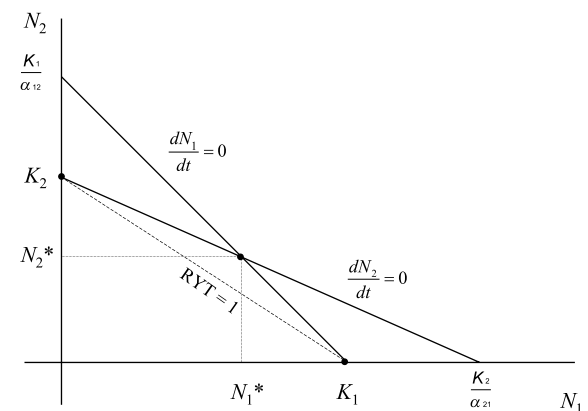


Fig. 1. Zero-growth isoclines for the Lotka-Volterra competition model when there is stable coexistence between the two species (solid lines). Stable coexistence occurs when $K_2/\alpha_{21} > K_1$ and $K_1/\alpha_{12} > K_2$. In this case, the stable equilibrium point (N_1^* , N_2^*) lies above the line $RYT = 1$ (dashed line) which connects the two monoculture equilibria ($K_1, 0$) and $(0, K_2)$.

point lies on this line. This amounts to requiring neutral coexistence, which violates the condition for stable coexistence. Thus, again no functional redundancy is possible by this standard in any stable community.

Transgressive overyielding vs redundancy

A more stringent test of functional complementarity than above is provided by transgressive overyielding, which occurs when a mixture outperforms the highest yielding monoculture (Harper 1977, Vandermeer 1989, Loreau 1998b). This test makes sense in agricultural sciences, where the best performing species or type can be selected and grown in monoculture. Its relevance to natural ecosystems, however, is more debatable (Hector et al. 2002). The null hypothesis against which transgressive overyielding is contrasted is not functional redundancy *sensu stricto* since species may differ in a variety of ways and yet fail to overyield the best performing species.

In the Lotka-Volterra model, transgressive overyielding occurs when:

$$N_1^* + N_2^* > K_2 = xK_1 \quad (8)$$

which simplifies into:

$$(1 - \alpha_{21})(1 - x\alpha_{12}) > 0 \quad (9)$$

Since the second bracketed term in the left-hand side of (9) is positive by inequality (2), this condition reduces to:

$$\alpha_{21} < 1 \quad (10)$$

It is straightforward to show that the coexistence condition (2) also necessarily implies $\alpha_{12} < 1$, and hence overyielding of the poorest yielding monoculture by the mixture. Thus, transgressive overyielding occurs provided that interspecific competition be smaller than intraspecific competition in both species. This requires stronger niche differentiation than is required for stable coexistence and functional complementarity since the latter are compatible with $\alpha_{21} > 1$.

Although transgressive overyielding is more stringent than complementarity and rejection of redundancy, it may be viewed as a test of a more liberal or 'weak' form of redundancy, in which differences in the monoculture yields of the various species are regarded as random variations around the mean, and rejection of redundancy requires that the yield of mixtures be outside the range of variation of monoculture yields.

Example: MacArthur's classical niche model

The Lotka-Volterra model is abstract and phenomenological, and subsumes a variety of forms of interspecific competition. Therefore it may be useful to provide a few examples using more mechanistic competition models.

One such model is MacArthur's (1972) classical niche model, in which species have niches described by normal (Gaussian) consumption curves along a resource gradient. In this model, if σ_1 and σ_2 are the standard deviations of the consumption curves of species 1 and 2, respectively (a measure of niche breadth), and d is the distance between their means, the competition coefficients in the equivalent Lotka-Volterra model are (Case 2000):

$$\alpha_{ij} = \frac{\sqrt{2}e^{-\frac{d^2}{2(\sigma_1^2 + \sigma_2^2)}}}{\sigma_j \sqrt{\frac{1}{\sigma_1^2} + \frac{1}{\sigma_2^2}}} = \frac{\sigma_i e^{-\frac{d^2}{4\sigma^2}}}{\sqrt{\sigma^2}} \quad (11)$$

