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Bridging parametric and nonparametric measures of species interactions

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Abstract

A central theme in ecological research is to understand how species interactions contribute to community dynamics. Indeed, species interactions are the basis of parametric (model-driven) and nonparametric (model-free) approaches in theoretical and empirical work. However, despite their different interpretation across these approaches, these measures have occasionally been used interchangeably, limiting our opportunity to use their differences to gain new insights about ecological systems. Here, we revisit two of the most used measures across these approaches: species interactions measured as *constant direct* effects (typically used in parametric approaches) and *local aggregated* effects (typically used in nonparametric approaches). We study these measures of species interactions under three categories: intra-specific, interspecific, and higher-order interactions. We show that these measures can be linked if and only if all species interactions are pairwise, demonstrate fundamental differences between inter and intra-specific interactions, and illustrate how and when these measures can be combined to gain further insights about non-equilibrium ecological dynamics and higher-order interactions.

Key-words: Higher-order Interactions, Interaction Matrix, Jacobian Matrix, Model-driven, Model-free, Non-equilibrium Dynamics

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Introduction

Theoretical and community ecology build upon the idea that species interact either directly or indirectly with other species (Abrams, 1987; Thompson, 2005; Morin, 2009; Vellend, 2016). Indeed, a central theme in ecological research is to understand how species interactions contribute to community dynamics (May, 1972; Pimm, 1982; Allesina & Tang, 2012; Fukami, 2015; Saavedra et al., 2017; Chesson, 2018). Even macro-ecological studies that do not explicitly model species interactions are built upon the idea of an existing balance among species interactions (Hubbell, 2005; Harte, 2011; Staniczenko et al., 2017). Thus, ever since Odum (Odum & Barrett, 2005), most ecologists classify species interactions not by their mechanisms, but according to the effects produced on the growth rate of populations (see Abrams 1987 for an extended discussion on this topic). Yet, this simple definition has different measures and interpretations across theoretical and empirical studies (Case, 2000), making necessary to understand how and when these measures can be linked.

In empirical and theoretical research, the effect of species interactions has been measured following parametric (model-driven) and nonparametric (model-free) approaches (Sugihara, 1994; Turchin, 2003). Typically, the parametric approach measures species interactions as *constant direct* effects, while the nonparametric approach measures them as *local aggregated* effects (Breiman et al., 2001). Both measures have their own strengths and weaknesses: Within parametric approaches, measures have a mechanistic or phenomenological interpretation of a direct effect between species, but the magnitude and dimension of such parametric measures are model-dependent (Cenci & Saavedra, 2018a; AlAdwani & Saavedra, 2019; Letten & Stouffer, 2019). Instead, within the nonparametric approach, measures can be estimated directly from data, but they are often hard to be biologically interpreted (Sugihara & May, 1990; Cenci et al., 2019). Additionally, regardless of the specific methods, the two approaches hold different conceptualizations about how species interactions can be decomposed: Within the parametric approach, measures can be decomposed into intra-specific (the effect of a species on itself), interspecific (the effect of a species on another), and higher-order interactions (the effect of two or more species on another). In contrast, within the nonparametric approach, measures can only be decomposed into intra-specific and interspecific interactions (Deyle et al., 2016; Ushio et al., 2018; Cenci & Saavedra, 2018b). Yet, it is unclear whether and how the decomposition of a species interaction can be bridged, and whether this bridge can provide new insights about ecological dynamics.

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Importantly, the subtle but central differences in the measure of species interactions between these two approaches have sometimes been a cause of confusion in the literature (Lawlor, 1980; Abrams, 1981). Take the complexity-stability debate as an example, one of the most controversial topics in theoretical and community ecology (May, 1972; McCann, 2000; Ives & Carpenter, 2007; Landi et al., 2018). As it has been shown (Logofet, 2005), much of the debate has been generated by aiming to generalize ecological dynamics and species interactions under a nonparametric approach. However, the merger between parametric and nonparametric approaches to species interactions in such context is only possible under the (often implicitly) assumption of a Lotka-Volterra model and equal equilibrium states for all species (Haydon, 1994; Novak et al., 2016; Vázquez et al., 2007). Thus, moving beyond these assumptions, it is pivotal to understand the different measures of species interactions and their transferability between the two approaches.

