

IDEAS AND PERSPECTIVE

The mechanistic basis for higher-order interactions and non-additivity in competitive communities

Andrew D. Letten^{1,2*} and
Daniel B. Stouffer¹

¹Centre for Integrative Ecology
University of Canterbury Christchurch 8140, New Zealand ²Institute of Integrative Biology Department of Environmental Systems Science
ETH Zürich 8092, Zürich, Switzerland

*Correspondence: E-mail:
andrew.letten@usys.ethz.ch

Abstract

Motivated by both analytical tractability and empirical practicality, community ecologists have long treated the species pair as the fundamental unit of study. This notwithstanding, the challenge of understanding more complex systems has repeatedly generated interest in the role of so-called higher-order interactions (HOIs) imposed by species beyond the focal pair. Here we argue that HOIs – defined as non-additive effects of density on *per capita* growth – are best interpreted as emergent properties of phenomenological models (e.g. Lotka–Volterra competition) rather than as distinct ‘ecological processes’ in their own right. Using simulations of consumer–resource models, we explore the mechanisms and system properties that give rise to HOIs in observational data. We demonstrate that HOIs emerge under all but the most restrictive of assumptions, and that incorporating non-additivity into phenomenological models improves the quantitative and qualitative accuracy of model predictions. Notably, we also observe that HOIs derive primarily from mechanisms and system properties that apply equally to single-species or pairwise systems as they do to more diverse communities. Consequently, there exists a strong mandate for further recognition of non-additive effects in both theoretical and empirical research.

Keywords

Coexistence. higher-order interactions. Lotka–Volterra. mechanistic models. non-additivity. resource competition.

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INTRODUCTION

For the last ~ 100 years (a conservative estimate for the age of ecology as a unique discipline), population and community ecologists have treated the ‘species pair’ as the fundamental unit of study (e.g. Gause 1934; MacArthur 1970; Chesson 2000). Indeed, multiple paradigmatic concepts, including the competitive exclusion principle, niche partitioning and alternative stable states, are grounded in the analysis of simple mathematical models for two interacting species (Gause 1934; MacArthur & Levins 1967; Vandermeer 1973; May 1977). In doing so, the implicit and explicit reductionist hope has always been that we can build up to a more complete understanding of more complex systems if we can understand the forces pushing and pulling between two species. To date, however, it still remains rather unclear under what circumstances it is reasonable to scale up from two species systems to more ‘realistic’ ecological communities, comprised of multiple species interacting at different intensities across multiple temporal and spatial scales.

Growing awareness of this gulf between theory and reality has increased interest in the role of indirect effects, which encompass a broad spectrum of species interactions impacted by intermediary species (i.e. one that does not belong to a focal pair) (Wootton 1993; Billick & Case 1994). Among these, there is particular interest in the role of the so-called higher-order interactions (HOIs) in mediating the dynamics of multi-species systems (Bailey *et al.* 2016; Grilli *et al.* 2017; Levine *et al.* 2017; Mayfield & Stouffer 2017; Saavedra *et al.* 2017; Terry *et al.* 2017; for earlier discussion, see Hutchinson

1947; Vandermeer 1969; Neill 1974; Levine 1976; Case & Bender 1981; Pomerantz 1981; Abrams 1983; Wootton 1993, Billick & Case 1994). In particular, the inclusion of HOIs in competition models has recently been shown to effectively explain the stability of high-dimensional systems (Bailey *et al.* 2016; Grilli *et al.* 2017), as well as provide a parsimonious predictor of population dynamics (Mayfield & Stouffer 2017).

According to most verbal definitions, HOIs are one of many possible indirect effects that can emerge in multispecies systems (Billick & Case 1994). In competitive systems, which are the focus of the current work, the reference to ‘higher order’ more precisely stems from the explicit, mathematical role HOIs play in extending standard phenomenological population-dynamic models. Under the simplest form of Lotka–Volterra competition, the *per capita* growth of each species is a linear function of its own density and those of its competitors; that is, the intra- and inter-specific effects vary additively with the densities of all co-occurring species. In this purely additive world, where the *per capita* interaction strengths between all pairs of species is unaffected by their own densities and/or that of other species, it is possible to predict the dynamics of multispecies systems simply by linking all pairwise dynamics together by way of an interaction chain (Wootton 1993; Billick & Case 1994; Levine *et al.* 2017). Unfortunately, we know from both first principles and observational evidence that the natural world rarely operates in an additive fashion (Strogatz 2014), and the effect one species has on another will likely vary depending on the identities and densities of co-occurring species (Abrams 1980a, 1983).

Box 1. Higher-order Lotka–Volterra competition

Following Mayfield & Stouffer (2017), we define higher-order interactions broadly as non-additive density-dependent effects on *per capita* fitness. Consider a standard Lotka–Volterra model,

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \sum_{j=1}^n \alpha_{ij} N_j \right) \quad (11)$$

where r_i is the *per capita* intrinsic rate of increase of the focal species, and the competition coefficients, α_{ij} , result in a realised rate of increase that is a linear, additive function of intra- and inter-specific density.

The inherent additive effect of density on *per capita* growth rate in the standard model is illustrated for a two-species system (blue line) in Fig. 1a, and for a three-species system (blue plane) in Fig. 1b. In order to incorporate intra-specific HOIs, we can extend the standard model through the inclusion of higher-order quadratic terms, such that,

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \sum_{j=1}^n \alpha_{ij} N_j - \sum_{j=1}^n \beta_{ijj} N_j^2 \right) \quad (12)$$

where β_{ijj} capture the cumulative impacts of intra-specific interactions on the focal species (illustrated by the green curve in Fig. 1a). Note, the identity of j may or may not be the same as the focal species.

Alternatively, to incorporate inter-specific HOIs, the model can take the form,

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \sum_{j=1}^n \alpha_{ij} N_j - \sum_{j=1}^n \sum_{k=j+1}^n \beta_{ijk} N_j N_k \right) \quad (13)$$

where β_{ijk} capture the cumulative impacts of inter-specific interactions on the focal species (illustrated by the beige surface in Fig. 1b). Here again, the identity of j may or may not be the same as the focal species, but the identity

Box 1 (Continued)

of k strictly excludes the focal species. Finally, a fully specified higher-order Lotka–Volterra model (including both intra- and inter-specific quadratic terms) would take the form,

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \sum_{j=1}^n \alpha_{ij} N_j - \sum_{j=1}^n \sum_{k=j+1}^n \beta_{ijk} N_j N_k - \sum_{j=1}^n \beta_{ijj} N_j^2 \right) \quad (14)$$

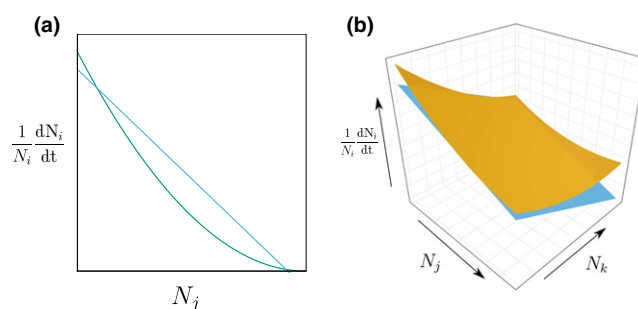


Figure 1 Illustrating higher-order interactions as non-additive density-dependant *per capita* growth functions. In (a), *per capita* growth of a focal species is an additive (blue) or non-additive (green) function of its own density or that of a competitor. In (b), *per capita* growth of a focal species is an additive (blue) or non-additive (beige) function of the densities of itself and another competitor or of two different competitors.

From a conventional multispecies (> 2) perspective, it follows that HOIs reflect the need to adjust the strength of phenomenological (e.g. Lotka–Volterra) pairwise interaction coefficients in the presence of more than two competitors through the inclusion of higher-order terms. Mathematically, however, there is nothing to prevent the inclusion of higher-order terms in less diverse models. For example, a higher-order logistic-growth equation for a single species could take the form: $\frac{dN}{dt} = rN(1 - \alpha N - \beta N^2)$ where the new β term captures the second-order, non-additive effects of intra-specific density on the *per capita* growth rate (see Box 1 for an overview of incorporating higher-order terms into competitive models). Notably, Lotka (1924) himself conceived the basic growth equations as the first terms in a Taylor approximation to a more complex model, and thus only being a reasonable representation of community dynamics around equilibria. MacArthur (1970) echoed this view in an influential paper providing a mechanistic derivation of

Lotka–Volterra competition. Indeed, much of the early discussion in the literature on HOIs overlaps closely with discussion of the constancy of the competition coefficients in the standard two species Lotka–Volterra model (Hutchinson 1947; Neill 1974; Pomerantz 1981; Abrams 1983; Billick & Case 1994). More recently, Mayfield & Stouffer (2017) defined HOIs as the suite of non-additive effects that emerge when interaction strengths vary with the density of both heterospecifics and conspecifics.

