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How trophic interaction strength depends on traits: A conceptual framework for representing multidimensional trophic niche spaces

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Abstract

A key problem in community ecology is to understand how individual-level traits give rise to population-level trophic interactions. Here we propose a synthetic framework based on ecological considerations to address this question systematically. We derive a general functional form for the dependence of trophic interaction coefficients on trophically relevant quantitative traits of consumers and resources. The derived expression encompasses—and thus allows a unified comparison of—several functional forms previously proposed in the literature. Furthermore, we show how a community's, potentially low-dimensional, effective trophic niche space is related to its higher-dimensional phenotypic trait space. In this manner, we give ecological meaning to the notion of the "dimensionality of trophic niche space". Our framework implies a method of directly measuring this dimensionality. We suggest a procedure for estimating the relevant parameters and verifying the assumptions underlying our derivation for empirical data.

1 Introduction

The ecological niche of an animal was originally conceived by Elton (1927) as 'its place in the biotic environment, its relation to food and enemies'. The niche concept is of fundamental importance in ecology and establishes a link between individual-level traits and population dynamics. However, despite decades of intense research and debate (Hutchinson, 1957, 1965; MacArthur, 1968; Whittaker and Levin, 1975; Pianka, 1983; Arthur, 1987; Leibold, 1995; Begon et al, 1996; Case and Leibold, 2003; Meszéna et al, 2006), no universal agreement has emerged as to how niches are to be formally represented, and fundamental questions remain unresolved.

Hutchinson (1957) conceptualized the niche of a species as a volume in a high-dimensional space, referred to as niche space. The availability of an ecological niche for a species depends, in a great variety of ways, on interactions between the species comprising an ecological community. These interactions, in turn, are affected by the phenotypic traits expressed by the interacting species. Cohen (1977) introduced the concept of *trophic niche space*, defined as the trophically relevant subspace of niche space. The position of a species within trophic niche space is defined by its *trophic traits* alone, that is, the traits relevant for determining trophic interactions. A first fundamental question raised by Cohen (1977) is how many dimensions the trophic niche space has or, equivalently, how many different *trophic traits* consumers and resources have. The topology of empirical food webs, for example, has variously been interpreted

as being indicative of for a low-dimensional (Cohen, 1977, 1978; Allesina et al, 2008) but also for a rather high-dimensional (Rossberg et al, 2006a; Rossberg, 2008) niche space, without consensus as to when one of these interpretations is more appropriate. A second fundamental question concerns the empirical identification of trophic traits. How are trophic traits related to the vast number of directly measurable, phenotypic, hereditary traits that characterize the physiology, anatomy, and behavior of the individuals of a species (hereafter: *phenotypic traits*)? Which objective criterion should be used to choose trophic traits, and how is the minimal number of such traits to be found? A third fundamental question addresses the quantitative relationship between trophic traits and phenotypic traits. Specifically, how can the former be expressed in terms of the latter?

These questions assert themselves with a vengeance in current models for describing the evolution of food webs (e.g., Caldarelli et al, 1998; Drossel et al, 2001; Christensen et al, 2002; Yoshida, 2003; Tokita and Yasutomi, 2003; Bastolla et al, 2005; Loeuille and Loreau, 2005; Ito and Ikegami, 2006; Rikvold, 2007; Rossberg et al, 2008; see also the review by Yoshida, 2006). These models inevitably face the problem of having to cast the niche concept into a specific mathematical form. The choices made are of central importance, since they can affect the predicted system-level properties of modeled communities. Solutions to this problem suggested to date, differ substantially, both in terms of how niches are represented through trophic traits and how traits give rise to trophic interactions. Some models simply consider the trophic links themselves as evolving traits (Yoshida, 2003; Tokita and Yasutomi, 2003; Bastolla et al, 2005; Rossberg et al, 2006b). In other models, links are determined by trophic traits of consumers and resources, which are then allowed to evolve (e.g., Caldarelli et al, 1998; Yoshida, 2003; Rossberg et al, 2006a; Ito and Ikegami, 2006; Laird and Jensen, 2006; Rossberg et al, 2008). Trophic traits, in turn, have been modeled as qualitative or categorical characters given by discrete numbers that describe the presence or absence of specific trophically relevant features (e.g., Drossel et al, 2001) or as quantitative characters given by continuous numbers (e.g., Yoshida, 2003). Both approaches have their merits. Categorical characters are better aligned with the practice of cladistics (Kitching et al, 1998) and do justice to the fact that a specific definition and associated measurement protocol used for quantifying a quantitative character in one species might be difficult to apply to other species. The use of quantitative characters, on the other hand, is motivated by the observation that phenotypes change continuously, in particular when considering population averages, and that even merely quantitative differences in trophic traits can have large impacts on the strengths of trophic interactions.

