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Disentangling nature, strength and stability issues in the characterization of population interactions

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ABSTRACT

Many recent reviews discuss the adequacy of definitions and metrics for the *strength* of population interactions. However, the discussion on the *beneficial* or *detrimental nature* of interactions is clearly absent, or at the most, inadvertently merged into the strength debate. This deficiency is emerging with the increasing interest in theoretical studies of interactions that shift in their *nature*; e.g. associations that present a mixture of mutualistic and antagonistic aspects, such as pollination; or species with changes in role, such as mutualistic ants that predate on aphid partners. By exploring these models, major controversies are revealed underlying some traditional perspectives: the original Levins' *community matrix* reformulated into *interaction* and *jacobian matrices*, that is, *interaction coefficients* reinterpreted as *partial derivatives*, fail to recognize the ecological context of interactions. The 'effect of one species on the other' is not necessarily quantified by 'the effect of varying species densities'; and shifts in the signs of jacobian elements do not correspond to shifts in types of interaction but to stability properties. Thus, the generalised use of these approaches must be revised. On the other hand, the comparison of ultimate performances of populations when growing alone or in association, here referred to as the *relative performance* approach, conceptually represents the original meaning of the *community matrix*. This conception, although measured at population levels, is a reflection of properties at the individual level. This article inspects and discusses the formalities and ecological contexts of these approaches to characterization by means of known population interaction models: linear and non-linear, variable and non-variable; aiming to disentangle crucial conceptions that are usually mingled in the literature: the *strength* (magnitude) and the *nature* (detrimental or beneficial) of the interaction, which are sometimes used interchangeably, and the *stability* properties of the system, which have been misleadingly associated with the latter.

1. Introduction

1.1. A variety of concepts and the necessity of clear definitions

The structure of a natural community is very much determined by the different types of interactions that occur among its populations; the dynamics of the community are thus significantly determined by the variations in these interactions. This has been the focal issue of numerous studies for years, mainly trying to understand patterns, within the theoretical and the empirical scopes. However, understanding requires, first, clear definitions, and then, clear purposes and ecological context.

When referring to *type of interaction* authors may be alluding to the concepts of *competition*, *mutualism*, *predation*; or rather to the *strength* or intensity of the effect of one species on another; or to whether the association is *beneficial* or *detrimental* for a species. Amazingly, some may be referring to all of them indistinctly. This is a first level of confusion: the vagueness.

In recent years, many reviews have discussed an appropriate way to define and measure the *strength* of population interactions. However, the discussion on the *nature* of the interaction, in the sense of being either detrimental or beneficial for each of the species involved, is clearly absent, or at the most inadvertently merged into the strength discussion. This issue is particularly relevant for those interactions whose outcome may vary along a continuum, as is the case in some mutualistic–antagonistic interactions, e.g. pollination; or the switch in role in some species, e.g. mutualistic ants predating on their aphid partners.

The *strength* of the interaction refers to the intensity of the effect of one species on the other; or its characterization within the continuum from weak to strong. We find a variety of criteria on this issue: Berlow et al. (1999) open their thorough theoretical–empirical analysis on species interactions with the general definition of strength as 'the magnitude of the effect of

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one species on the abundance of another', to ultimately establish that the different indices, experimental protocols and models that exist for measuring and representing this magnitude may yield quite different outcomes. Equally exhaustive and compelling are the reviews by Abrams (2001), Chase et al. (2002), Kokkoris et al. (2002), Berlow et al. (2004) and Wootton and Emmerson (2005) regarding this challenging topic; they all agree on the necessity of clear definitions and clear ecological purposes. However, most of these works on population interactions, although being generic in the kinds of indices reported, focus their analysis on a particular kind of interaction, or on one trophic level. For instance, Kokkoris et al. (2002) and Christianou and Kokkoris (2008) deal with competition, whereas Laska and Wootton (1998), Berlow et al. (1999, 2004) and Abrams (2001) deal with predator–prey interactions. Therefore, a proper definition or discussion on the nature of the interaction is not an issue; in these works the model already explicitly represents a particular type of interaction.

On the other hand, in the literature we find that interactions are reported as mutualistic, competitive, predator–prey, among others; yet the precise definition for each type varies among authors. An apparently general consensus, however, indicates that the type of interaction between two populations is defined in terms of the beneficial or detrimental nature of the association for each species. The confusion arises when this nature needs to be measured. *What* do we measure? *When* do we measure? An association might be beneficial for the survivorship of the individuals of a species, or enhance the partner's population growth rate or its equilibrium density, but simultaneously carry detrimental effects on other components like size, developmental rate, etc. (see e.g. May, 1973, 1981; Addicott, 1984; Abrams, 1987; Thompson, 1988; Murray, 1989). Some authors consider the long-term response of partners in the interaction to each other's presence (e.g. van Baalen and Jansen, 2001; de Mazancourt et al., 2005), which gives rise to yet different definitions based on evolutionary considerations. Sometimes we find that the terms *strength* and *type* of interaction are used interchangeably (e.g. Neill, 1974; Bender et al., 1984; Adler and Morris, 1994; Laska and Wootton, 1998; McPeek and Peckarsky, 1998).