Irrespective of the number of species required to form an HOI, it is useful to recognise HOIs for what they are: emergent properties of the phenomenological models routinely used to study competition. While it is tempting to consider HOIs as ecological processes in their own right, in reality they are only a phenomenological representation of underlying non-additive processes. Consequently, fitting higher-order models to data can tell us something about the where, when, and what of HOIs, but they tell us little about the how and why. This is especially true given that any number of system properties and processes can result in non-additive dynamics. In order to understand the mechanistic basis of HOIs, we are better served by turning to more mechanistic models of competition in which non-additive dynamics emerge implicitly (e.g. through saturating growth functions in consumer-resource models), without the need to invoke higher-order terms (Abrams 1980a, 1983; Levine *et al.* 2017). Taking a mechanistic approach can enable us to tease apart and

compare the causal factors that lead to the emergent non-additivity we characterise as HOIs.

Here, we combine mechanistic and phenomenological modelling approaches to disentangle the mechanistic drivers of HOIs that emerge through resource competition. We begin by laying the necessary theoretical foundations for a mechanistic understanding of HOIs, before simulating data from a suite of general consumer-resource models to assess the frequency and magnitude of emergent non-additivity arising under different assumptions about the dynamics of resource competition. The results of this analysis show that HOIs are the rule rather than the exception. We then evaluate the analytical implications of HOIs for species coexistence and community stability. Finally, we conclude with an overview of the significance of acknowledging non-additivity for our current and future understanding of community dynamics.

MECHANISING HIGHER-ORDER INTERACTIONS

Although the line between phenomenological and mechanistic models is not always clear cut (Bolker 2008), from the perspective of resource competition the distinction is fairly transparent. We can distinguish a phenomenological model, such as Lotka–Volterra, as one in which *per capita* growth is modelled as a direct function of conspecific and heterospecific densities. The implication is that the product of competitor densities and their accompanying proportionality constants provides a suitable proxy for the underlying competitive process. We might assume these interactions arise via resource competition (MacArthur 1970), but we don't know what resources they are competing for or how each species utilises them. Despite these abstractions, one of the advantages of a phenomenological approach is that we don't need to have this latter information if we want to infer model parameters empirically, either by experiments or field observations. Furthermore, the dimensionality of the system of equations is only as large as the number of competitors; that is, two competitors lead to two equations. In contrast, *per capita* growth in a mechanistic model of resource competition is modelled as an explicit function of resource availability. Here, intra- and inter-specific feedbacks on growth rates arise solely through the depletion of shared resources. As such, mechanistic models require one to keep track of more variables. In addition to an equation for each consumer, an additional equation is required for each resource. Moreover, to parametrise a mechanistic model, we need to know which are the key limiting resources in the system.

Within the above verbal description, we already see some terminological ambiguity in moving between phenomenological and mechanistic perspectives. The alpha coefficients in a Lotka–Volterra model represent *direct* pairwise effects, with *indirect* effects emerging either through a non-focal species having a density mediated domino-effect on the dynamics of a focal pair via an interaction chain (e.g. an intransitive loop), or through a non-focal species modifying the *per capita* level interaction strength between a focal pair (HOI, sensu Wootton 1993; Levine *et al.* 2017). In contrast, in a mechanistic model, *all* interactions are indirect, irrespective of whether the

community comprises a single or a thousand consumers. At the same time, from a continuous-time mechanistic perspective, there is no clear means of distinguishing between interaction chains and HOIs since the former is only an extreme case of negligible non-additivity (we expand on this point in the discussion). As a result, we believe the question we should instead be asking is under what conditions do we expect to observe non-negligible non-additivity?

There already exists a considerable body of literature investigating the additivity of competition coefficients on analytical and empirical grounds in both pairwise and multi-species systems (Hutchinson 1947; Neill 1974; Abrams 1980a; Pomerantz 1981; Abrams 1983; Billick & Case 1994). The empirical evidence for non-constant competition coefficients is undeniable (Levine *et al.* 2017), but perhaps more compelling is the analytical work that has been carried out to assess the tendency for non-additivity from first principles. As a start, we can learn a lot from the necessary constraints MacArthur (1970) was forced to impose in order to translate resource competition into a Lotka–Volterra form. Chief amongst there were (i) logistic resource supply, (ii) linear consumer functional responses, and (iii) a time-scale separation between consumer dynamics and resource dynamics based on the assumption that resource dynamics are significantly faster than consumer dynamics. A number of researchers have since shown that relaxing these assumptions will typically result in non-additive *per capita* growth functions, with Peter Abrams' contributions on this topic being particularly noteworthy (Abrams 1980a, 1983; Abrams *et al.* 2008).

Analytical work indicates that non-additivity can emerge under a broad spectrum of conditions. What remains to be seen is to what extent the inclusion of higher-order terms in phenomenological models improves predictive accuracy, and/or is critical to mapping the qualitative end-points of a community (e.g. correctly identifying coexistence vs. exclusion). One way we can investigate this is by statistically fitting standard and higher-order Lotka–Volterra models to data generated from simulations of mechanistic consumer-resource models, where we have full knowledge of underlying processes. This allows us to evaluate both the robustness of static fits to the observed data as well as the relative fidelity of parameterised phenomenological models to the dynamics of the original data generating mechanistic model (see Fig. 2). What makes a simulation approach additionally attractive is that it is representative of the process taken by empiricists in parametrising phenomenological models from experimental or observational data, albeit with one key contrast in that it is perfectly deterministic.

TESTING FOR HIGHER-ORDER INTERACTIONS IN A PERFECT WORLD

Model formulation

To investigate the prevalence and significance of HOIs arising from resource competition, we first generated synthetic 'observed' data from simulations of a suite of basic consumer-resource models (see Fig. 2 for an illustration of the process). All models took the general form,

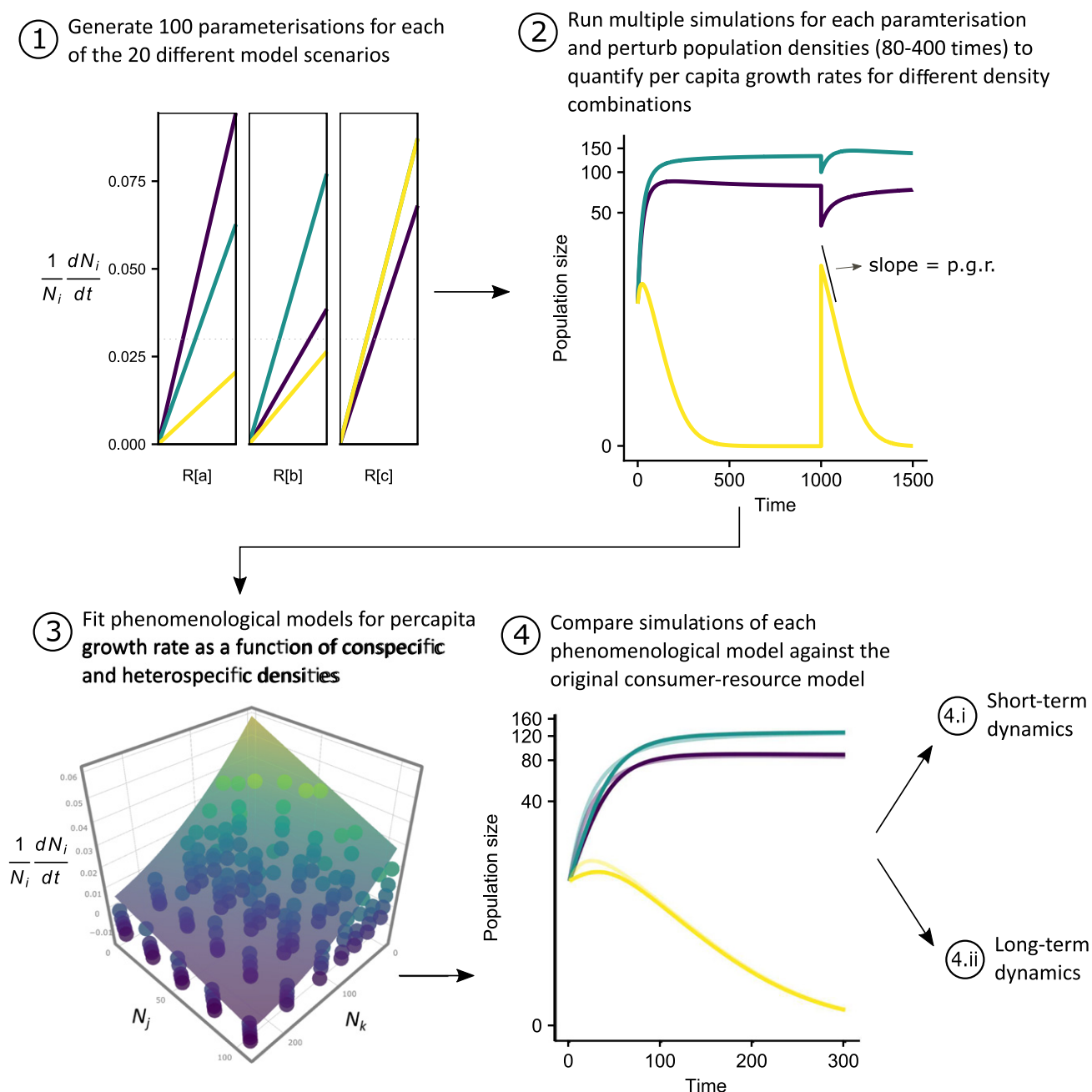


Figure 2 Illustrating a simulation approach to testing HOIs. (1) Linear functional responses for three consumers competing for three resources. (2) A single iteration of the data generation step via density perturbations. (3) The fitted higher-order *per capita* growth rate surface for purple as function of yellow and turquoise. In the illustrated fit, purple is treated as being at negligible density and so the plane tracks the upper most quantiles of purple's potential *per capita* growth rate. The vertical depth of the point data is indicative of the effect of purple's own population density on its growth rate, in combination with its two competitors. (4) Re-simulated trajectories of the three competitors from a fully specified higher-order model (solid lines), against the corresponding trajectories from the original mechanistic model (partially transparent lines).