The aim of this study is to develop a general theory of how phenotypic traits determine trophic interaction strengths. We start from a generic characterization of the dependence of interaction strengths on the phenotypic traits of resources and consumers (Eq. (3)). This characterization can be verified and parametrized based on field data (Appendix A). We then map phenotypic traits onto a hierarchy of trophic traits, with the latter being ranked according to their importance in determining trophic interaction strengths. This hierarchy, when truncated at a given level of accuracy, gives a formal and objective meaning to the concepts of trophic niche space and its dimensionality. Based on the truncated hierarchy, we derive an approximate expression for interaction strength as

a function of trophic traits (Eq. (4)). This result clarifies how trophic traits can be chosen to characterize the trophic vulnerability of resources and the foraging strategies and capabilities of consumers in a shared trophic niche space. This finding naturally leads to interpreting the strengths of trophic links in terms of a match between the vulnerability traits of resources and the foraging traits of consumers. Derived from a generic ansatz, our results allow us to integrate several different models proposed in the literature for determining trophic interaction strength into a unified framework.

2 Theory

We focus on trophic interactions between species because for this type of interaction theory is historically most developed and because trophic interactions are obviously essential for all species but primary producers. It is, however, not difficult to apply our theory to other types of interaction, such as those between pollinators and plants. Also, the interacting units considered below can equally well be interpreted as individuals or as higher taxa, rather than as species, depending on the perspective that is most appropriate and illuminating for any specific application.

2.1 Dependence of interaction strengths on phenotypic traits

Following general practice in food-web modeling, we assume that trophic interactions are pairwise, that is, for each pair of species (r, c) there is an interaction strength $a_{rc} \geq 0$ characterizing the intrinsic efficiency or likelihood that c eats r. In nature, trophic interactions involving three or more species do exist (e.g., herbivores hiding within plants from predators), but may not be as important in determining macroecological and macroevolutionary patterns as pairwise interactions, and are therefore not considered here. The trophic energy flows from r to c depends not only on the interaction strength a_{rc} but also on the densities, abundances, or biomasses (densities for short) of r, c, and other species, in a form that is usually described by a functional response. In general, such a functional response may be affected by phenotypic traits of c, such as handling times. We assume that the trophic energy flow to c is determined at most by the matrix a_{rc}, the densities of all species, and some phenotypic traits of c. The phenotypic traits of species other than c affect the direct flows to c only *via* the pairwise interaction strengths a_{rc}, and each a_{rc} depends only on the phenotypic traits of r and c, but not on their densities.

The specific forms in which interaction strengths a_{rc} enter a community model can vary considerably. Among the various measures of interaction strength tabulated by Berlow et al (2004), a_{rc} may refer to the an element of community's demographic matrix (there denoted as interaction matrix) or the maximum consumption rate of r by c, on a per-capita or a per-biomass basis. In a typical expression for the type-II functional response of a consumer c to N resource species of densities ρ_i $(i = 1, ..., N)$, the interaction strengths enter as

$$\frac{a_{ic}\rho_i}{1 + \tau_c \sum_k a_{kj}\rho_k},\tag{1}$$

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where τ_c scales the consumer's handling time. Many other forms are conceivable and are encompassed by our general analysis below.

Observations show that food webs possess many more weak than strong trophic links (Kenny and Loehle, 1991; Ulanowicz and Wolff, 1991). We thus adopt a logarithmic scale for link strength by developing our framework in terms of $\ln a_{rc}$. (Should a_{rc} have a unit, the unit is removed by division with a normalizing constant before taking the logarithm.) Working on a logarithmic scale requires the technical assumption that there is at least the tiniest probability for any consumer species to eat individuals of any other species, including its own, so that a_{rc} is always positive and $\ln a_{rc}$ is always defined. This does not preclude the possibility that a_{rc} is so small for many consumer-resource pairs that trophic interactions between them are never observed.

Plants, or other producers, can be included in the formalism in several ways. One is to distinguish formally between producers and consumers, and admit producers only in the roles of resources but not as consumers (e.g., Yoshida, 2003). Another is to avoid a formal distinction between producers and consumers by stretching the idea of small $a_{rc} > 0$ even further; at the same time admitting borderline cases such as parasitic or carnivorous plants in a natural way. The formulation here is following the second approach.

We denote by $\mathbf{t}_i$ the m-dimensional vector of numerical values of phenotypic traits characterizing species i. We conceive of the trait vectors $\mathbf{t}_i$ as being high-dimensional, providing a nearly complete characterization of the average phenotype of a species.

Not all phenotypic trait values or combinations thereof are physiologically sustainable and anatomically or ecologically feasible. That is, there are (hypothetical) combinations of phenotypic traits for which it is impossible for a species to sustain its population even when sufficient resources are available and no competitors or natural enemies are present. We assume that the sustainable region of phenotypic trait space is bounded, i.e., there is a $t_{\max}$ such that all trait vectors $\mathbf{t}$ with $|\mathbf{t}| > t_{\max}$ are unsustainable. Satisfying this assumption might require a suitable nonlinear transformation of trait vectors (e.g., by taking logarithms, reciprocal values, etc.).