Here, we revisit two of the most used measures of species interactions across the parametric and nonparametric approaches. We study species interactions under three categories: intra-specific, interspecific, and higher-order interactions. In the reminder, we begin by presenting a brief summary of how species interactions are typically measured within each approach. Then, we show that these measures can be linked if and only if all species interactions are pairwise (i.e., no higher-order interactions present) regardless of the dynamics assumed. Next, we demonstrate that interspecific interactions are more transferable across measures than intra-specific interactions. Finally, we discuss how and when these measures can be combined to gain further insights about non-equilibrium ecological dynamics and higher-order interactions.

Two different approaches, two different measures

Parametric approach: constant direct effects

Typically, the parametric approach measures species interactions as constant direct effects (mechanistic or phenomenological) between species (Case, 2000; Song et al., 2020), and completely relies on knowledge about the governing population dynamics (Box 1 Eqn. 1). The pairwise formalism of population dynamics (Box 1 Eqn. 3) has been the basis of this approach. The matrix $\mathbf{A} = \{a_{ij}\}$ is called the *interaction matrix*, encoding the strength of pairwise, constant, direct effects (note these effects can be non-additive (Billick & Case, 1994)). Despite the diversity of population dynamics models (i.e., the form of functional responses), the sign pattern of the interaction matrix $\mathbf{A}$ is usually fixed and interpreted as the type of pairwise direct effect, such as: mutualism, competition, predation, or null (Abrams, 1987; Callaway et al., 2002; Chamberlain

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et al., 2014; Song et al., 2020). Note that an alternative measure of the parametric pairwise interaction strength is $\frac{\partial f_i}{\partial N_j}$ (Carrara et al., 2015; Xiao et al., 2017), biologically interpreted as the change in the per capita growth rate of species i under a small change in density of species j. However, this measure has received less attention as it is more difficult to estimate given its time-varying and model-sensitive properties.

Box 1: Parametric Approach: population dynamics models

Generally, the population dynamics of S interacting species have been described either as continuous ordinary differential equations (Case, 2000),

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i f_i(N_1, \ldots, N_S), \tag{1}$$

or discrete difference equations

$$N_{i+1} = N_i f_i(N_1, \ldots, N_S), \tag{2}$$

where N_i is the abundance (or biomass) of species i, and f_i is the per capita growth rate of species i. Note that the term $N_i(t)$ on the right-hand side of both equations has been imposed to prohibit reaching negative abundances (Strogatz, 2014). Because the parametric and nonparametric approaches have similar treatments to continuous or discrete dynamics, our discussion is exclusively focused on continuous dynamics.

Pairwise formalism: Assuming all direct effects to be pairwise (Lotka, 1926; Volterra, 1926), the general population dynamics (Eqn. 1) can be written as

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i(\underbrace{r_i}_{\text{intrinsic growth}} + \underbrace{a_{ii}s_i(N_i)}_{\text{intra-specific}} + \underbrace{\sum_{j\neq i} a_{ij}g_{ij}(N_i, N_j)}_{\text{interspecific}}), \tag{3}$$

where r_i represents the intrinsic growth rate of species i (no density dependency), a_{ij} represents the constant, direct, intra- (if $i = j$) and interspecific effect (if $i \neq j$), and $s_i(N_i)$ and $g_{ij}(N_i, N_j)$ represent the functional form of the intra- and interspecific direct effects, respectively. Note that the constant, direct effects a_{ij} can be the result of indirect mechanisms depending on the level of resolution of the model (MacArthur & Levins, 1967; Abrams, 1987). Additionally, the functional forms are not restricted to be linear and can incorporate non-additive effects (Billick & Case, 1994; Letten & Stouffer, 2019; Tilman, 1982). Yet, a general constraint on $g_{ij}(N_i, N_j)$ is that $\frac{\partial g_{ij}(N_i,N_j)}{\partial N_j}$ has to be positive (i.e., the larger the abundance, the larger the effect). The classic example of Eqn. (3) is the Lotka-Voletrra dynamics (Lotka, 1926; Volterra, 1926), where $s_i(N_i) = N_i$, and $g_{ij}(N_i, N_j) = N_j$.