$$\frac{dN_i}{dt} = N_i(\mu_i(R_1, R_2, \dots) - m) \quad (1)$$

$$\frac{dR_j}{dt} = \Psi_j(R_j) - \sum_{i=1}^n Q_{ij}\mu_{ij}(R_j)N_i \quad (2)$$

where N_i is the population density of consumer i , R_j is the density/concentration of resource j , $\mu_i(R_j)$ is the *per capita* consumer functional response of consumer i , m is the *per*

capita mortality rate, $\Psi_j(R_j)$ is the resource supply function, and Q_{ij} is the resource quota of consumer i on resource j .

From this general form, different model scenarios are distinguished by: (i) the form of the consumer functional response; (ii) the form of the resource supply function; (iii) the class of resource; and (iv) the number of consumers/resources.

We allow the consumer growth function to take one of two forms: (i) linear,

$$\mu_{ij}(R_j) = a_{ij}R_j \quad (3)$$

where a_{ij} is a constant of proportionality, or (ii) nonlinear (Monod),

$$\mu_{ij}(R_j) = \mu_{max_{ij}} \frac{R_j}{k_{ij} + R_j} \quad (4)$$

where $\mu_{max_{ij}}$ is the maximum growth rate and k_{ij} is the half saturation constant for consumer i on resource j .

We also explore two options for the resource supply function. Specifically, we either assume that the resources are biological and grow logistically,

$$\Psi_j(R_j) = r_j R_j \left(1 - \frac{R_j}{K_j}\right) \quad (5)$$

where r_j is the resource intrinsic rate of increase and K_j is the resource carrying capacity; or we assume abiotic resources that are supplied to the systems at a fixed concentration and rate (as in a chemostat),

$$\Psi_j(R_j) = d(S_j - R_j) \quad (6)$$

where d represents the flux of resources into and out of the system.

In the case of multiple resources, we then further distinguish between whether each resource is essential to consumer growth following Leibig's law of the minimum, in which case,

$$\mu_i(R_1, R_2, \dots, R_n) = \min(\mu_i(R_1), \mu_i(R_2), \dots, \mu_i(R_n)); \quad (7)$$

or the resources are substitutable such that:

$$\mu_i(R_1, R_2, \dots, R_n) = \mu_i(R_1) + \mu_i(R_2) + \dots + \mu_i(R_n) \quad (8)$$

Finally, we varied the number of consumers in the system from one to three inclusively, with an equivalent number of resources in each case. For 2 consumer functional responses $\times$ 2 resource supply functions $\times$ 2 resource classes $\times$ 3 levels of consumer/resource richness, this resulted in a full complement of 20 model formulations of resource competition (note for a single consumer utilising a single resource there is no distinction in resource class).

Model parametrisation

For each model formulation, we generated 100 random parametrisations for the consumer functional response(s). In the linear case, for each consumer's response to each resource, a was sampled 100 times from a uniform distribution with a lower limit of 0.015 and an upper limit of 0.1. In the nonlinear case, for each consumer's response to each resource, k was sampled 100 times from a uniform distribution with a lower limit of 0.1 and an upper limit of 5, while μ_{max} was held fixed at 0.1. Resource quota, Q , was parametrised in proportion (1 $\times$, 10 $\times$, 100 $\times$ or 1000 $\times$) to the a and k parameters of the consumer functional responses across all models, with slight distinctions in the allocation procedure depending on the functional response, resource type and the number of consumers/resources. The simplest case was for a single consumer, where Q was simply given by a or k . For two

consumers and two resources. In the linear case, the resource quota Q was given a value proportional to a of the corresponding resource if resources were substitutable, or the alternative resource if resources were essential; in the nonlinear case, the resource quota Q was given a value proportional to k of the corresponding resource if resources were essential, or the alternative resource if resources were substitutable. Finally, for three consumers and three resources, the relative size of each consumer's Q for each resource was given by a random shuffling of each consumer's a or k values.

To ensure that growth rates would be tightly linked to changes in density, we parametrised resource dynamics to be at least an order of magnitude faster than consumer dynamics. This assumption is equivalent to the time-scale separation commonly applied in analytical treatments of consumer-resource dynamics (MacArthur 1970; Chesson 1990, see Appendix S2). For logistically growing resources, this is done by increasing the magnitude of the resource logistic growth parameter, r . To achieve the same effect for constantly supplied resources, it was necessary to decouple consumer mortality, m , from the inflow/outflow rate, d , as would be the case in a chemostat if a filter on the output slowed the washout rate (Smith & Waltman 1995) or, in a less artificial scenario, if consumers are motile and therefore able to actively avoid being washed out (e.g. fish in a stream).

Data generation

To generate idealised observational data, we performed a series of repeated simulations for each of 100 parametrisations of the 20 different model scenarios. After a short burn-in period of 1000 time-steps (10 000 numerical iterations, equivalent to ~ 15 –100 generations) that allowed for the system to approach its stable equilibrium, consumer densities were perturbed up and down over ~ 80 –400 density combinations up to and including each consumer's carrying capacity in monoculture (see Appendix S1 in Supporting Information for a detailed description of how perturbation densities were calculated).

We then measured the *per capita* growth rate for each consumer given its own density and the density of its competitors. We obtained an 'instantaneous' measure of this *per capita* growth by taking the first derivative of a spline model fit for the natural log of density as a function of time (across one time-step [10 numerical iterations] beginning one timestep after densities were perturbed). All simulations were run with the LSODA solver using the deSolve package v1.20 (Soetaert *et al.* 2010) in R v3.4.2.

Phenomenological (α and β) parameter inference

With the data-generated for each of the valid parametrisations (max 100) of each model, we fit four Lotka–Volterra-type models of varying complexity: (i) standard Lotka–Volterra model; (ii) Lotka–Volterra model with inter-specific HOIs; (iii) Lotka–Volterra model with intra-specific HOIs; and (iv) Lotka–Volterra model with both inter and intra-specific HOIs (see Box 1). Owing to occasional, randomly-drawn parameter combinations that resulted in unsolvable numerical solutions,

note that the number of valid parametrisations for six model scenarios involving logistically growing resources was < 100 (see simulation tallies in Table S1 in the Supporting Information). For each valid parametrisation, we fit the model to the full data and in select cases (multiple consumers competing for logistically growing resources) also a subset of the data excluding perturbations densities that yielded ‘spurious’ nonlinearities due to minimum *per capita* growth rates being bounded from below by the mortality rate. We refer to these as spurious because they arise from the ecologically unrealistic simultaneous perturbation of multiple competitors close to their respective monoculture carrying capacities. In the case of multiple consumers competing for logistically growing resources, we present the results for the sub-setted data in the main text and for the full data in the supplementary material (see Figs S1–S2 in Supporting Information). All models were fit as standard polynomial linear regressions in R v3.4.2.

Goodness of fit: static training and dynamic testing

In order to evaluate the explanatory power of the phenomenological model fits, we obtained the R^2 for each of the valid parametrisations of each scenario. Note that the potential to generate infinite data via simulation precludes the use of classical significance testing (White *et al.* 2014) or even information-criteria-based model selection (McElreath 2015). The superficial limitation of using R^2 is that it will always increase with additional parameters. As such, there is a risk of concluding that a more complex model is superior even when overfit to the observed data. At the same time, we know *a priori* that all four models are strictly speaking misspecified, in that they do not represent the true data-generating process. However, because we can reproduce the data generating-process exactly with the mechanistic models, we can compare the predictive accuracy of each Lotka–Volterra model dynamically against the original mechanistic version. This two-step procedure can be viewed as analogous to the use of a training dataset and a test dataset in cross validation; an overfit model, with a larger statically fit R^2 , will produce larger errors in dynamic simulations when contrasted against a better fit model with a smaller statically fit R^2 (the potential of a fully specified HOI model to overfit the observed data is illustrated in Fig. S4 in the Supporting Information for an example model scenario).