Variations in the *strength* of the interaction may involve also variations in the *nature* of the interaction itself. When the strength of the interaction is the result of the costs and benefits involved in the association—which may depend, for instance, on species abundances or ecological settings—the net outcome, or type, of the interaction may vary along a continuum of positive to negative values. This occurs, for instance, in some associations classically considered as mutualisms such as ants and homopterans, or epibionts and hosts in aquatic environments, or pollinators and plants, among many others (see e.g. Addicott, 1979; Cushman and Addicott, 1991; Bronstein, 1994; Wahl and Hay, 1995; Addicott and Bao, 1999). The increasing attention to the study of mutualistic and variable population interactions in general denotes that the static perception of population interactions is taking a turn. This is leading to a more complete comprehension of the whole picture and of the complexity of ways in which individuals from different populations may interact (deeper discussion on this issue in Thompson, 1988; mathematical approach in Hernandez, 1998; Hochberg et al., 2000; Hernandez and Barradas, 2003; Zhang, 2003; Neuhauser and Fargione, 2004).

1.2. Quantifying: indices… help or mingle?

The second level of confusion: What, when, how do we measure?

Levins (1968) defined the *community matrix* to describe interactions between populations. No formal mathematics is involved, just interaction coefficients taken out from a Lotka–Volterra system. The elements a_{ij} of the matrix are 'competition coefficients', or 'predator–prey pairs a_{ij} and a_{ji}, if they have opposite sign'. May's (1973) formulation extends the *community matrix* to 'an entity which, on the one hand, summarizes the biology of the community of interacting species near equilibrium and, on the other hand, has mathematical properties which describes the system's stability'. The sign structure of this matrix is directly tied to the classification of mutualism (+ +), competition (− −), predator–prey (+ −), etc.; its eigenvalues describe the stability properties of the system at equilibrium.

Since then, the usage of this concept, and especially its usage as an index, has varied among authors. Two very similar but subtly different conceptions of community matrix are on the table. Authors just choose one for their work; or use both with alternative names such as *interaction matrix*—to describe types of interaction, or *jacobian matrix*—for stability analysis. However, the original meaning and purpose of the concept has wandered away, leading to confusion.

Although all the reviews cited above agree on the necessity of a clear definition of interaction strength, they mostly start at a point that already includes a misleading conception: a sort of taken-for-granted transitivity in the usage of *community matrix, interaction matrix* and *jacobian matrix*; which is true only for particular cases. This is unravelled only when the nature of the interaction is taken into account, which in turn comes into light when those interactions whose nature can switch between detrimental and beneficial are taken into account.

Hence, it is essential to disentangle not only these conceptions surrounding the classical community matrix definition, but yet another commonly used view that I want to bring into the discussion. This is the notion that an association is considered beneficial if the population reaches higher equilibrium densities than it does when growing alone, detrimental if these are lower. All these conceptions study effects that act on properties at the individual level but that have a reflection at the population level.

There is no doubt that the lack of a global agreement on these issues represents a problem for the analysis of the dynamics of interacting populations, conveys errors in the interpretation of results and hinders the possibility of adequate comparisons among outcomes from different papers. Both theoretical and empirical approaches demand accurate and specific definitions on the concept and meaning of population interactions, but when trying to find a proper frame for characterization we face a problem that embodies subtleties from too many angles. In this paper I focus the discussion on specific theoretical approaches to the definition of population interactions, aiming to: properly distinguish between *nature* and *strength* of interactions, examine the appropriateness of the parameters used to measure them, and include variable interactions in the whole picture, that is, consider those cases in which the nature of the interaction itself is dynamic. The crucial ultimate issue is the necessary consistency between the mathematical and the ecological contexts.

2. Approaches to defining type of interaction

The dynamics of two interacting populations with densities N_1 and N_2 can be modelled by the system

$$\frac{dN_1}{dt} = F_1(N_1, N_2) \equiv N_1 f_1(N_1, N_2)$$

$$\frac{dN_2}{dt} = F_2(N_1, N_2) \equiv N_2 f_2(N_1, N_2) \qquad (1)$$

where F_i is the total population growth rate of species i and f_i the *per capita* growth rate, as a function of population abundances.