Higher-order formalism: Assuming higher-order effects as the direct effects among more than two species (Billick & Case, 1994; Kleinhesselink et al., 2019), the general population dynamics (Eqn. 1) can be rewritten as

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i(\overbrace{r_i}^{\text{intrinsic growth}} + \underbrace{a_{ii}s_i(N_i)}_{\text{intra-specific}} + \overbrace{\sum_{j\neq i} a_{ij}g_{ij}(N_i, N_j)}^{\text{inter-specific}} + \underbrace{\sum_{j\neq k; j,k\neq i} b_{ijk}h_{ijk}(N_i, N_j, N_k) + \cdots}_{\text{higher order}}), \tag{4}$$

where b_{ijk} represents the constant, direct, triple-wise effect(O'Dwyer, 2018; Letten & Stouffer, 2019), and $h_{ijk}(N_i, N_j, N_k)$ represents the functional form of the triple-wise direct effect among species i, j, and k. Other higher-order direct effects (such as quadruple-wise effect) can be similarly defined (but see AlAdwani & Saavedra 2019).

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While the pairwise formalism ignores higher-order direct effects, the parametric approach can also be applied to a higher-order formalism of the general population dynamics (Box 1 Eqn. 4). In this other formalism, higher-order effects correspond to direct effects among more than two species (which is fundamentally different from other definitions such as indirect effects or non-additive effects, see Billick & Case 1994). For example, b_{ijk} (see Box 1) corresponds to the constant change in the per capita growth rate of species i under a small change in density of species j and k. The parametric approach, regardless of the specific formalism, can be applied under the assumptions of equilibrium and non-equilibrium dynamics (Case, 2000).

Nonparametric approach: local aggregated effects

Typically, the nonparametric approach measures species interactions as the local (state-dependent) aggregated (direct and indirect) effects between two species. Different from the parametric approach, the nonparametric one does not assume any particular governing population dynamics (Sugihara & May, 1990; Ye et al., 2015). Because the local aggregated effect counts all the pathways (including indirect or higher-order effects) at a given point in time, it can only be defined pairwise (Deyle et al., 2016; Ushio et al., 2018; Cenci & Saavedra, 2018b). That is, the nonparametric pairwise interaction between two species is measured as the change in the growth rate of species i under a small change in density of species j. Formally, this can be written as

$$J_{ij} = \frac{\partial dN_i(t)/dt}{\partial N_j} = N_i \frac{\partial f_i}{\partial N_j} + \delta_{ij} f_i, \tag{5}$$

where the Kronecker delta δ_{ij} is 1 if $i = j$, 0 otherwise. The matrix $\mathbf{J} = \{J_{ij}\}$ is called the *Jacobian matrix*. Similarly, this approach can be applied to both equilibrium (May, 1972; Allesina & Tang, 2012) and non-equilibrium dynamics (Sugihara, 1994; Ushio et al., 2018; Cenci & Saavedra, 2019). Note that under equilibrium dynamics, the Jacobian matrix has also been called the *community matrix* (Levins, 1968; May, 1972; Case, 2000).

The translucent mirror between measures

Intra-specific interactions

Under the parametric approach, a negative, constant, direct, intra-specific effect a_{ii} is often considered as *self-regulation* or *intra-specific density dependence* (Case, 2000). However, under the nonparametric approach, the interpretation of the local aggregated intra-specific term J_{ii} is

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more complex. For example, following the general parametric formalism defined in Eqn. (4), the elements of the Jacobian matrix are defined as

$$J_{ii} = r_i + a_{ii}(s_i + N_i\frac{\partial s_i}{\partial N_i}) + \sum_{j\neq i} a_{ij}(g_{ij} + N_i\frac{\partial g_{ij}}{\partial N_i}) + \sum_{j\neq k; j,k\neq i} b_{ijk}(h_{ijk} + N_i\frac{\partial h_{ijk}}{\partial N_i}) + \cdots \quad (6)$$

and when the system is at equilibrium, it reduces to

$$J^*_{ii} = a_{ii}N_i\frac{\partial s_{ii}}{\partial N_i} + \sum_{j\neq i} a_{ij}N_i\frac{\partial g_{ij}}{\partial N_i} + \sum_{j\neq k; j,k\neq i} b_{ijk}N_i\frac{\partial h_{ijk}}{\partial N_i} + \cdots . \quad (7)$$

Therefore, regardless of the presence of higher-order effects (whether b_{ijk} are all zeros) or the system is at the equilibrium ($\frac{\mathrm{d}N_i}{\mathrm{d}t} = 0$), the term J_{ii} measures the local aggregated effect across all the pathways under which species i can affect itself (not only the self-loop from i to i).