To evaluate the accuracy of each model we obtained a dynamic measure of McFadden’s pseudo- R^2 :

$$R^2 = 1 - \frac{\ln L(M_p)}{\ln L(M_{null})} \quad (9)$$

where the numerator in the fraction is the log-likelihood of a phenomenological model and the denominator is the log-likelihood of the relevant null model. To quantify the log-likelihoods, we simulated all five models (1 mechanistic + 4 phenomenological) using the perturbation densities implemented in the data generation step as the initial values. Each simulation was run for 20 time-steps (200 numerical iterations, equivalent to ~ 0.3 – 2 generations) with the absolute average error calculated as the average difference across the time-series between the density of each consumer in each of the four

phenomenological models relative to their density in the consumer-resource model, and then finally averaged over consumers. As the null model, we held the initial values fixed and subtracted them from the recorded state of the consumer-resource model over the same 20 time-steps. Because some combinations of phenomenological parameters (particularly in the case of quadratic terms) exhibit pathological behaviour where population size blow-up to infinity, simulations in which average differences exceeded 100 000 individuals were excluded.

We calculated the log-likelihood for each of the 100 parametrisations of each phenomenological model and the null model as:

$$L(M) = m \ln \left(\left(\sum_{i=1}^m \overline{|(y_i - x_i)|} \right) / m \right) \quad (10)$$

where y_i (abundance in mechanistic model) and x_i (abundance in phenomenological model) is the average over the 20 time-steps of each simulation run of the mechanistic model and the phenomenological/null models respectively, and m is the number of simulations per parametrisation (i.e. different starting values) (Mangan *et al.* 2017). Note that rather than stochastic error, here we are treating the functional misspecification of the model as the error on the basis that we know with certainty that the phenomenological models do not represent the original data-generating process. The final output of the analysis of short-term dynamics is a distribution of 100 pseudo- R^2 representing each phenomenological model’s correspondence to each of the 20 data-generating consumer-resource model scenarios. Note that the absolute value of the pseudo- R^2 values is partially a function of the dynamic speed of the model, and therefore contingent on the number of time-steps evaluated. Because our interest here is on the relative performance of the different phenomenological models under a given mechanistic scenario, we therefore present the results as the difference in goodness of fit (ΔR^2) between each HOI model and the reference standard Lotka–Volterra model. For consistency, we do the same for the static fits, but provide the absolute R^2 of the static fit of the standard model as a reference in each figure.

In Table S1 of the Supporting Information, we provide a breakdown of the following for each model scenario: the number of valid mechanistic parametrisations; the average number of original perturbations; and the average number of perturbations after excluding those in which all consumers exhibited minimum bounded growth rates due to population perturbations well above equilibrium; and the average number of simulations excluded due to blown-up population sizes.

Supplementary analyses

In addition to the core analyses, we conducted a number of additional simulations aimed at testing the sensitivity and robustness of the data generation and fitting procedure. This included: (i) rerunning all simulations (incl. data generation) while constraining perturbation densities to be below half of each species’ carrying capacity to evaluate the effect of a reduced perturbation range on emergent non-additivity; (ii)

rerunning all simulations to evaluate the effect of a longer post-perturbation sampling interval (100 time steps) on emergent non-additivity (quantifying *per capita* growth rate as $\log[N_{t+1} - N_t]/\Delta t$); and (iii) comparing logistic growth parameters obtained via simulation with those derived analytically using the approach described in Appendix S2 of the Supporting Information for the only model for which we know *a priori* should recapitulate logistic population growth (i.e. a single consumer with a linear functional response to a logistically growing resource).

Results

One consumer and one resource

The training and test data ΔR^2 s for a single consumer utilising a single logistically growing resource are shown in Fig. 3. When the consumer has a linear functional response to resource availability, the standard version of Lotka–Volterra competition performs as well as the HOI model including quadratic intra-specific terms for both the static training data and the dynamic test data, with both being indistinguishable from unity. Though not particularly illuminating, this numerical result is reassuringly consistent with MacArthur's analytical derivation of resource competition in Lotka–Volterra form (MacArthur 1970; Abrams 1980a; an analytical derivation for this model is provided in Appendix S2). As proof of the robustness of our

fitting procedure, we are also able to show that the parameters obtained via simulation of this model recover the analytically derived parameters to within three significant figures (Fig. S3). We nevertheless found that a shift to nonlinear consumer functional responses already led to the model including quadratic intra-specific terms performing better on both the training and test data. This simulation result can be derived analytically and is consistent with several analytical studies (Abrams 1980a, 1983; Abrams *et al.* 2008) demonstrating that the phenomenological Lotka–Volterra competition coefficients will typically be a non-constant function of population densities when consumer functional responses are nonlinear (see Appendix S2 in the Supporting Information).

For a single species utilising a single resource under constant supply, the most striking result is that the relative performance of the higher-order model is greatest ($\Delta R^2 \sim 0.24$) when the consumer functional response is linear (Fig. 3, Appendix S2). Intuitively, we might assume this arises from some dynamic peculiar to chemostat-type resource supply, but the reality is that any deviation from logistic resource supply will result in non-additive dynamics (O'Dwyer 2018). Several previous studies have already shown analytically that non-logistic resource supply will generate non-constant competition coefficients, even if the consumer functional responses are linear (Abrams 1980a, 1983). As recently put succinctly by O'Dwyer (2018), 'to obtain something as familiar as logistic growth ... we must assume logistic growth 'all the way down'. The somewhat counter-intuitive observation here is that the effect of introducing a saturating consumer functional response is to increase the relative performance of the standard Lotka–Volterra model. The underlying explanation is that, under constant resource supply, the functional relationship between *per capita* growth rates and consumer densities is concave-up, leading to positive quadratic HOIs. In contrast, the effect of a saturating consumer functional response (i.e. *per capita* growth rate as a function of resource concentration) is to cause the functional relationship between *per capita* growth rates and consumer densities to be concave-down, leading to negative quadratic HOIs. This is because at low consumer population density, resources are at high density, and therefore a small increase in population density depletes resource concentrations in the saturating region of the consumer functional response, where the effect on *per capita* growth rate is minimal. Once densities become larger, the rate at which *per capita* growth rate declines as resources become more scarce increases, hence giving rise to a concave-down phenomenological functional response (i.e. *per capita* growth rate as a function of density). In combination, these two sources of non-additivity work to partially cancel each other out (see eqns 5, 9 and 10 of Appendix S2) and ultimately reduce the difference in the performance between the standard model and the higher-order model.

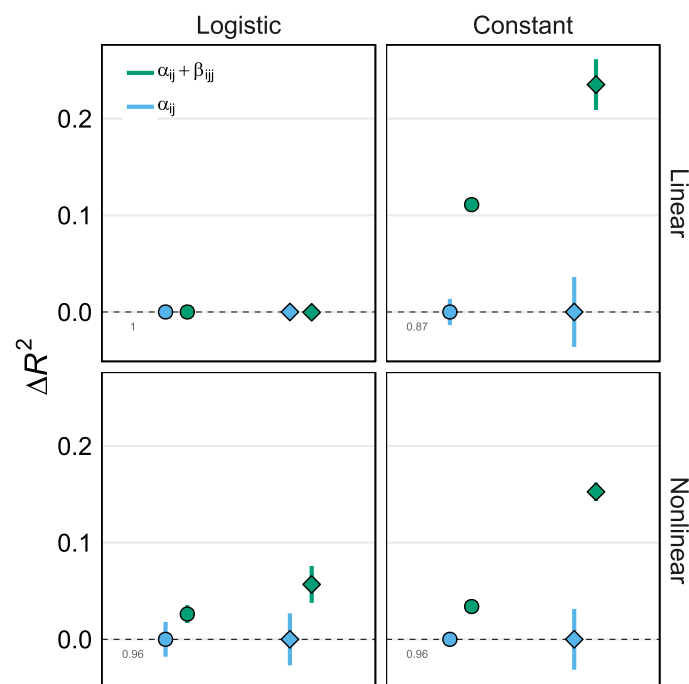


Figure 3 Difference in goodness of fit (ΔR^2) for HOI models relative to a standard Lotka–Volterra model fitted to data generated from a consumer–resource model for a single consumer. ΔR^2 for the training data (static fits) are indicated with circles; ΔR^2 for the test data (dynamic fits) are indicated with diamonds. The number in bottom left of each panel gives the R^2 for the standard Lotka–Volterra model (static fit). Number of parameters in each model: 'alpha' = 2; 'alpha + beta (intra)' = 3. All error bars denote standard errors.