We now examine the dependence of $\ln a_{rc}$ on the traits of an arbitrary resource species r and an arbitrary consumer species c. The indices r and c are suppressed where the dependence on r and/or c is clear from the context. We denote by $\mathbf{v}$ the $2m$-dimensional vector obtained by concatenating the trait vectors $\mathbf{t}_r$ and $\mathbf{t}_c$, that is,

$$\mathbf{v} = \begin{pmatrix} \mathbf{t_r} \\ \mathbf{t_c} \end{pmatrix}. \tag{2}$$

The vector $\mathbf{v}$ therefore characterizes a consumer-resource pair.

By definition, the interaction strength a_{rc} is a function of $\mathbf{v}$ alone. A general functional form describing this relationship needs to respect several considerations. First, food-web dynamics are most affected by resource-consumer pairs (trophic links) with large interaction strengths. The description of a_{rc} should therefore be able to accurately model $\ln a_{rc}$ where it is large, that is, near its maximum; for values of $\mathbf{v}$ where a_{rc} is close to zero, less accuracy in $\ln a_{rc}$ is required. Second, to admit a mathematical analysis, the functional form should not be overly complex. Third, it should be possible to describe all qualitatively
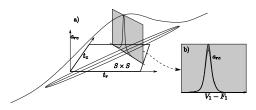
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Figure 1: Schematic illustration of the projection technique used for the dimensional reduction of niche space, for the case that the phenotypic single-species trait space is one-dimensional ($m = 1$). The corresponding single trait might, for example, characterize the preferred habitat. The sustainable range is some interval S on this niche axis. (a) All sustainable values of $\mathbf{v} = (t_r \; t_c)^{\mathrm{T}}$ are located within a square $S \times S$. The ellipsis in the t_r-t_c-plane indicates the range where the interaction strength a_{rc} attains sizable values. Along the short axis of this ellipse a_{rc} varies considerably within $S \times S$, while along its long axis this variation is small. (b) The projection of $\mathbf{v}$ onto the short axis (parametrized by the match between trophic traits, $V_1 - F_1$) is therefore sufficient for an approximate determination of a_{rc}. Since the starting point is here already a one-dimensional niche space, the projection does not lead to the dimensional reduction realized in cases with larger m, which are more difficult to visualize.

different ways in which interaction strengths may depend on a phenotypic trait: it may increase or decrease steadily and thus reach its maximum at the edge of the sustainable region of trait space, or is may exhibit a minimum or maximum somewhere within this range. The quadratic polynomial

$$\ln a_{rc} = \ln a_0 + \mathbf{b}^{\mathrm{T}} \mathbf{v} + \frac{1}{2} \mathbf{v}^{\mathrm{T}} C \mathbf{v} \tag{3}$$

is perhaps the simplest general functional form satisfying these criteria. In this expression, a_0 is a positive scalar, $\mathbf{b}$ is a vector of length $2m$, and C is a symmetric $2m \times 2m$ matrix. We stress that Eq. (3) should not generally be interpreted as an expansion of $\ln a_{rc}$ around $\mathbf{v} = 0$ or at the point at which interaction strength attains its maximum (which might be outside the sustainable region of trait space). Rather, the quadratic polynomial is chosen so as to best approximate a_{rc} across the sustainable region. A judicious parametrization of phenotypic traits in $\mathbf{t}$ can improve the accuracy of this representation; we will come back to this point in Discussion.

Eq. (3) determines the interaction strength between any two species r and c with trait vectors t_r and t_c: therefore, the values a_0, $\mathbf{b}$, and C characterize an entire community, rather than just one specific species pair. Notice that, while our framework allows for cross-feeding between any pair of species, a_{rc} will often be significant in one direction and negligible in the other. In Appendix A we propose a specific scheme for estimating $\mathbf{b}$ and C in Eq. (3) from empirical data on interaction strengths (e.g., records of observed interactions) and phenotypic traits. It is thus possible to evaluate for any particular empirical application whether Eq. (3) provides an adequate representation. Enabling such direct empirical verification, our theory goes beyond many other theoretical approaches to describing the dependence of trophic interaction strength on phenotypic traits.

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2.2 Dependence of interaction strengths on trophic traits

Starting from the general representation of the dependence of trophic interaction strength on the phenotypic traits of consumer-resource pairs in the form of Eq. (3), we derive in Appendix B the approximation

$$a_{rc} = a_1 \exp\left[V^* + F^* + \frac{1}{2}\sum_{i=1}^{n}\lambda_i(V_i - F_i)^2\right],\tag{4}$$

with constants n, a_1, and λ_i $(i = 1, ..., n)$. The *vulnerability traits* V^* and V_i depend only on the phenotypic traits of the resource r while the *foraging traits* F^* and F_i depend only on the phenotypic traits of the consumer c. Vulnerability and foraging traits together define a species' trophic traits, since they alone suffice to determine, in this approximation, the strength of trophic interactions. Eq. (4) is obtained by a truncation of the hierarchy of eigenvectors of the matrix C, retaining only the eigenvectors with the n dominating eigenvalues. (Since C is symmetric, all its eigenvalues are real.) The choice of n depends on the structure of the eigenvalue spectrum of C and the desired accuracy. Technically, this approximation is similar to a principle component analysis.

