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**Detecting Higher Order Competitive Interactions**

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# Abstract

Almost every species on earth interacts with more than one competitor. When species simultaneously interact with two or more competitor species, higher order interactions (HOIs) can emerge and invalidate the application of classical theories of species competition. In order to extend pairwise ecological theory to multi-species communities it is critical to understand how often and by what mechanisms HOIs arise. In this paper we discuss the difficulties inherent in defining HOIs and propose a definition for HOIs that distinguishes them from non-linear density dependence and emphasizes their consequences for predicting multispecies competition. We then use a simple mechanistic resource competition simulation to illustrate how HOIs can be detected using phenomenological models and discuss the mechanistic basis for HOIs. In our example, we simulate resource competition between three annual plant species differing in their phenology and their functional response to resource depletion. We then fit a phenomenological competition model to the outcome of simulated competition and evaluate whether the effects of multispecies competition are equal to the sum of single species effects. We find that the strength of HOIs vary with phenology in our simulation: species that grow later in the season experience stronger HOIs because the competitive environment they experience is strongly affected by species growing earlier in the season. We conclude that HOIs are likely to arise in systems where resource availability declines rapidly and individual size increases rapidly over the course of a single growing season.

*Key words: competition, coexistence theory, phenology, annual plants*

# Introduction

Over the course of their lifetime, most organisms interact with a diversity of predators, pathogens and competitors. Despite this, most classical models in community ecology summarize species interactions assuming that the per capita effect of one species on another is independent of the densities of other species in the system. Such models have been critical to the development of modern coexistence theory (Chesson 2000, Levine et al. 2017), and imply that the dynamics of multi-species species competition can be predicted if we have an accurate understanding of the interactions between each pair of species. This concept is also central to recent efforts to relate species’ and community functional traits to the outcome of their competitive dynamics (Kraft et al. 2015).

The potential for higher order interactions (HOIs) between species challenges the core assumption of many foundational models in ecology (Neill 1974, Mayfield and Stouffer 2017, Levine et al. 2017, Grilli et al. 2017). The conceptual importance of HOIs is clear: if HOIs are prevalent even a perfect understanding of competition between pairs of species may not be sufficient to describe the dynamics of communities with more than two species (Neill 1974, Billick and Case 1994, Levine et al. 2017). The presence of HOIs challenges classical definitions of coexistence and the niche that rest on the assumption that intraspecific and interspecific interactions are fixed strength (Levine et al. 2017). In the extreme, HOIs may permit coexistence in communities of three or more species that are unable to coexist as species pairs (Grilli et al. 2017).

Although there has been a revival in ecologists’ interest in the implications of HOIs for community coexistence the field still lacks a consensus definition of HOIs and robust methods to detect them in empirical data. The difficulty in defining HOIs was apparent early on (Vandermeer 1969, Neill 1974, Case and Bender 1981, Pomerantz 1981). Early discussions defined an HOI only within the context of a standard Lotka-Volterra competition model (Vandermeer 1969). Billick and Case (1994) attempted to define HOIs more generally as the presence of non-additive effects between species, but this definition was itself problematic (Adler and Morris 1994). A recent paper by Mayfield and Stouffer (2017) included non-linear intra- and inter-specific interaction terms in their definition of HOI, which deviates from the original emphasis on interactions between more than two species. In another recent paper, Grilli et al. (2017) demonstrate the implications HOIs could have for multispecies coexistence, but their example of HOIs are strictly speaking not interaction modifications at all, and fit more accurately within the definition of indirect interaction chains (Levine et al. 2017). The renewed interest in HOIs and their potentially profound implications for modeling multispecies communities demand a clear definition of what they are and a worked example showing how HOIs could be detected in the kind of empirical data ecologists actually collect.

In addition, the mechanisms that do and do not generate higher order interactions between competing species are unclear. Ecologists know that higher order interactions emerge organically in many mechanistic competition models (Abrams 1983, O’Dwyer 2018). This has two key implications: first, since mechanistic models generate HOIs without the addition of explicit HOI terms, one might argue that the issue is essentially an artificial construct of phenomenological models. However, the question of whether perfect knowledge of pairwise interactions is sufficient to predict the dynamics of more complex systems is fundamentally phenomenological and thus can only be investigated in the context of phenomenological interactions. Second, if mechanistic models almost unavoidably generate HOIs (Abrams 1983), the scarcity of rigorous demonstrations of HOIs in nature represents a glaring gap in our knowledge of competition—the logistical challenge of studying multispecies competition notwithstanding. An investigation of the mechanistic basis of HOIs would help ecologists predict when and where HOIs are most likely to emerge—and may help explain why phenomenological models without HOIs have been successfully applied in many communities.