Multiple consumers and multiple essential resources

Doubling the number of consumers and resources has little impact on the relative performance of the standard and higher-order models when the consumers have linear functional responses and the resources are essential and grow logistically (Fig. 4). In contrast, the introduction of nonlinear

functional responses results in a significant improvement in the model including *both* inter- and intra-specific quadratic terms relative to the other three models, as is most pronounced in the test data in the lower left panel of Fig. 4. With the addition of a third consumer and third logistically growing essential resource, the fully specified higher-order model exhibits a marked improvement over the other models in both the training and test data and in spite of consumers having linear functional responses. This is likely attributable to abrupt switches in the resources each consumer is most limited by, coupled with the tendency for at least one resource to be driven to scarcity when multiple resources are available, leading to abrupt changes in interaction strengths (Abrams 1980a,b). Although resource exclusion can arise when two consumers compete for two logistically growing resources, it should emerge much

more frequently in the case of three or more resources (Abrams 1998). When consumer functional responses are non-linear, the fully specified model again shows substantially stronger performance for three-consumer systems.

Paralleling the pattern seen for a single consumer (Fig. 3), the switch to constant resource supply results in a marked drop in performance in the standard Lotka–Volterra model; this is even true in two consumer systems with linear functional responses (Fig. 5). Notably, however, the jump to three consumers and three resources is not characterised by the same upward trend in the relative performance of the fully specified HOI model exhibited by logistically growing essential resources. We suspect this can be at least partly attributed to the inability of consumers to temporarily drive resources to extinction in a system with constant resource supply.

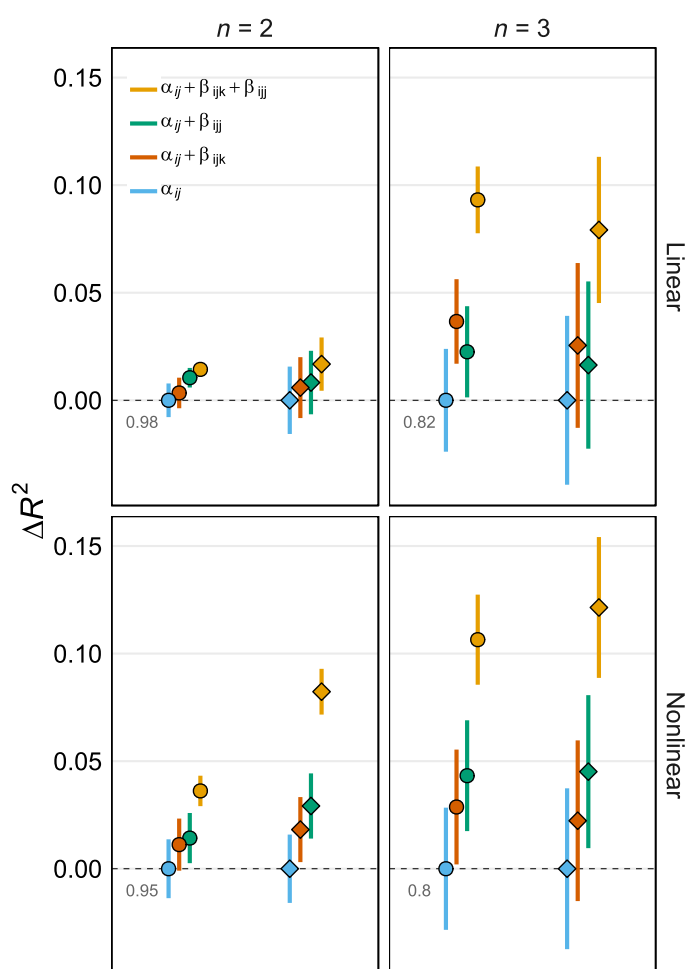


Figure 4 Difference in goodness of fit (ΔR^2) for HOI models relative to a standard Lotka–Volterra model fitted to data generated from a consumer-resource model for two and three consumers utilising an equivalent number of *logistically growing, essential* resources. ΔR^2 for the training data (static fits) are indicated with circles; ΔR^2 for the test data (dynamic fits) are indicated with diamonds. The number in bottom left of each panel gives the R^2 for the standard Lotka–Volterra model (static fit). Number of parameters in each model (2 consumers/3 consumers): ‘alpha’ = 6/12; ‘alpha + beta (inter)’ = 8/21; ‘alpha + beta (intra)’ = 10/21; ‘alpha + beta (inter & intra)’ = 12/30. All error bars denote standard errors.

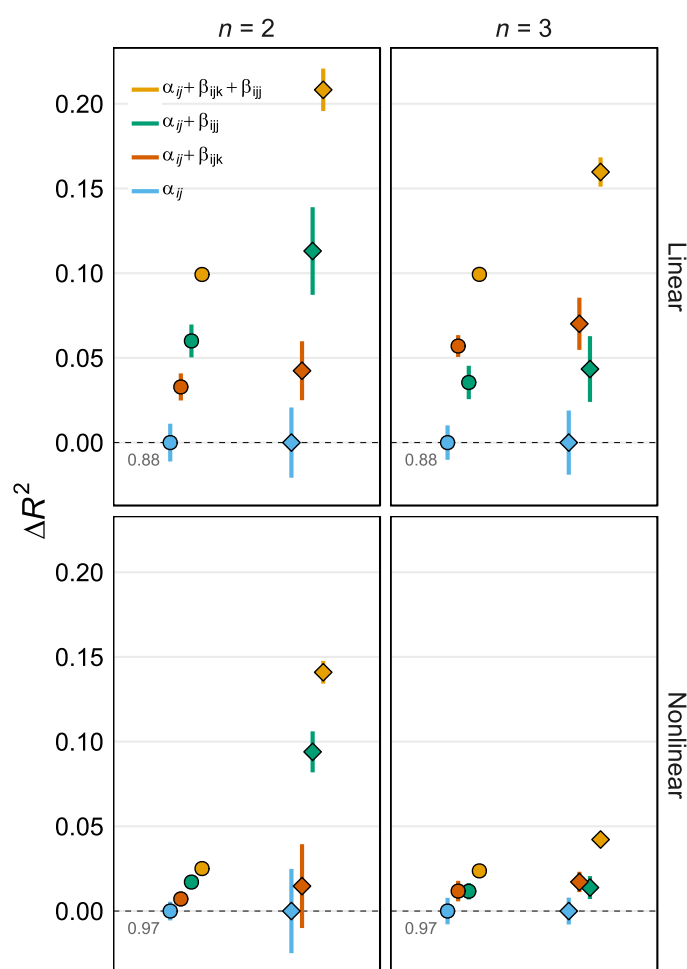


Figure 5 Difference in goodness of fit (ΔR^2) for HOI models relative to a standard Lotka–Volterra model fitted to data generated from a consumer-resource model for two and three consumers utilising an equivalent number of *essential* resources under *constant* supply. ΔR^2 for the training data (static fits) are indicated with circles; ΔR^2 for the test data (dynamic fits) are indicated with diamonds. The number in bottom left of each panel gives the R^2 for the standard Lotka–Volterra model (static fit). Number of parameters in each model (2 consumers/3 consumers): ‘alpha’ = 6/12; ‘alpha + beta (inter)’ = 8/21; ‘alpha + beta (intra)’ = 10/21; ‘alpha + beta (inter & intra)’ = 12/30. All error bars denote standard errors.

Multiple consumers and multiple substitutable resources

The switch to substitutable resources makes little substantive difference to the above observations (Figs 6 and 7). The only somewhat surprising exception is that the fully specified model doesn't see the same marked increase in performance from two to three consumer systems under logistic resource growth as it did for essential resources (Fig. 4). This is notable because resource extinction can still arise at, or below, equilibrium population sizes, when resources are substitutable (assuming logistic growth). It is nevertheless possible that quadratic functions provide a poor fit to the types of non-linearities generated from resource extinction (a point we will expand upon in the discussion). Furthermore, unlike for essential resources, changes in the ratio of available resources