Hence, it is natural to ask what is the link between a_{ii} and J_{ii}. In general, a negative sign in J_{ii} does not imply a constant direct self-regulation ($a_{ii} < 0$), and vice versa (Somorjai & Goswami, 1972; Haydon, 1994). This property can be easily illustrated using the logistic population dynamics of a single species,

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = r_iN_i(1 - \frac{a_{ii}N_i}{K_i}), \quad (8)$$

where r_i, K_i, and a_{ii} correspond to the intrinsic growth rate, the carrying capacity, and the direct self-regulation of the single species i, respectively. At equilibrium ($N^*_i = K_i$), the constant, direct, intra-specific effect is given by $a_{ii} = -\frac{1}{K_i}$, which is interpreted as a constant self-regulation. In turn, from Eqn. (7) the Jacobian J_{ii} equals $r_i(1-\frac{2N_i}{K_i})$, which is always positive when $N_i < K_i/2$, negative otherwise. This implies that, in general, the interpretation measures of intra-specific interactions across the parametric and nonparametric are not the same.

Then, when can J_{ii} be transferable into a_{ii}? If we require that the signs of a_{ii} and J_{ii} be the same, we need the system at equilibrium following Lotka-Volterra dynamics. If we additionally require that $a_{ii} = J_{ii}$, then on top of the two previous requirements, we need all equilibrium abundances to be exactly the same (May & Mac Arthur, 1972; Song & Saavedra, 2018). While it is not explicit, note that previous work (May, 1972; Coyte et al., 2015) on the complexity-stability debate operates under these assumptions.

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Interspecific interactions

Assuming that all direct effects are pairwise as described in Eqn. (3), the local, aggregated, interspecific effect can be derived as

$$J_{ij} \quad = \quad a_{ij} N_i \frac{\partial g_{ij}}{\partial N_j} \; (i \neq j), \tag{9}$$

which only includes the direct effect (functional form) g_{ij} between species i and j. Under this assumption, J_{ij} and $a_{ij}(i \neq j)$ always have the same sign because $\frac{\partial g_{ij}}{\partial N_j} > 0$ (biologically, this means that effects are stronger with larger species abundances).

Instead, assuming that direct interactions include higher-order effects as in Eqn. (4), the Jacobian (the local aggregated effects) can be derived as

$$J_{ij} \quad = \quad a_{ij} N_j \frac{\partial g_{ij}}{\partial N_j} + \sum_{k \neq i,j} b_{ijk} \frac{\partial h_{ijk}}{\partial N_j} + \cdots \; (i \neq j), \tag{10}$$

where J_{ij} encodes not only the direct interspecific effects, but also the higher-order effects coming from species other than species i and j. Therefore, J_{ij} can be interpreted as the local (state-dependent) direct effect between species i and j *if and only if* all (parametric) direct effects are pairwise. That is, under higher-order effects, there is no link between (parametric) a_{ij} and (nonparametric) J_{ij} interspecific interactions. This also shows that the interspecific J_{ij} $(i \neq j)$ is fundamentally different from the intra-specific J_{ii}.

Leveraging on the difference in measures

Importantly, the difference in measures can offer an opportunity to gain further insights about non-equilibrium ecological dynamics and higher-order interactions without modeling them (AlAdwani & Saavedra, 2019). For example, focusing on dynamics and building from the classic complexity-stability debate (May, 1972), it is assumed that a community can be dynamically stable only if most of the constant, direct, intra-specific terms are negative ($a_{ii} < 0$), i.e., if "the population of each species would by itself be stable" (May, 1972). This assumption comes from the observation that dynamical stability requires that most of the local, aggregated, intra-specific terms are also negative ($J_{ii} < 0$) (May, 1972; Yodzis, 1980; Sterner et al., 1997; Moore & de Ruiter, 2012; McCann, 2011; Barabás et al., 2017). Yet, there is few empirical evidence to support the addition of direct self-regulation ($a_{ii} < 0$) for primary consumers and top predators (Pimm & Lawton, 1977; Tilman, 1982; Chesson, 2013), which would make most systems unstable.