In this paper we discuss the difficulties in defining HOIs, the pitfalls inherent detecting HOIs with phenomenological models, and the potential mechanisms that generate HOIs. To illustrate our definition and to highlight the mechanism that can generate HOIs we construct a simple mechanistic resource competition model that captures key features of the kind of empirical data that ecologists often collect when studying natural populations. We use the mechanistic model to simulate a virtual field experiment on the effects of competition on individual performance. We then fit phenomenological models to the simulated data in order to assess the presence of HOIs. Our virtual experiment demonstrates that HOIs may indeed be common even in relatively simple mechanistic competition. Importantly, we suggest that systems in which competitors vary in timing of resource uptake are likely to show HOIs, and that HOIs will likely be stronger for species maturing later in the growing season. Our worked example also shows how the strength and even the direction of HOIs are dependent on the structure of the phenomenological model being fit to the data.

## What counts as a higher order interaction?

Competition occurs when individuals consume the same limiting resource, such that increases in consumer densities reduce the availability of resources, which in turn changes the population growth rate of the consumers (Meszéna et al. 2006). Thus, resource competition is an indirect effect of individuals on one another mediated by shared resources. The commonly used phenomenological definition of competition simplifies the representation of the interaction by focusing on the net effect of the indirect interaction without tracking the status of shared resources. At the population-level, phenomenological competition is measured as the reduction in a per-capita population growth rate due to an increase in density of individuals of the same trophic level (Chesson 2000).

The great benefit of modeling competition phenomenologically is that such models can be fitted to empirical data for any pair of species without making assumptions about which resources or environmental factors are limiting to their populations (e.g. (Kraft et al. 2015)). This power, however, comes with complications. Phenomenological models require choosing a functional form for the effects of species density on population performance. As we will show this choice fundamentally dictates how we define species interactions and the how we could detect higher order interactions (Adler and Morris 1994).

In order to construct a useful definition for HOIs, we start from what we see as the important implication HOIs have for community dynamics: the presence of HOIs means that even if an ecologist had perfect knowledge of how each pair of species compete against one another, the ecologist would be unable to predict the dynamics of a community with more than two species. While this may sound mysterious, HOIs can arise from a simple modification of standard competition models: if we assume, as is done in the classical Lotka-Volterra model, that interactions between species are independent of the broader competitive environment, then this means there are no HOIs; if on the other hand, interactions between species depend on the density of other species then this leads to HOIs (see (Billick and Case 1994)). Thus HOIs and interaction modification are often discussed as two sides of the same coin (Adler and Morris 1994).

Nevertheless, recent theoretical and empirical papers have defined HOIs in other ways. For instance, Grilli et al. (2017) show HOIs emerging in a model of forest dynamics even without interaction modifications. However, what the authors call HOIs in their model are essentially indirect effects or interaction chains (sensu (Levine et al. 2017). These appear to be HOIs on the time scale of the longest-lived life stage in the competing populations because their model does not explicitly track the density of competitors during early stages of competition.

In a study of annual plant competition, Mayfield and Stouffer (2017) define as HOIs any polynomial terms of species density in their demographic model that improve the statistical fit to the data. Thus, their definition includes interactions between intraspecific and interspecific density and even quadratic terms involving the density of a single species. While including these terms as HOIs simplifies their statistical detection, and maps clearly onto what a mathematician thinks of as a “higher order” term, these HOIs have different implications for community dynamics than the definition we emphasize. For instance, including quadratic density terms within the definition of HOIs may seem inconsistent with idea that HOIs result from interaction modification: i.e. how can a species modify its own competitive effect?