where

$$\sigma^2 = \frac{\sigma_1^2 + \sigma_2^2}{2} \quad (12)$$

As in any Lotka-Volterra system, stable coexistence entails functional complementarity according to the RYT criterion and is incompatible with perfect redundancy as defined above. Transgressive overyielding, however, is not guaranteed. Condition (10) becomes:

$$d^2 > 4\sigma^2 \ln\left(\frac{\sigma_2}{\sqrt{\sigma^2}}\right) \quad (13)$$

Thus, transgressive overyielding is facilitated by greater niche differentiation along the resource gradient (larger d and smaller σ^2), and by greater similarity in niche breadth (when $\sigma_1 = \sigma_2$, $\sigma_2 = \sqrt{\sigma^2}$, and the right-hand side of (11) vanishes). When niches have identical breadth, any niche differentiation ($d > 0$) is sufficient to generate transgressive overyielding. On the other hand, when niches have identical optima ($d = 0$), no difference in niche breadth can make for transgressive overyielding.

Example: the competition-colonisation trade-off model

Hastings's (1980) and Tilman's (1994) model of interspecific competition for space, in which coexistence is allowed by a trade-off between competition and colonisation abilities, can be viewed as a model of interference competition in which there is a trade-off between the ability for interference competition and the ability to use more resources and hence maintain a higher carrying capacity (Adler and Mosquera 2000, Kokkoris et al. 2002). This model can be rewritten as a non-spatial Lotka-Volterra model with the following transformations:

$$r_i = c_i - m_i \quad (14.a)$$

$$K_i = 1 - m_i/c_i \quad (14.b)$$

$$\alpha_{ij} = 1 + c_j/c_i \quad j < i \\ = 0, \quad j > i \quad (14.c)$$

where c_i and m_i are the colonisation rate and mortality rate, respectively, of species i .

It is apparent from Eq. 14.c that the competition coefficient measuring interference from the species with the smaller carrying capacity (species 1) on the species with the larger carrying capacity (species 2) is greater than 1, which violates condition (10) and thus precludes transgressive overyielding.

Discussion: is coexistence compatible with functional redundancy?

The above analysis of the classical Lotka-Volterra model suggests that stable coexistence is incompatible with functional redundancy as assessed by either the RYT or the perfect redundancy criterion. Stable coexistence requires differences between species which automatically lead to functional complementarity and differences between the yields of mixtures and monocultures. A weaker version of functional redundancy, i.e. that mixture yields lie within the range of variation of monoculture yields, however, is compatible with stable coexistence. This weaker version is rejected when transgressive overyielding occurs. Analysis of MacArthur's classical niche model shows that transgressive overyielding requires a strong enough niche differentiation. Such a level of niche differentiation can be absent altogether for some coexistence mechanisms such as the competition-colonisation trade-off. It is interesting to note that much of the debate on the interpretation of recent biodiversity experiments (Huston et al. 2000, Loreau et al. 2001) has revolved precisely around the issue of whether transgressive overyielding is the key criterion to assess functional differences among biodiversity treatments. When defined more strictly and consistently, functional redundancy should be rejected when there are non-random differences among species in their monoculture yields or when functional complementarity is detected by the RYT approach.

These conclusions, however, apply to equilibrium coexistence in Lotka-Volterra systems. How robust are they likely to be to departures from the assumptions underlying the model and the equilibrium analysis? Non-equilibrium coexistence is possible when either the external environment or species interactions within the system change through time. In the short term, transient non-equilibrium coexistence can obscure functional complementarity and allow functional redundancy (Pacala and Tilman 2002). For such coexistence to persist in the long term, however, species must have different responses to environmental fluctuations, which may be interpreted as a form of temporal niche differentiation (Chesson 2000). Although the quantita-

tive details may differ greatly from the Lotka-Volterra model, long-term non-equilibrium coexistence also requires niche differentiation, which should tend to generate higher yields on average in mixtures than in monocultures (Yachi and Loreau 1999, Chesson et al. 2002).

Natural systems often differ from the Lotka-Volterra model in being open to spatial exchanges with neighbouring communities. Immigration through source-sink or mass effects can maintain local species diversity even in the absence of any form of local niche differentiation, which may lead to local productivity staying constant or even decreasing with increasing diversity (Shmida and Ellner 1984, Loreau and Mouquet 1999). At the regional scale, however, stable coexistence requires spatial niche differentiation among habitats (Mouquet and Loreau 2002). Such a spatial niche differentiation is likely to also make more diverse regional systems more productive (Chesson et al. 2002). Niche differentiation and overyielding are transferred from the local to the regional scale in this coexistence mechanism.