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This apparent contradiction arises from the ill perception that a negative J_{ii} requires a negative a_{ii}. However, recalling the link between J_{ii} and a_{ii} (Eqn. 6), J_{ii} can be expressed in the absence of self-regulation ($a_{ii} = 0$) as

$$J_{ii} = \begin{cases} r_i + \sum_{j \neq i} a_{ij}(g_{ij} + N_i \frac{\partial g_{ij}}{\partial N_i}) + \sum_{j \neq k; j,k \neq i} b_{ijk}(h_{ijk} + \frac{\partial h_{ijk}}{\partial N_i}) + \cdots, & \text{if non-equilibrium} \\ \sum_{j \neq i} a_{ij} N_i \frac{\partial g_{ij}}{\partial N_i} + \sum_{j \neq k; j,k \neq i} b_{ijk} N_i \frac{\partial h_{ijk}}{\partial N_i} + \cdots, & \text{if equilibrium.} \end{cases} \tag{11}$$

This implies that a negative J_{ii} (in equilibrium and non-equilibrium dynamics) in a non-self-regulated species i (i.e., $a_{ii} \geq 0$) can arise simply by satisfying two conditions (Song et al., 2018): (1) a negative intrinsic growth rate (i.e., $r_i < 0$), and (2) at least one negative, constant, direct, interspecific effect (i.e., $a_{ij} < 0$). Figure 1 shows a simple example in a 3-species food chain: both the consumer and the top predator have no constant, direct self-regulation; yet they can exhibit negative, local, aggregated, intra-specific effects. In contrast, the primary producer does have constant, direct self-regulation; yet it does not always exhibit a negative, local, aggregated, intra-specific effect. Hence, apart (or instead) of local aggregated self-regulation mechanisms, these (or other conditions) can be taken as stabilization sources of ecological communities.

Shifting our focus to higher-order interactions, the different interpretations of J_{ij} in the presence of higher-order effects can be useful to detect their existence. For example, it has been found that J_{ij} can change its sign across time in a community (Ushio et al., 2018). If we assume that the governing population dynamics only consists of pairwise direct effects (Eqn. 3), then this result should be interpreted as the change of the type of the constant, direct, interspecific effect (i.e., the sign of the parameters in the governing population dynamics have to change). However, if we assume that the governing population dynamics is fixed, then this result should be interpreted as the presence of higher-order direct effects. Figure 2 shows a simple three-species competing system with and without higher-order direct effects that illustrate these points. Of course, the assumption relies on our belief of how nature operates. For example, previous work (Ushio et al., 2018) has assumed that the governing population dynamics is fixed, implying the presence of higher-order direct effects.

Discussion

Traditionally, the parametric and nonparametric approaches have considered different measures and interpretations of species interactions. That is, species interactions are measured as constant-direct and local-aggregated effects within the parametric and nonparametric approaches,

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respectively. However, their interpretations have been occasionally used interchangeably (e.g., when describing the stability conditions of an ecological community (May, 1972; Coyte et al., 2015)), limiting our opportunity to use their differences to gain new insights about ecological systems. In this line, here we have provided a bridge between these two approaches (measures) and illustrated its utility. In particular, we have shown three fundamental properties of species interactions. First, the local, aggregated, intra-specific effect summarizes all potential pathways one species impacts itself, which can be negative without any direct, self-regulation mechanism (see Fig. 1). Second, the local, aggregated, interspecific effect only measures the direct effect between two species if and only if the population dynamics does not have any higher-order direct effects (see Fig. 2A-B). Third, higher-order direct effects can be detected by studying interaction changes within a nonparametric approach (Figure 2C-D).

Species interactions are a multidimensional concept (Callaway et al., 2002), which naturally resulted in multiple definitions, ranging from mechanistically motivated characterizations to highly phenomenological representations (White & Marshall, 2019). However, despite the fact that these definitions are distinct mathematical entities, their construction implies that they must be inherently linked given that they all describe properties of species interactions. Importantly, most of the definitions can be classified as either parametric or nonparametric. The parametric approach decomposes species interaction in *biologically interpretable* intra-specific, interspecific, and high-order direct effects. In turn, the nonparametric approach decomposes species interactions in *computationally feasible* intra-specific and interspecific aggregated effects. Therefore, instead of linking specific definitions case-by-case, we have bridge these two approaches by focusing on their high-level conceptual links.