A similar set of issues was pointed out early on by Pomerantz (1981) who argued that a distinction needed to be made between HOIs and non-linear density dependence. In the most widely used models for effects of competition, such as the Beverton-Holt, Hassell and Ricker models, per capita growth rate is assumed to be a nonlinear function of competitor density (Hassell and Comins 1976). In each of these models the effect of each additional competitor on growth declines as more competitors are added. This could be interpreted as a kind of interaction modification among *individuals within* species. Like Pomerantz (1981) however, we advocate restricting higher order interactions to cases where individuals of one species modifies the effect of individuals of other species.

*Defining Higher Order Interactions*

To formally define higher order interactions and avoid the pitfalls of prior attempts to do so, we return to the key conceptual issues that HOIs imply: the presence of emergent properties in multispecies communities. Or equivalently, that dynamics in multispecies communities cannot be neatly decomposed into separate competitive effects of each species on each other species. Emergent properties at the community level, or non-independence of competitive effects arise due to interaction modification between competitors. Following from this and building on past efforts by Billick and Case (1994) and Adler and Morris (1994), we propose the following general mathematical definition.

We start with a general phenomenological model for species competition in discrete time (though the equivalent definition applies in continuous time):

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where on the left-hand side is the per capita growth rate of species at time , , is a species specific parameter defining the average per capita population growth rate in the absence of competitors, and the function gives the competitor-influenced per capita population growth rate as a function of total competition , which determined by the density of all competitors in the community. While is technically dependent on —it cannot be measured without specifying some function for per capita growth rate—we believe that separating the two is heuristically valuable as a way to differentiate non-linear demographic responses from HOIs. For instance, in the most widely used models for density dependent population growth is non-linear: in the Ricker model , whereas in the Beverton-Holt or Hassel model

An HOI occurs whenever cannot be expressed as a sum of individual species effects. Mathematically this means that for any function of only a single species *j’s* density. HOIs are therefore any additional terms in the summation of that involve functions of more than one species’ density. Following this definition, there are no HOIs in the standard Ricker and Beverton-Holt models because, despite the nonlinear effects of on per capita growth, is a weighted sum of species densities, , where is the competitive effect of each individual of species on species . In fact, one advantage of our definition of HOIs over earlier definitions (e.g. Billick and Case 1994) is that it does not require that each species’ growth depend linearly on density. For example, could be a sum of quadratic functions of each species’ density: (Mayfield and Stouffer 2017). While the effects of density are non-linear in this formulation of , this does not imply HOIs because each species’ contribution to total competition does not depend on the density of any other species ( depends only on *nj*). Our definition of HOIs does include cases where intraspecific competition is modified by the density of another species. This means that HOIs as defined here can occur even in interactions between two species (Billick and Case 1994, Mayfield and Stouffer 2017).

# HOIs in a mechanistic resource competition model

To illustrate how we might detect and understand the mechanisms generating HOIs in empirical data on species interactions, we simulate competition among annual plants for a single shared resource using a mechanistic resource competition model. We then fit species’ responses to interspecific competition using a simple phenomenological competition model. By considering the cases in which higher order interactions emerge in this phenomenological description of the system, we can address the processes causing these interactions develop.

Our mechanistic model is inspired by California annual plant communities. In this system, rainfall generally starts in the early winter and gradually declines through the spring while temperature and evaporative demand increase. Plants germinate in the winter and grow until they begin to flower in spring. By summer, most plants have completed flowering and produce seeds and die. In our model, we track a single pool of generic soil resources, most easily thought of as water given its timing of availability. Importantly, this pool is not resupplied during the growing season. As spring progresses, plants grow larger and use up the pool of stored soil resources. Because growth is resource dependent in our model, plant growth slows and eventually net growth is negative as resources are depleted. We make the assumption that when net plant growth stops, the optimal behavior of the plants is to stop producing vegetative biomass and start producing seeds (Cohen 1976).

The model is expressed as a set of differential equations,

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where gives the resource availability at time , and gives the resource supply rate. The final term expresses the loss of resources due to uptake by plants. Plant biomass of species at time is given by , *s* is the number of species in the community and is the resource dependent uptake function for species *i*. We simulate a Mediterranean climate by setting initial resource availability high, , and setting the resource supply rate to zero—resource availability starts out high and is gradually depleted (Figure 2 a).