Thus, spatial and temporal environmental variability makes functional redundancy possible at small spatial and temporal scales, but is unlikely to make it possible at the scales at which environmental variations occur. What other conditions, then, are likely to make functional redundancy compatible with coexistence in natural systems?

First, functional redundancy may arise when species are equivalent competitors and coexistence obeys the neutral theory (Hubbell 2001). In this case, species have confounded isoclines in the Lotka-Volterra model, which leads to neutral stability and perfect functional redundancy. For this theory to apply to natural systems, species should experience pure random drift and have no niche differences that determine their local competitive ability and their spatial and temporal responses to environmental gradients. Although ecological knowledge can easily falsify these hypotheses in many instances, it is still unclear whether quasi-neutral coexistence may be an appropriate description of reality at some spatial and temporal scales.

Second, the Lotka-Volterra model may be viewed as providing a linear approximation of per capita growth rates, which may more generally be non-linear. It is this linearity of per capita growth rates which generates the linearity of the zero-growth isoclines (Fig. 1). Concave-up non-linear isoclines allow stable equilibrium points to lie on or below the line $RYT = 1$ which connects the two monoculture equilibria (Fig. 2). In the event that the equilibrium point lies on, or sufficiently close to, the line $RYT = 1$, stable coexistence now becomes compatible with functional redundancy as assessed by either the RYT or the perfect redundancy criterion. Concave-up non-linear isoclines have been demonstrated in a *Drosophila* experimental system precisely to explain why stable

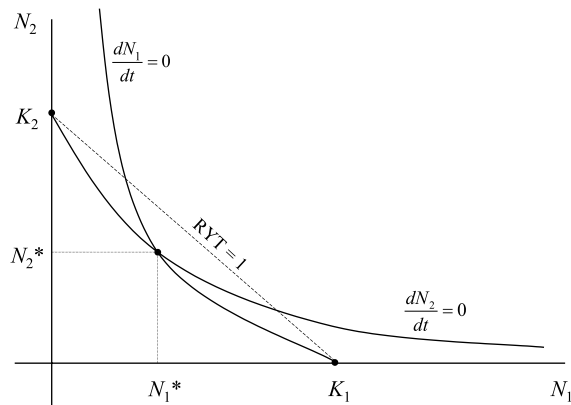


Fig. 2. Stable coexistence in a model with concave-up non-linear zero-growth isoclines (solid lines). In this case, the stable equilibrium point (N_1^* , N_2^*) may lie below the line $RYT = 1$ (dashed line) which connects the two monoculture equilibria (K_1 , 0) and (0, K_2).

coexistence is compatible with underyielding and why this does not invalidate competition theory (Gilpin and Justice 1972). How frequent they are in nature is still largely unknown.

Lastly, it should be recalled that the results obtained with the Lotka-Volterra model concern biomass and yield measures that are proportional to biomass, as is often assumed in annual plants. The Lotka-Volterra model does not describe resource consumption and loss explicitly and therefore does not make any direct prediction on productivity or other functional impacts of competing species. In species for which productivity is poorly correlated with biomass, as is often the case with trees and animals, productivity or other ecosystem processes might be unrelated to conditions that allow stable coexistence, and more mechanistic approaches would be necessary to predict the relationship between productivity and coexistence.

To conclude, functional redundancy has often been assumed as an intuitive null hypothesis in biodiversity experiments, but theory based on the classical Lotka-Volterra competition model shows that functional redundancy *sensu stricto* is incompatible with stable coexistence. Spatial and temporal environmental variability may provide room for functional redundancy at small spatial and temporal scales, but is not expected to do so at the larger scales at which environmental variations help maintain coexistence. Neutral coexistence of equivalent competitors, non-linear per capita growth rates, and lack of correlation between functional impact and biomass are potential candidates for the presence of functional redundancy in ecosystems. Overall, there is a striking parallel between the conditions that allow stable coexistence and those that allow overyielding. This leads to an intriguing question: is the recent debate over biodiversity and ecosystem

functioning simply a continuation of the debate over the factors that maintain diversity in ecological communities?

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