We hope this *Note* can open a dialogue between the parametric and the nonparametric approaches. The parametric approach has dominated community ecology (Kingsland, 2015), while the nonparametric approach has received increasing attention in the past decade (Deyle et al., 2016; Ushio et al., 2018; Cenci & Saavedra, 2019). While both approaches have shaped our understanding of ecological dynamics, little is known about when and how we can transfer the knowledge from one approach to another. Importantly, we have shown that the transferability is necessary and provides a new perspective that each approach itself cannot offer. For example, the Achilles' heel of the parametric approach is to evaluate whether the model has included enough details of the system under investigation. Indeed, if we assume a pairwise formalism, while the system is actually governed by a high-order formalism (Box 1), then we are likely to make false predictions of the system (Letten & Stouffer, 2019). However, the computational methods emerging from the parametric approach are difficult to distinguish (e.g., functional

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responses and higher-order interactions) (AlAdwani & Saavedra, 2019). Yet, relying upon the computational feasibility of the nonparametric approach (Martin et al., 2018; Deyle et al., 2016; Cenci & Saavedra, 2019), we may be able to distinguish the nature of species interactions acting on a system. Therefore, we believe that a better understanding of the measures used across parametric and nonparametric approaches can improve our knowledge of species interactions and ecological dynamics in general.

Competing financial interests

The authors declare no competing financial interests.

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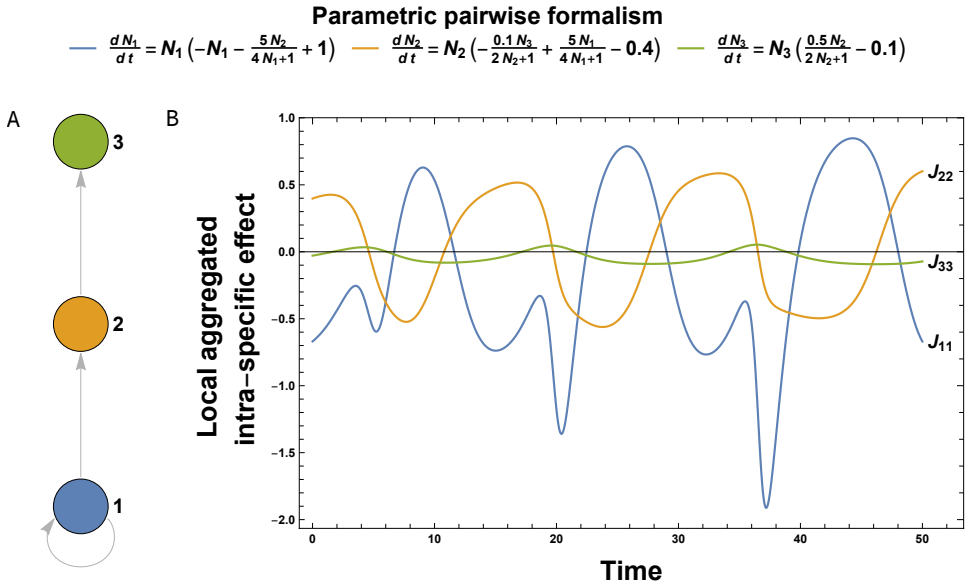

Figure 1: Local, aggregated, intra-specific effects can be negative without a direct self-regulation mechanism. Panel (A) shows a simple 3-level trophic chain with a primary producer (bottom circle), a consumer (middle circle), and a top predator (top circle). These species are linked by arrows showing the standard energy/biomass flow. Note that only the primary producer has a constant direct self-regulation (typically used in parametric approaches), i.e., $a_{11} < 0$, whereas $a_{22} = a_{33} = 0$. The governing equations describing the population dynamics of the 3-species trophic chain are shown on the top. Panel (B) shows the local (state-dependent), aggregated, intra-specific effects J_{ii} (typically used in nonparametric approaches) when the trophic chain is governed by a type II functional response (parameters are taken from Ref. (Hastings & Powell, 1991)). Top predator (J_{33}) shows mostly negative, local, aggregated effects to itself; whereas both the consumer (J_{22}) and the primary producer (J_{11}) show anti-correlated oscillatory sign patterns of local, aggregated effects to themselves.