Growth of each species is simulated with a piecewise differential equation dependent on resource availability,

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where, is the total biomass of species , is a resource conversion factor, is a per biomass respiration and tissue loss rate, and as in the first equation, is a function giving resource uptake rate. The growth of each species stops when meaning that biomass gained is equal to biomass lost to respiration and maintenance. The optimal behavior of the plant at this point is to stop growing and convert all biomass to seed mass. We impose this behavior on the model by setting growth to zero when resources fall to this point.

Different species are likely to have different rates of resource uptake and growth. In our simulation, we assume a trade-off between rates of resource uptake at high resource availability and rates of resource uptake at low resource availability (Figure 2c). This means that species which grow rapidly early in the season when resource availability is high will stop growing and produce seed earlier (Figure 2b). In contrast, species that grow slower early in the growing season are able to persist later into the season when resource availability is low.

This trade-off between species in early and late season growth rates is produced by giving each species a saturating Monod resource uptake function (Miller and Klausmeier 2017),

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|  |  | (4) |

where, is the maximum rate of resource capture and is the half-saturation constant of resource capture. In our simulations the species with the highest maximum resource uptake rate , has the highest half-saturation constant , and the species with slowest maximum resource uptake rate has the lowest half-saturation constant. The resource uptake curves result in species-specific growth and phenology for the three species we model here, and term ‘early’, ‘mid’ and ‘late’ (Figure 2). The differences in the timing of growth of species in this model recreates important functional differences between species observed empirically in this system (Godoy and Levine 2013).

So far, we have described a model of growth dynamics in continuous time *u* within a single generation. By contrast, for fitting the phenomenological competition models, we track the total population size of each generation at a discrete annual time . To calculate the total population size of each species in year we take each species’ maximum vegetative biomass during the growing season, multiply that by a conversion factor to get total number of seeds produced. Thus,

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where is the number of seeds produced at the end of the growing season, and therefore available to start the next years population growth. We assume that there is no seed mortality between years and all seeds germinate. We simulate these dynamics using the ordinary differential equation solvers package desolve in the statistical program R (R Core Team 2015). Simulation parameters and code to run the simulations are given in the supporting information.

Finally, we used this mechanistic model to simulate plant growth when faced with a range of densities of one or two other competitors, and from these simulated data we fit a phenomenological competition model. In the simulated experiment each of the three species are grown against increasing densities of either one interspecific competitor species or two interspecific competitor species at once. For each simulation, we calculated the per capita reproductive output of the focal species and fit the phenomenological competition models described in the next section to our simulated experimental data.

## Phenomenological annual plant model

We model annual plant competition in terms of the decline in per capita reproductive output with increasing density of competitors at the start of the growing season (). We tested two different phenomenological competition models. The first has been used in a number of empirical studies of annual plant competition e.g. (Kraft et al. 2015),

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where denotes maximum per capita reproductive output, is the per capita competitive effect of species on and is a species-specific parameter controlling how steep fecundity declines with competition in general.

We also fit a second model in which the effects of each species are modified with a separate exponent where

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This allows species to have per capita effects that depend on density but the competitive effects of each species are still assumed to be additive. We fit separate competition models for each of three species using the nls package in R. We defined for each species as the per capita fecundity in the absence of any competitors and fixed this as a constant when fitting the models.

In order to detect HOIs and measure their strength we fit the phenomenological model to cases where each focal species faced increasing densities of only one other competitor species at a time. Once we had shown that phenomenological models fit these pairwise dynamics adequately we used the models to predict species fecundity in the case where the focal species simultaneously faces two interspecific competitor species. If species effects are additive, then our model fit to density gradients of a single competitor species should be able to predict the joint effect of competition from two competitor species together. However, if there are HOIs then the sum of species effects will not be equal to the observed effect of multiple species. We use the deviation between the per capita fecundity of each species predicted by the additive phenomenological model and the per capita fecundity observed in the simulations as a measure of the effect of HOIs. Importantly, this approach does not require that we specify the functional form of the higher order interaction term.