The trophic traits V_i and F_i for $i = 1, \ldots, n$ are obtained as projections of the phenotypic trait vectors $\mathbf{t}$ onto the trophically most relevant axes of trait space. The main idea is illustrated in Fig. 1; details are provided in Appendix B. The trophic baseline traits V^* and F^* describe the interaction strength $a_1 \exp(V^* + F^*)$ that results when all vulnerability traits and foraging traits are matched, $V_i = F_i$ for $i = 1, ..., n$. Strong contributions to F^* come from phenotypic traits of c for which all quadratic effects are relatively small, since these traits always facilitate or hinder foraging. Likewise, strong contributions to V^* come from phenotypic traits of r for which all quadratic effects are relatively small, since these traits always increase or decrease defense against foraging. Examples are, respectively, the maximum speed of locomotion or the armor strength of resources. Increasing the former strengthens the interaction between r and c by enhancing F^*, while increasing the latter weakens this interaction by reducing V^*.

The sum of quadratic terms in Eq. (4) formalizes the idea that trophic interactions are determined by matches between trophic traits of consumers and resources in a shared trophic niche space. Specifically, when all λ_i $(i = 1, \ldots, n)$ are negative, trophic interactions are strongest when the consumer has foraging traits F_i that equal the corresponding vulnerability traits V_i of the resource. As an illustration, consider the color F_i at which a consumer's eyes are maximally sensitive in relation with the dominant color V_i of a resource's body. Positive values λ_i may be less likely to occur in natural systems. They imply that the trophic interaction is weakest for a particular match of consumer and resource traits, and thus correspond to defense strategies specialized to particular kinds of consumers. Conceivable cases of this type would be camouflages that are efficient only when viewed at a particular distance or from a particular angle, as defenses against consumers searching for prey from particular heights or positions.

In comparison with Eq. (3), Eq. (4) affords a substantial reduction of ecological complexity when the number $2n + 2$ of trophic traits is much smaller than the number $2m$ of phenotypic traits, that is, when $n \ll m$. Two reasons

suggest that this relation is widely fulfilled in natural systems. First, the trophic effects of many phenotypic traits are negligible, and second, the trophic effects of groups of other phenotypic traits are similar and they can to good accuracy be summed up in single trophic trait variables. Whether $n \ll m$ indeed holds for a particular natural system and for a particular set of phenotypic traits is an empirical question. Our theory allows answering this question in two steps: by identifying the most suitable trophic traits as described in Appendix B and by confirming that Eq. (4) achieves a satisfactory degree of accuracy across the sustainable region of trophic niche space.

The trophic traits V^*, F^*, V_i, F_i of a species are derived from its phenotypic trait vector and determine its place in a $(2n+2)$-dimensional space. As explained above, the trophic baseline traits V^* and F^* only determine a species' overall vulnerability and foraging capacity, and hence are not involved in the assessment of species interactions in terms of trait matches. For the latter purpose, we can represent each possible species by a point (V, F) in the $2n$-dimensional space spanned by the coordinates V_i and F_i. Hutchinson's 1957 ecological niche space may either be conceived as identical with the traits space encompassing all conceivable trait vectors $\mathbf{t}$, or as its restriction to the traits or trait combinations that are ecologically relevant. In either case, this ecologically niche space will generally be larger than the $2n$-dimensional space spanned by V_i and F_i, since some phenotypic traits have non-trophic ecological implications. The $2n$-dimensional space spanned by V_i and F_i is therefore a sub-space of the ecological niche space. However, Eq. (4) shows that a different but equivalent representation may be more illuminating: each species can be represented by two points V and F in an n-dimensional space, with coordinates V_i and F_i, respectively. This space is the community's trophic niche space: while V determines a species' niche in its role as resource, F determines its niche in its role as consumer, and the vicinity of V and F for species pairs determines their trophic interactions. Independent of whether n is large or small it can be interpreted as the number of dimensions of trophic niche space. Applying our framework, the old problem of determining the dimensionality of trophic niche space (Cohen, 1977) is therefore reduced to the much more practical task of estimating from empirical data the quadratic polynomial (3).