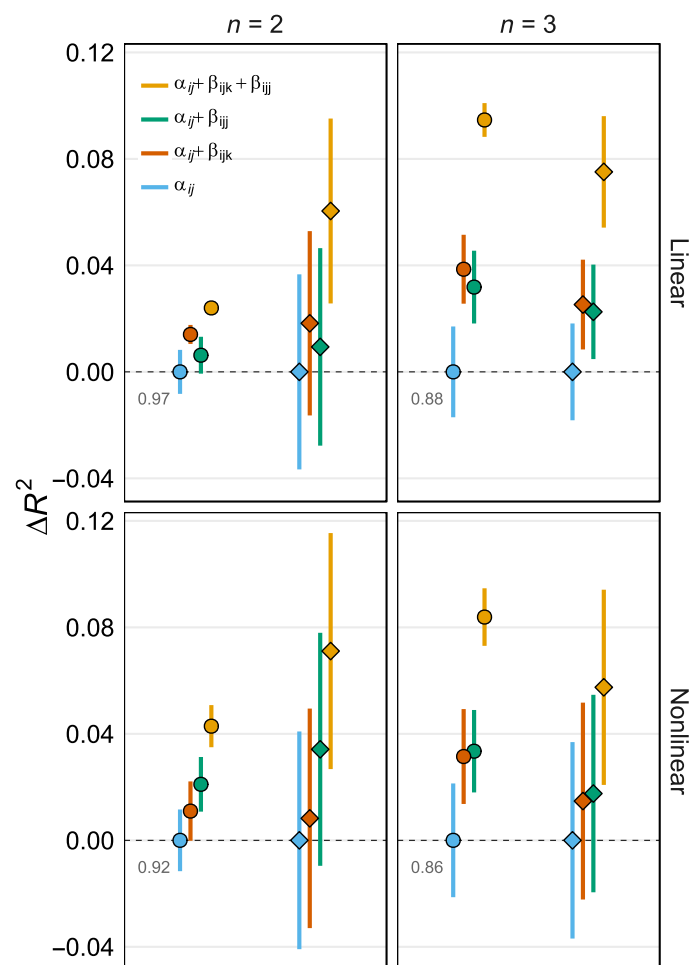


Figure 6 Difference in goodness of fit (ΔR^2) for HOI models relative to a standard Lotka–Volterra model fitted to data generated from a consumer–resource model for two and three consumers utilising an equivalent number of *logistically growing, substitutable* resources. ΔR^2 for the training data (static fits) are indicated with circles; ΔR^2 for the test data (dynamic fits) are indicated with diamonds. The number in bottom left of each panel gives the R^2 for the standard Lotka–Volterra model (static fit). Number of parameters in each model (2 consumers/3 consumers): ‘alpha’ = 6/12; ‘alpha + beta (inter)’ = 8/21; ‘alpha + beta (intra)’ = 10/21; ‘alpha + beta (inter & intra)’ = 12/30. All error bars denote standard errors.

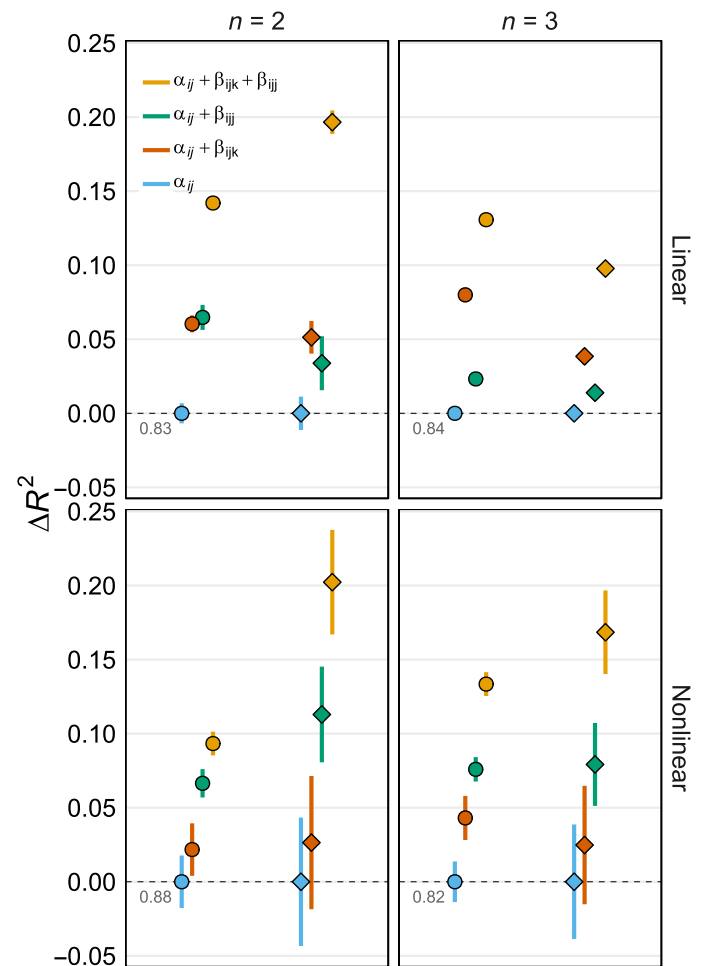


Figure 7 Difference in goodness of fit (ΔR^2) for HOI models relative to a standard Lotka–Volterra model fitted to data generated from a consumer–resource model for two and three consumers utilising an equivalent number of *substitutable* resources under *constant* supply. ΔR^2 for the training data (static fits) are indicated with circles; ΔR^2 for the test data (dynamic fits) are indicated with diamonds. The number in bottom left of each panel gives the R^2 for the standard Lotka–Volterra model (static fit). Number of parameters in each model (2 consumers/3 consumers): ‘alpha’ = 6/12; ‘alpha + beta (inter)’ = 8/21; ‘alpha + beta (intra)’ = 10/21; ‘alpha + beta (inter & intra)’ = 12/30. All error bars denote standard errors.

do not change the identity of the most limiting resource, which likely contributes to the abrupt shifts seen for logistically growing essential resources (Letten *et al.* 2017).

For both single and multiple consumers and resources, the results obtained when the time scale over which we estimated *per capita* growth rates was increased by two orders of magnitude were broadly consistent with those described above (Figs S5–S9); this indicates that the data-generation procedure is robust even to a non-instantaneous measure of *per capita* growth rate. In contrast, the results obtained when the range of perturbation densities was narrowed to below each species carrying capacities exhibited a marked increase in the relative performance of the standard Lotka–Volterra model (Figs S10–S14).

COEXISTENCE IN A NON-ADDITIVE WORLD

In the preceding analysis, we evaluated the accuracy of different higher-order models solely on the basis of their short-term accuracy across a broad range of initial population sizes. Nevertheless, it is possible for a model to be a closer approximation to the data-generating process in the short-term but be a weak predictor of its long-run state, and vice versa. In order to evaluate long-term model accuracy and the implications of HOIs for analyses of coexistence and stability, we ran additional simulations for 3000 time-steps of each phenomenological model using the end state (after 1500 time-steps) of the corresponding consumer-resource model as the initial state values. We then evaluated the qualitative accuracy (correct or incorrect) of each model in matching the end state (i.e. the identities of coexisting and excluded consumers) of the data generating model after the same number of time steps.

The comparative accuracy of the standard Lotka–Volterra model and the fully specified HOI model in qualitatively matching the end-state of each simulation is shown in Fig. 8. In each of the 16 simulation scenarios, the HOI model performed as well (4/16) or better (12/16) than the standard model. The baseline accuracy for the standard LV model was nevertheless already between 96–100% for two consumers and between 87–100% for three consumers. It must be noted that Fig. 8 only presents the results for those simulations in which the populations didn't blow-up for one or both model forms. Compared to the short-term simulations (which were terminated after 20 time-steps), a larger number of simulations exhibited pathological behaviour when allowed to proceed indefinitely. The average number of simulations in which population sizes blew up was just two for the standard model

compared to nine for the fully specified HOI model. In the case of the intermediate intra-specific HOI model (not shown in Fig. 8) an average of 31 out of a maximum of 100 simulations resulted in blown up population sizes. This shouldn't be surprising given the quadratic form of the HOI model, but it does highlight some of the potential subtleties encountered when fitting higher-order models.

Perhaps a more pressing limitation to the incorporation of HOIs into our understanding of the dynamics of multi-species systems is the derivation of intuitive analytical criteria for predicting coexistence and partitioning apart the various contributory factors (Levine *et al.* 2017; Letten *et al.* 2018). For two species systems, we frequently rely on the mutual invasibility criterion, which states that two species can coexist if both can invade from low density when the other is at its monoculture carrying capacity. This is satisfied under pairwise Lotka–Volterra competition when the intra-specific competition coefficients are greater than the inter-specific coefficients for both species. There also exist convenient, competition-coefficient-based formulae for partitioning apart the contributions of fitness and niche differences to coexistence (Chesson 2013). Unfortunately, the mutual invasibility criterion is no longer foolproof for non-additive models or in systems with three or more species (Gilpin 1975; Stouffer *et al.* 2018); and even in the absence of HOIs, pairwise coexistence is not a reliable indicator of multispecies coexistence (Barabás *et al.* 2016; Levine *et al.* 2017; Saavedra *et al.* 2017). Recently, Saavedra *et al.* (2017) developed a structural approach for evaluating coexistence in multi-species systems that critically bypasses the dependency on invasibility criteria. The method for now remains constrained to standard Lotka–Volterra models parametrised in the form of an interaction chain (but see Cenci & Saavedra 2018), but in the context of the current work it provides a useful tool to illustrate the (in)fidelity of Lotka–Volterra models to their mechanistic counterparts and the potential importance of HOIs in explaining coexistence.

Even without HOIs, there are many ways in which the dynamics of three species can depart from those expected based on pairwise dynamics. A textbook scenario for illustrating the novelty of multi-species systems takes the form of a game of rock-paper-scissors, or what is more technically referred to as an intransitive loop (Kerr *et al.* 2002; Stouffer *et al.* 2018): species A excludes B, B excludes C, and C excludes A. Even though no single species pair can coexist, the triplet nevertheless persists when together. Parametrising a pairwise Lotka–Volterra model to exhibit intransitive dynamics is as simple as introducing a set of pairwise competition coefficients corresponding to a third competitor, such that each species excludes and is excluded by one other species. Importantly, there needn't be any non-additivity for this mechanism to stabilize coexistence.