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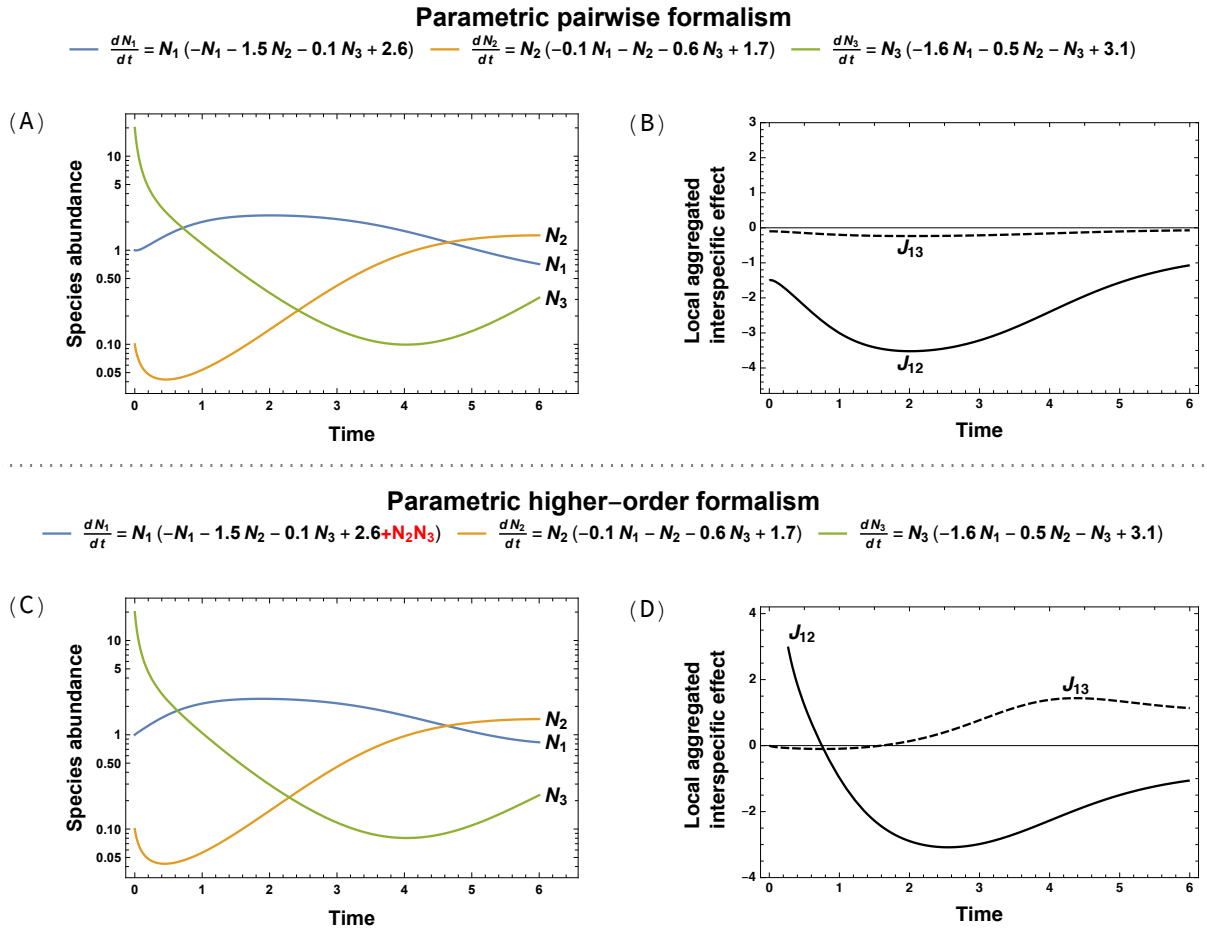

Figure 2: Local, aggregated, interspecific effects and constant, direct effects have the same sign if and only if all direct effects are pairwise based (i.e., absent of higher-order direct effects). Panels (A)-(B): Three competing species are governed by Lotka-Volterra dynamics without any higher-order direct effects (shown above panels; parameters adopted from Saavedra et al. 2017). Panel (A) shows the time series of species abundances. Panel (B) shows the corresponding local, aggregated, interspecific effects (typically used in nonparametric approaches) that species 2 and 3 have on species 1, where both J_{13} and J_{12} are always negative. Panels (C)-(D): Three competing species are governed by Lotka-Volterra dynamics with an added higher-order direct effect from species 2 and 3 on species 1 (highlighted in red; shown above panels). This formulation of higher-order effects is conceptually inspired by Levine et al. 2017 and mathematically adopted from Letten & Stouffer 2019). Panel (C) shows the time series of species abundances, which exhibit similar patterns as the model without higher-order interactions shown in Panel (A). However, Panel (D) shows that both J_{12} and J_{13} change their sign, which are fundamentally different from the patterns shown in Panel (B).