While there is no general guarantee that the dependence of trophic traits on phenotypic traits is such that all trophic traits can be chosen independently for a given species, this becomes likely when $n \ll m$: With many potentially relevant phenotypic traits, those determining foraging capacities are likely to be different from those determining vulnerabilities. Largely independent foraging and vulnerability traits may indeed be required to understand the observed differences between the rates at which species evolve in their roles as resources and as consumers (Rossberg et al, 2006a; Bersier and Kehrli, 2008). Naturally, one must expects some phenotypic traits to strongly affect both foraging and vulnerability of species. Examples are body size or the preferred height above or depth below ground. In general, however, such phenotypic traits will determine the values of trophic traits only in combination with other phenotypic traits. Consider, for example, the predator-prey body-mass ratio PPMR, that is, the difference between logarithmic body masses of consumers and their resources $\log M_c - \log M_r$, which has been shown to be a good predictor of trophic interactions (Brose et al, 2006). While trophic interactions are generally more likely to occur within a certain intermediate range of the PPMR (Otto et al, 2007;

Troost et al, 2008), the prey-size preference of a predator is not determined by its body size alone (Jennings et al, 2002), but also depends on its mode of foraging, the shape of its ingestive organ, and many other characteristics. Usually, the corresponding term in Eq. (4) will therefore not describe a simple size matching based on $V_i = \log M_r$ and $F_i = \log M_c - D$ for some constant D, but other phenotypic traits will enter F_i and V_i, leading to numerically independent values of F_i and V_i for a given species. In short, since foraging and vulnerability traits are derived as linear combinations of very many phenotypic traits, functional dependencies between trophic traits are likely to be rare.

3 Comparison with other approaches

Here we briefly review five alternative approaches from the literature for determining trophic interaction strengths from traits, and show how our synthetic framework enables interpreting these formally different approaches in a unified fashion. Reformulating the existing approaches in this manner draws attention to some special assumptions that might be difficult to motivate from the vantage point of our more general framework. This raises the question how these assumptions affect the community-level structure and dynamics of the resulting model food webs.

The Webworld model refers to a family of models initially introduced by Caldarelli et al (1998), which has been developed further in the works of Drossel et al (2001), Lugo and McKane (2008), and many others. Each species is characterized by a set of L realized categorical characters picked from a larger set of K possible categorical characters: the L traits are assigned the value 1, while the remaining $K - L$ traits are assigned the value 0. In the framework developed above, $\mathbf{t} \in \{0, 1\}^K$ with the sustainable region of trait space given by $|\mathbf{t}|^2 = L$. Link strengths are determined according to $a_{rc} = \max(0, \mathbf{t}_r^{\mathrm{T}} W \mathbf{t}_c)$, where W is a zero-mean, antisymmetric random matrix. Apart from replacing the maximum function by an exponential, this is equivalent to Eq. (3) with $a_0 = 1$, $\mathbf{b} = 0$, and C having a block structure

$$C = \begin{pmatrix} 0 & W \\ W^{\mathrm{T}} & 0 \end{pmatrix}. \tag{5}$$

With the prescription for W by Drossel et al (2001), and also with the variants proposed by Lugo and McKane (2008), one finds numerically, quite independent of the details, that (i) eigenvalues always come in quadruples (with each eigenvalue λ having a multiplicity two and being accompanied by the eigenvalue $-\lambda$ also of multiplicity two) and (ii) otherwise eigenvalues are spread fairly evenly across a range from $-\lambda_{\max}$ to $\lambda_{\max}$. Hence, in this model, no efficient dimensional reduction with $n \ll m$ is possible. As a result, a species' foraging and vulnerability traits are not independent, which might impose constraints on the food-web topologies derived from this model.

Yoshida (2003) employed a hybrid model involving both the autonomous evolution of trophic links and the evolution of trophic traits determining trophic links. The strength of trophic links was determined in two steps. First, trophic traits determine the probability for establishing a trophic link. Second, if established, a link's strength is independently drawn at random. Here we only consider the first step, interpreting the linking probability as a trait-mediated

interaction strength. In Yoshida's model, species are, among others, characterized by ten vulnerability traits and, independently, by ten corresponding foraging traits, all chosen from within a hypercube. The probability of establishing a link between a consumer and a resource is given by the fraction of the consumer's foraging traits that differ from the resource's corresponding vulnerability traits by less than a certain niche width w. A similar form can be obtained by setting $V^* = F^* = 0$, and $\lambda_i = -w^{-2}$ (for all i) in Eq. (4), which yields

$$a_{rc} = a_1 \exp\left[-\frac{1}{2w^2} \sum_{i=1}^{n} (V_i - F_i)^2\right]. \qquad (6)$$

In both cases, all directions of trophic niche-space are treated equally, and the interaction strength (or probability) is a function of the differences between vulnerability and foraging traits only. However, while the contours of the matching kernel in Eq. (6) are simple hypersphere, they are more complex in the model of Yoshida: specifically, the linking probability is elevated around ten hyperplanes normal to the niche axes, more elevated along the pairwise intersections of these hyperplanes and even further elevated along higher-order intersections. While such a specific structure would be difficult to motivate within the general framework introduced above, Yoshida's model did inspire the choice of a functional form for the interaction strength very similar to Eq. (6) in the population-dynamical matching model (Rossberg et al, 2008).