Under a consumer-resource model, intransitivity can emerge when three consumers compete for three essential resources and each has the largest impact on the resource it is the second most limited by (Huisman & Weissing 2001). We parametrised a consumer-resource model to generate intransitive dynamics amongst three consumers competing for three logistically growing essential resources (Fig. 9a,b). We then simulated the model using the same approach described under the

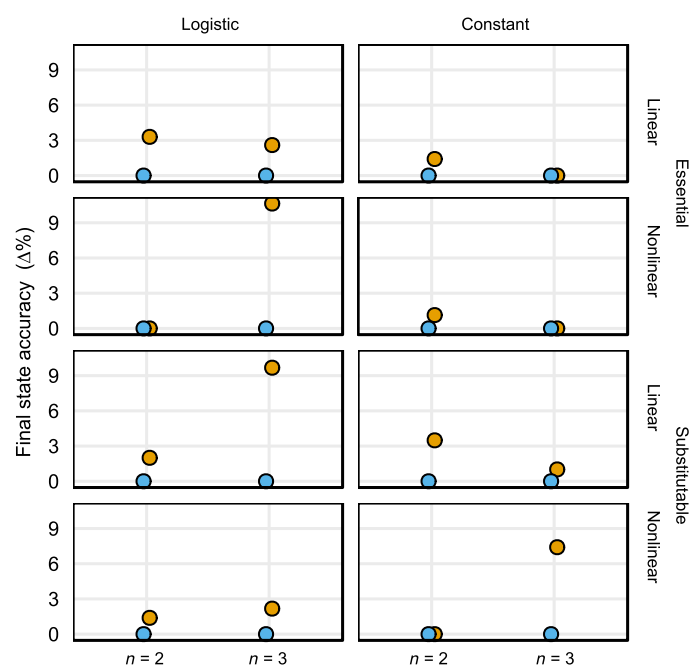


Figure 8 Percentage difference in qualitative accuracy of the fully specified HOI model (beige) relative to the standard Lotka–Volterra model (blue).

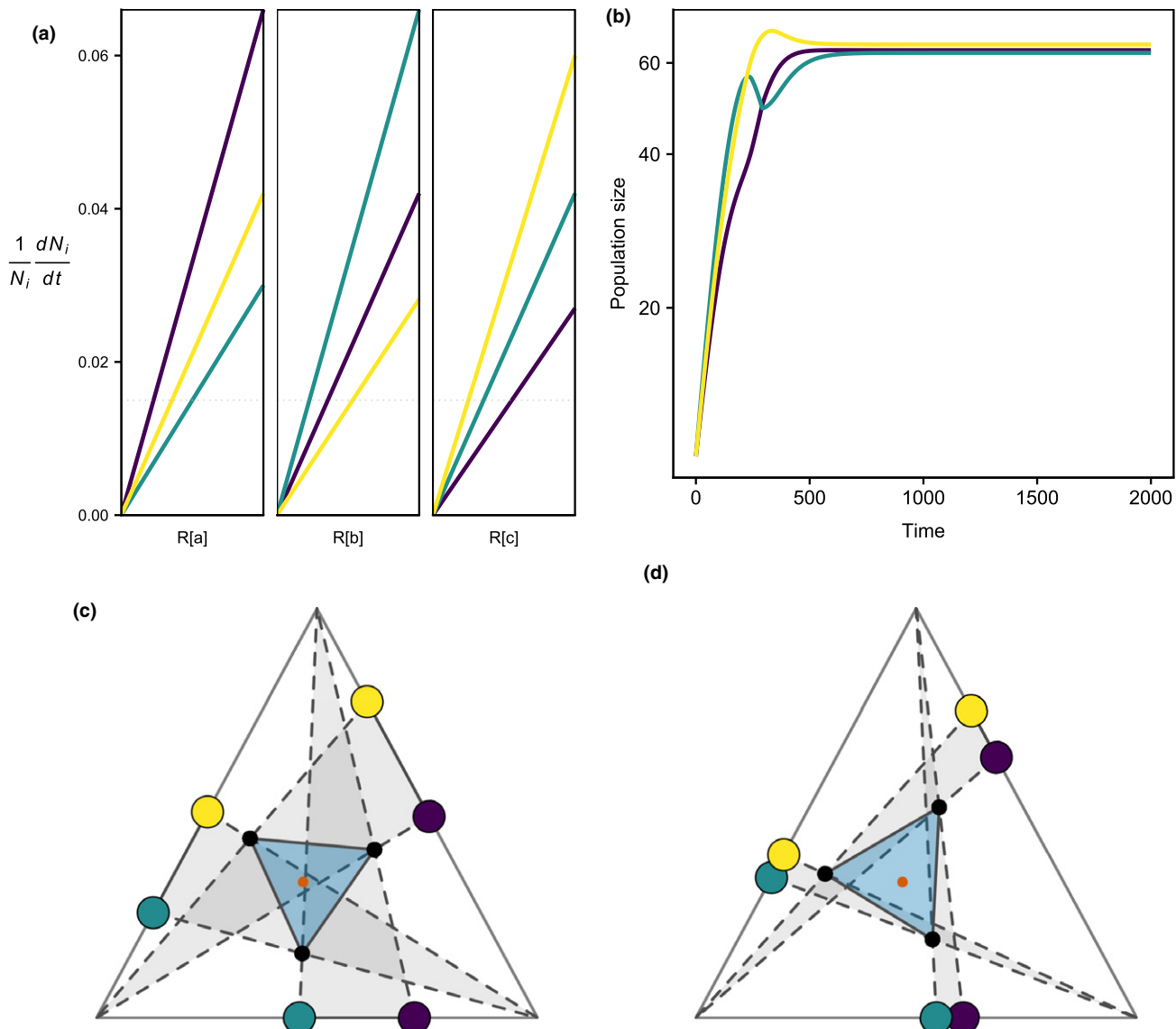


Figure 9 Structural representation of a resource-competition-based intransitive loop. (a) Linear *per capita* functional responses for three consumers to three logistically growing essential resources, with each competitor limited by a different resource. (b) Consumer time series when initiated from the same population sizes. (c) Structural feasibility domain using alphas from a standard Lotka–Volterra model. (d) Structural feasibility domain using alphas from a Lotka–Volterra model including higher-order inter-specific terms.

previous section to generate ‘observed’ data from which we can then infer the competition coefficients of standard and higher-order models. We then followed the approach described in Saavedra *et al.* (2017) to obtain structural representations for the coexistence criteria. Briefly, this approach evaluates the set of intrinsic growth rates consistent with feasible communities (all $N_i > 0$ at equilibrium) given the constraints set by the matrix of competition coefficients (see Saavedra *et al.* 2017).

Figure 9c shows the feasibility domain (set of intrinsic growth rates leading to feasible equilibria) for each pair of species (grey triangles) and for the triplet (grey-blue triangle) derived from the fit of a standard Lotka–Volterra model. The existence of a region in which the feasibility domains for all species pairs intersect indicates that there is a vector of

intrinsic growth rates for which all pairs can coexist and the triplet can coexist (the small interior grey triangle formed by the intersection of the pairwise feasibility domains falls completely within the grey-blue interior triangle giving the feasibility domain of the triplet). In this instance, the actual vector of intrinsic growth rates inferred from the model fits, denoted by the orange dot, falls in a region where the triplet can still coexist but species 1 and 2 are unable to coexist as a pair. This is, however, at odds with the known dynamics of the original data-generating consumer resource-model, and thus reflects the failure of the standard Lotka–Volterra model to accurately capture the system’s true dynamics.

In Fig. 9d, we regenerate the pairwise and triplet feasibility domains using the pairwise coefficients from a model that also includes inter-specific higher-order terms. The difference now

is that the inferred vector of intrinsic growth rates falls within a region where the triplet can coexist due to intransitivity but none of the pairs can coexist alone. This representation is faithful to the dynamics of the data-generating mechanistic model. The reason why the standard Lotka–Volterra model misrepresents the system is it doesn't capture its inherent non-additivity. In contrast, the inclusion of higher-order terms in the model improves the fit to the data and thus provides better estimates for the pairwise alpha coefficients near to the equilibrium. This then is a direct illustration of Lotka's (1924), and later MacArthur's (1970), oft forgotten words of caution on the conception of Lotka–Volterra as a Taylor approximation around the equilibrium.

To add our own words of caution, it is critical to emphasise that the reason we were able to confidently evaluate the feasibility domain based solely on the alpha coefficients from a higher-order model is because: (i) we know there exists a fixed point equilibrium (Fig. 9b); and (ii) we know it is the only non-trivial equilibrium. However, intransitivity and/or non-additivity can also give rise to cyclical dynamics resulting in large deviations in population densities around the mean, in which case the higher-order terms will have a greater influence on the long-run community state.