In a model developed by Loeuille and Loreau (2005), trophic interactions between a consumer and a resource are determined by their body masses M_c and M_r alone. The defining equation is a special case of Eq. (4), with $V^*, F^* = 0$, $n = 1$, $\lambda_1 < 0$, $V_1 = M_r$, and $F_1 = M_c - d_1$, where $d_1 > 0$ is the body-mass difference that allows predators to consumer their prey most efficiently. In addition, the matching kernel is truncated above $M_r \geq M_c$. A representation of trophic traits in terms of logarithmic masses (e.g., $V_1 = \ln M_r$, $F_1 = \ln M_c - d_1$) might have been more appropriate, because it leads to preferred mass ratios (e.g., $M_c/M_r = \exp d_1$), which is more in line with observations (Warren and Lawton, 1987; Warren, 1989; Cohen et al, 1993; Memmott et al, 2000; Brose et al, 2006) than preferred mass differences.

A simple, more general model for food-webs based on a one-dimensional niche space can be constructed by associating each species with four quantitative characters t_1, ..., t_4, setting $V_1 = t_1$, $F_1 = t_2$, $V^* = t_3$, and $F^* = t_4$, and choosing parameters in Eq. (4) such that

$$\ln a_{rc} = V^* + F^* - (V_1 - F_1)^2. \qquad (7)$$

The classical niche model for describing food-web topology (Williams and Martinez, 2000) naturally arises from Eq. (7) by focusing on the special case $V^* = t_3 = 0$, choosing triplets (t_1, t_2, t_4) independently for each species from a distribution particular to this model (see Williams and Martinez, 2000), and considering a trophic link as present whenever $\ln a_{rc} > 0$. A consumer's "niche center" is then controlled by F_1, and the "niche width" by F^*, which implies that, in this model, a consumer's trophic generality is positively correlated with its maximum link strength.

One can also consider the other extreme, by examining food-web topologies determined by a large number of independent traits. The matching model (Ross-

berg et al, 2006a) represents this approach. Trait matching as implemented in this model can be reproduced by an interaction strength as in Eq. (6) with large n, if one restricts admissible trait values to the alternatives $V_i = \pm c_1$ and $F_i = \pm c_2$ with constants c_1 and c_2. The value of $\ln a_{rc}$ is then fully determined by the number of cases for which the signs of $V_i = \pm c_1$ and $F_i = \pm c_2$ are matched. When considering a trophic link as present when $\ln a_{rc}$, and therefore the number of trait matches, exceeds a given threshold, a food-web topology is obtained. In the matching model, however, a second condition needs to be satisfied for establishing trophic links: the mean body mass of a consumer species cannot be smaller than a certain fraction of that of its resource species. With this unrealistically sharp threshold for the predator-prey mass ratio, it is difficult to combine the two conditions the matching model uses for establishing links into a thresholded interaction strength of the general form defined by Eq. (4). It would be interesting to check whether the good fit of the matching model with empirical data can be reproduced when recasting the matching model in such a generalized form.

4   Discussion

The past two decades have seen a growing interest in food-web modeling and there is now a substantial number of models aimed at reproducing the demographic and evolutionary dynamics of large ecological communities. These models have increased our understanding of macroecology and can potentially be used to address many questions related to the conservation and management of biodiversity and living resources. In practice, however, the application and wider acceptance of these models is restricted by a lack of understanding of their range of validity and their resultant limitations. Questions naturally arise as to whether such models offer sufficiently detailed representations of the complexity of real ecosystems. Here we have proposed a general framework for framing some of these questions in such a way as to make them accessible to direct empirical investigation.

The route from phenotypic traits to the expressions of interaction strength in terms of trophic traits necessarily involves some simplifying assumptions. In our framework, the most important of these is arguably that logarithmic interaction strength can be expressed as a quadratic polynomial in phenotypic traits (Eq. (3)). While this assumption may at first glace seem too restrictive, it should be kept in mind that the adequate choice and suitable nonlinear transformation of phenotypic traits can significantly improve the accuracy of this representation, allowing higher-order dependencies among the traits to be implicitly included. Consider, for example, a species that uses warning calls as a defense against predation. For these calls to be efficient, the species should not only show (1) a behaviour to emit warning calls in dangerous situations, but should also have (2) an audio-sensory apparatus to register them and (3) a behavioural repertoire to react appropriately. Thus, for warning calls to be efficient, at least three different kinds of traits $\tilde{t}_1$, $\tilde{t}_2$, $\tilde{t}_3$ must come together synergistically. In order to incorporate this into the quadratic form (3), one could, in the simplest case, transform the phenotypic traits by a nonlinear mapping B such that one component of $\mathbf{t} = B(\tilde{\mathbf{t}})$ equals $t_1 = \tilde{t}_1 \cdot \tilde{t}_2 \cdot \tilde{t}_3$, and two further components are chosen such as to make this transformation invertible

(up to a few singular points), e.g., by setting $t_2 = \tilde{t}_2$, $t_3 = \tilde{t}_3$. Further work might also extend the results presented here by expanding the representation of trophic interaction strength to third or higher order, or by making use of the mathematical concept of manifolds as non-linear generalizations of the linear sub-spaces of trait space we worked with.

Until now, no formal framework systematically related phenotypic traits to trophic traits. Consequently, evolutionary food-web models so far had to incorporate trophic traits in an *ad-hoc* manner. A major promise of the theory presented here is the unification of these disparate approaches within a synthetic framework, thus enabling comparisons and broadening the basis for scientific exchanges and discussions. We believe that models of interaction strength that can be derived from general, verifiable ecological considerations will make food-web models more reliable and conclusions drawn from them more trustworthy, thus strengthening the role that food-web research can play in ecology.

5 Acknowledgements

A Empirical determination of parameters relating phenotypic traits and interaction strength

In this appendix we shortly describe a procedure for estimating the pre-factor a_0, the vector $\mathbf{b}$ and the matrix C in the expression for the interaction strength Eq. (3), based on measured trait vectors t_i and in- teraction strengths $\hat{a}_{ij}$ for all pairs of species (i, j) in a community of N species.

Presumably the most laborious aspect of this procedure is the mea- surement of the empirical interaction strengths $\hat{a}_{ij}$. In principle it would be desirable to obtain these quantities from measured functional re- sponses. Due to practical constraints, one will often assume linear functional responses and, for each pair (i, j), estimate the interaction strength $\hat{a}_{ij}$ as the biomass flow density from species i to species j divided by the biomass densities of i and j (other curren- cies of flows and abundances can be used as well). A set of phenotypic traits, adequate for the community under consideration, has to be defined and the traits have to be measured for each species. One phenotypic trait vector t_i is obtained for each species i. Finding the parameters entering the expression for the interaction strength Eq. (3) might, at first sight, appear to be a general- ized linear regression problem. In practice, however, many empirical interaction

strengths will be zero, which requires ad hoc assumptions when go- ing over to the logarithmic scale. Ignoring these data points is not an option, since the fact that one species does not consume another is important ecological information. For these reasons, we propose using non-linear regression of a_{ij} directly to fit the parameters, i.e., choosing parameters in such as way that, in a well-defined sense, the residual errors

$$\epsilon_{ij} = \hat{a}_{ij} - a_0 \exp \mathbf{b} \begin{pmatrix} t_i \\ t_j \end{pmatrix} + \frac{1}{2} \begin{pmatrix} t_i \\ t_j \end{pmatrix}^{\mathrm{T}} C \begin{pmatrix} t_i \\ t_j \end{pmatrix} \tag{8}$$

are minimized. The standard assumption of independent, normally distributed errors suggests least-square fitting, i.e., a choice of a_0, $\mathbf{b}$, and C so that the sum $\sum_{i,j} \epsilon_{ij}^2$ is minimized. More complex error models lead to other criteria, e.g., via likelihood maximization, and might suggest weighting errors differently. However, it has to be kept in mind when solving this problem that the particular form we assumed for the de- pendence of interaction strength on phenotypic traits was motivated by qualitative considerations. One should therefore not generally expect more than a semi-quantitative approximation of the data by this expression. The residuals ϵ_{ij} thus combine contributions from measurement errors of the $\hat{a}_{ij}$ with approximation errors. Rather than weighting each data point (i,j) according to the accuracy of the measured interaction strength a_{ij} , we therefore recommend to weight the data more evenly. The total number of parameters to be fitted is $1 + 3m + 2m2$, where m is the number of traits considered. For $m = 10$, this corresponds to 231 parameters and the number of measured $\hat{a}_{ij}$ should be significantly larger than this. These data require- ments might first appear daunting. However, for most resource-consumer pairs (i,j) expert knowledge will be sufficient to exclude trophic interactions, and $\hat{a}_{ij}$ can then be set to zero without measurements. Expert knowledge will also be sufficient to exclude significant effects of certain phenotypic traits on either foraging or vulnerability. The corresponding entries in b and C can then be set to zero a priori, reducing the number of parameters to be estimated, and thus the demands on data. For the validation of our model of interaction strength we recommend, again keeping its semi-quantitative nature in mind, to inspect graphs relating measured interaction strengths to the predictions by our model with fitted parameters. Strong outliers that are not explained by measurement errors in $\hat{a}_{ij}$ do not necessarily show that the model is inappropriate, they could also indicate that important phenotypic traits have not been included in the analysis. Inspection of the underlying ecology and inclusion of the relevant phe- notypic traits should improve the correlation between measurements and model pre- diction. If the trophic niche space of a community is high-dimensional, that is, if the number of relevant trophic traits is large, the number of relevant phe- notypic traits must be large, too. It may then be difficult in practice to achieve good model fits, even when the underlying model is a good description. This sit- uation can be identified by verifying that (i) the correlation between predicted and measured interaction strength improves as the number m of phenotypic traits considered increases, even when carefully guarding against over-fitting and (ii) the dimensionality of trophic niche space continues to increase with m. When only enhanced correlations (i) are observed with increasing m, but not increased dimensionality (ii), this is a signature of a low-dimensional niche space with the few relevant trophic traits depending on a large number of phenotypic

traits. When the correlation between model and data does not improve with the number of traits considered, this indicates that the models given by Eq. (8) or, equivalently, by Eq. (3) may be inappropriate. The main assumption underlying our theory is thus open to empirical falsification.