DISCUSSION

The prospect of extending our understanding of community dynamics from simple, tractable systems to more realistic, complex systems has fostered a revival in the study of HOIs (Bailey *et al.* 2016; Grilli *et al.* 2017; Levine *et al.* 2017; Mayfield & Stouffer 2017; Saavedra *et al.* 2017; Terry *et al.* 2017). To date, however, there has been little emphasis on the mechanistic origins of the emergent non-additivity that these HOIs aim to capture. Here we have shown that HOIs – defined as non-additive effects of density on *per capita* growth – are pervasive and emerge under even the most restrictive of mechanistic assumptions (e.g. non-logistic resource supply). We have also demonstrated the utility of HOIs in phenomenological models in terms of better approximating both short-term dynamics and final community states. At the same time, our study has made it clear that there remains considerable nuance regarding how one should best define, implement and interpret HOI models.

The hope of improving our predictive understanding of more complex (non-pairwise) systems has been a central motivation for much work on HOIs (Bailey *et al.* 2016; Grilli *et al.* 2017; Levine *et al.* 2017; Mayfield & Stouffer 2017; Saavedra *et al.* 2017). Although we did find that HOIs conspicuously improve predictive accuracy, we also see from a mechanistic perspective that HOIs are just as likely to be driven by interactions between individuals belonging to just one or two species as they are by interactions between individuals belonging to three separate species. Through the mechanistic lens, there is therefore little rationale for only perceiving HOIs as a problem when confronted by three (or more) species. The exception that proves the rule is the marked jump in relative performance by the fully specified HOI model when going from two to three species with linear functional responses competing for logistically growing essential resources (Fig. 4).

That five of the other seven core scenarios actually show a decrease in the performance of the fully specified HOI model is testament to the equally important role of non-logistic resource supply and/or resource extinction in generating non-additivity. It is equally instructive to note, in the case of logistically growing resources, that the change to a nonlinear functional response in a two-species system results in a similar increase in higher-order model performance as the change from two to three species with linear functional responses. The implication is that nonlinear functional responses, which are a species level attribute, also have an effect on phenomenological non-additivity that is comparable to the addition of a third consumer.

Independent to the dimensionality of HOIs, there also remain both theoretical and empirical hurdles to the implementation of higher-order phenomenological models. Perhaps foremost of the immediate obstacles is the sometime pathological behaviour of quadratic *per capita* growth functions, illustrated by the not infrequent population explosion in our long-term dynamic simulations of higher-order models. That this pathological behaviour seems to arise at a lower frequency in models incorporating all higher-order terms offers, one hypothetical solution, that is, fit a more complex model; however, this is clearly far from ideal. Increasingly complexity not only flies in the face of the *raison d'être* of modelling, but it also presents a near insurmountable challenge to empiricists. Fitting a fully specified higher-order model for three competitors required inferring no less than 30 parameters. Generating sufficient data synthetically is one thing, but acquiring it from experimental or observational data on real organisms is a considerable undertaking. A greater, longer-term challenge is to discover a pathology-free yet parameter-sparse, nonlinear function that captures the broadest spectrum of phenomenological non-additivities. Various Lotka–Volterra derivatives, including quotient and exponential forms in annual plant models (Hart *et al.* 2018), perhaps offer the most promising avenues of development. At the same time, the ever accelerating sophistication of hierarchical statistical models is increasingly helping researchers to obtain robust parameter estimates in spite of low degrees of freedom (McElreath 2015). Needless to say, there is plenty of room for empiricists, theoreticians and statisticians to make valuable contributions to this evolving research program.

Alongside challenges to model-fitting, we clearly still lack appropriate tools for evaluating criteria and contributions to coexistence in the presence of HOIs, at least from a phenomenological perspective. Structural techniques (e.g. Saavedra *et al.* 2017) provide a powerful tool when dynamics come close to approximating an interaction chain (i.e. exhibit negligible non-additivity). Furthermore, for systems exhibiting point equilibria, incorporating HOIs into model fits might afford much closer approximations to the dynamics near equilibria. At the same time, however, to the extent that HOIs improve approximations around equilibria, we can also assume that they increase the instability and structural sensitivity of system behaviour, such that small changes to population sizes or parameters are more likely to lead to qualitative shifts in system state (Adamson & Morozov 2012; Aldebert *et al.* 2016). At this stage, a recently-developed approach for

evaluating the structural stability of nonlinear population dynamics offers a promising route to the development of reliable criteria for evaluating coexistence in the presence of HOIs (Cenci & Saavedra 2018). Nevertheless, it should also be noted that the performance of the standard Lotka–Volterra model in the analysis of the long-run state in our simulations was often not far off that of the fully specified model (max 9%, Fig. 8). In other words, although HOIs are certainly important for accurately quantifying population abundances, they may not always be critical for capturing the qualitative properties of a system. Furthermore, as might be expected, the performance of the higher-order models relative to the standard Lotka–Volterra model was markedly reduced when the perturbation densities were limited to below half each species' carrying capacity (Figs S5–S9), indicating the latter provides improved predictions when densities fluctuate over a narrower range. Taken together, these results suggest that linear approximations may suffice when it comes to coexistence analysis in some instances, particularly when evaluating dynamics near to fixed points.

It also remains open to debate to what extent HOIs represent distinct phenomena from so-called interaction chains (or what Billick & Case (1994) refer to as indirect effects as distinct from HOIs). To look at the equations that define a mechanistic model of resource competition, there is no distinction. The only way to conceive of HOIs through a mechanistic lens is to ask whether a given system is characterised phenomenologically by *per capita* growth rates that are non-additive functions of consumer densities. Consequently, the distinction is mechanistically artefactual. Rather than being a unique dynamic, an interaction chain might be viewed more precisely as a corner-case under which the emergent dynamics exhibit negligible non-additivity. This viewpoint breaks with previous treatments of HOIs and interaction chains where they have been represented as fundamentally distinct (Billick & Case 1994; Levine *et al.* 2017). One argument is that HOIs and interaction chains operate over different time-scales, with the former having instantaneous effects and the latter being characterised by the time-lag it takes for densities to build up or mediate population dynamics (Billick & Case 1994; Levine *et al.* 2017). The problem with this distinction is that it is reasonable to assume that the strength of the HOI is itself density dependent. Even if we consider plastic or behaviourally mediated traits such as plant rooting depth, the extent to which an individual plant switches to a different depth in the presence of a particular competitor will typically depend on the number of that particular competitor surrounding it. It is also telling that delineating HOIs from interaction chains in any empirical system will be sensitive to the formulation of the model used to fit the data (e.g. classic Lotka–Volterra vs. Beverton–Holt vs. the Ricker model). Ultimately, these phenomena lie along a continuum, with additive interactions on one end and non-additive interactions on the other. It might be possible to find anecdotal ecological examples that provide a compelling fit to each end of this spectrum, but our expectation is that the vast majority of scenarios can be located in the vast grey area in between.

Considering our results as a whole, we ultimately found it more useful to cast HOIs as a non-additivity problem as opposed to the multi-species problem they are most

commonly associated with. This of course does not negate the critical challenge of understanding when multi-species (> 2) dynamics will deviate from those predicted from pairwise interactions due to emergent indirect effects. Nevertheless, given the aforementioned ambiguity in distinguishing between additive and non-additive interactions in multi-species systems, we would argue a clearer way forward is to avoid conflating questions relating to indirect effects with those relating to non-additivity. This is not to say they are independent of each other – they clearly are not – but rather that, to a first approximation, they represent orthogonal concerns.

CONCLUSION

MacArthur (1970) began his mechanistic derivation of Lotka–Volterra competition by recognising the equations' conception as a coarse mathematical approximation. With the passage of time and ecology's shift to more and more complex empirical systems, this crucial qualification seemingly fell by the wayside. As a result, it simultaneously fuelled a proliferation of empirical model fitting (Park 1948; Vandermeer 1969; Law & Watkinson 1987; Antonovics & Kareiva 1988) and reactionary critiques of the proverbial straw man (Tilman 1987; Hall 1988). Our analysis and discussion therefore shines a critical light on the merits and demerits of both positions. On the one hand, we have shown that higher-order interactions emerge under even the most basic mechanistic assumptions; on the other, the basic system of equations were only ever intended as an analytical tool rather than as a carbon copy of the full dynamics of real-world systems. Almost 50 years from MacArthur's influential paper, it seems the time is ripe for re-embracing community ecology's canonical equations in a suitably expanded form.

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AUTHORSHIP

ADL and DBS designed the study, ADL performed analysis, and ADL and DBS wrote the manuscript.

DATA ACCESSIBILITY STATEMENT

The code and simulation output supporting are available through Figshare: <http://dx.doi.org/10.6084/m9.figshare.7583276>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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