B Identification of trophic traits

The following describes the detailed procedure for deriving Eq. (4) from Eq. (3).

By the spectral decomposition theorem, the symmetric matrix C can be represented as $C = \sum_i \mathbf{e}_i \lambda_i \mathbf{e}_i^{\mathrm{T}}$ in terms of an orthonormal set of $2m$ eigenvectors $\mathbf{e}_i$ and the corresponding real eigenvalues λ_i. Without loss of generality, we assume that the eigenvalues are sorted so that $|\lambda_1| \geq |\lambda_2| \geq ... \geq |\lambda_{2m}|$. Now, define for each $i = 1, ..., 2m$ partial eigenvectors $\mathbf{e}_i', \mathbf{e}_i'' \in R^m$ representing the components of $\mathbf{e}_i$ referring to resource and consumer, respectively, that is

$$\mathbf{e}_i = \begin{pmatrix} \mathbf{e}_i' \\ \mathbf{e}_i'' \end{pmatrix}. \tag{9}$$

The $2m$-dimensional vector $\mathbf{v}$ can now be represented as

$$\mathbf{v} = \sum_{i=1}^{2m} \mathbf{e}_i \left(\mathbf{e}_i^{\mathrm{T}} \mathbf{v} \right) = \sum_{i=1}^{2m} \mathbf{e}_i (V_i - G_i) \tag{10}$$

with vulnerability traits $V_1, ..., V_{2m}$ of r and corresponding (raw) foraging traits $G_1, ..., G_{2m}$ of c defined by

$$V_i := \mathbf{e}_i'^{\mathrm{T}} \mathbf{t}_r, \quad G_i := -\mathbf{e}_i''^{\mathrm{T}} \mathbf{t}_c. \tag{11}$$

Note that, since the $2m$ values V_i are determined by linear projections of the m components of $\mathbf{t}_r$, at most m values V_i are independent. Similarly, there are at least m linear relationships between the $2m$ values G_i.

Putting Eq. (10) into expression (3) for $\ln a_{rc}$ yields

$$\ln a_{rc} = \ln a_0 + \sum_{i=1}^{2m} \mathbf{b}^{\mathrm{T}} \mathbf{e}_i (V_i - G_i) + \frac{1}{2} \sum_{i=1}^{2m} \lambda_i (V_i - G_i)^2. \tag{12}$$

To simplify this expression, consider the last sum first. Note that the upper bound $|\mathbf{t}| < t_{\max}$ (see Sec. 2) implies an upper bound on $|V_i - G_i|$: With $|\mathbf{v}|^2 = |\mathbf{t}_r|^2 + |\mathbf{t}_c|^2 \leq 2t_{\max}^2$ one obtains

$$|V_i - G_i| = |\mathbf{e}_i^{\mathrm{T}} \mathbf{v}| \leq \sqrt{2}\, t_{\max}. \tag{13}$$

Dropping terms with small $|\lambda_i|$ from the second sum will therefore often yield good approximations for $\ln a_{rc}$.

Denote by n the number of terms in the sum that need to be retained to maintain a given level of model accuracy. Define the lumped linear traits (note the lower bounds of the sums) by

$$V^* := \sum_{i=n+1}^{2m} \mathbf{b}^{\mathrm{T}} \mathbf{e}_i V_i \quad \text{and} \quad F^* := -\sum_{i=n+1}^{2m} \mathbf{b}^{\mathrm{T}} \mathbf{e}_i G_i, \tag{14}$$

the offsets between matched vulnerability and raw foraging traits

$$d_i := \frac{\mathbf{b}^{\mathrm{T}} \mathbf{e}_i}{\lambda_i} \quad (i = 1, \ldots, n), \tag{15}$$

the (adjusted) foraging traits

$$F_i := G_i - d_i \quad (i = 1, \ldots, n), \tag{16}$$

and the scaling factor

$$a_1 = a_0 \cdot \exp\left(-\sum_{i=1}^{n} \lambda_i d_i^2 / 2\right). \tag{17}$$

Putting these definitions into Eq. (4), i.e.,

$$\ln a_{rc} = \ln a_1 + V^* + F^* + \frac{1}{2} \sum_{i=1}^{n} \lambda_i (V_i - F_i)^2,$$

it is readily verified that this is equivalent to Eq. (12) with the second sum truncated at $i = n$. As discussed in Sec. 2, chances are good that the first $2n$ values V_i and F_i $(i = 1, \ldots n)$ of a species are all numerically (but not necessarily statistically) independent from each other, even though this is certainly not the case for the original set of $2 \times 2m$ values V_i and G_i $(i = 1 \ldots, 2m)$ defined by Eq. (11).

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