# Evidence for HOIs

For all three species we found that the modified phenomenological competition model with varying exponents (equation 7) fit the simulated data accurately whereas the standard model (equation 6) only fit the data for the early species (Figure 3; Figure S 1). When we tested how well the models fit to competition from one species at a time predicted the simultaneous effects of two species’, we found weak HOIs for the early season species and stronger HOIs for the mid and late-season species (Figure 4). For the early species, the observed strength of competition from two species together was close to the sum of the two species’ individual effects (Figure 5). For the mid and late season species, the observed strength of competition did not equal the sum of the single species effects (Figure 5 b, c). Specifically, assuming that species effects were additive led us to underpredict the total strength of competition on the mid-season species (Figure 5 b), and overpredicted the strength of competition on the late species (Figure 5 c). In short, our phenomenological models accurately described single competition but this did not predict the net effect of two species competition. This shows that competitors’ effects changed depending on the density of other competing species, and by our definition this is a HOI.

Our simulation shows that even in a relatively simple resource competition model the effects of multi-species competition may not be equal to the sum of the individual species effects. Comparing the observed effects of multispecies competition to the sum of the separate species’ effect is a useful way to determine the presence of HOIs without assuming a specific functional form for the HOIs. This makes it a diagnostic tool, not a way to predict multispecies community dynamics.

*What Causes Higher Order Interactions?*

In this model, HOIs emerge because species growth and resource uptake rates are dependent on the current availability of resources in the system (Figure 2 c). This means that as species use resources they not only affect the growth rates of their competitors, but they can also affect the net interaction between their competitors. For instance, the early species has the most rapid growth and resource uptake rate early in the season when resource concentrations are high and it has a strong impact on early season resource availability. This shifts the resource uptake rates of the mid and late season species left along their resource uptake curves. Figure 6a shows how the timeseries of resource uptake rates of the mid and late season species shift earlier in response to the change in resource availability caused by the early season species. Because the mid and late season species resource uptake curves are shaped differently, this reduces the uptake rate of the mid-season species more than the late season species during the period of time when both species are active, that is until the mid-season species stops growing (gray vertical lines Figure 6 a). Taking the time averaged resource uptake rates of each species over this period shows the effect more clearly: the average resource uptake rate of the mid-season species declines much more than that of the late season species in response to the early season species (Figure 6 b).

Differences in how much the species resource uptake rates change explain the direction of the HOI effect of the early and mid-season species on the late season species: in the presence of the early season species, the late season species gets a larger share of the resource pool it competes for with the mid-season species, and the joint effect of competition is less than additive (Figure 4 c; Figure 5 b). The same dynamics cause the mid-season species to experience stronger than additive competition from the early and late species together: in the presence of the early season species, the mid-season species gets a smaller share of the resource pool it competes for with the late season species (Figure 4 b; Figure 5 b).

By contrast, the early species is only weakly affected by HOIs (Figure 5). In principle, resource uptake by the late season species should reduce the early season species’ average resource uptake rate more than it does the mid-season species, thereby strengthening the effect of competition on the early species. However, this effect is very weak because the late season species grows much slower early in the season than either of its competitor and so it has minimal impact on resource availability. Meanwhile, the mid-season species does not significantly change the resource uptake rate of the late season species because the late species’ resource uptake curve is flat over the range of resource availabilities that the early species is active (Figure 2).

The origin of HOIs in this system are consistent with the arguments in favor of HOIs put forward by Abrams (1983). Abrams argued that HOIs should occur when competing species have different non-linear responses to resource availability. In our simulation, the resource uptake and growth rates of the competing species follow a Monod or type II functional response to resource availability (Figure 2c). This means that competition between pairs of species depends upon the level of resources available. Since species also influence the resource concentration itself, it follows that competition between any pair of species is influenced by the presence of other species in the community—the definition of a HOI.

What makes our example more complicated, but perhaps more realistic, is that unlike in classical resource competition models, resources do not reach an equilibrium during the course of our simulation. Rather, they are constantly declining throughout the season (Figure 2 a). Deriving competition coefficients from a mechanistic resource competition model often requires first solving for stable resource equilibria and then calculating the first order sensitivity of the growth rate of each species to the resource availability and the sensitivity of the resource to the consumers (Tilman 1977, Meszéna et al. 2006, Letten et al. 2017). However, we believe that in many natural systems, such as those involving annual plants, the pace of resource dynamics may be as rapid as the change in consumer biomass. This makes deriving competition coefficients analytically much more difficult, perhaps impossible (O’Dwyer 2018). The great advantage of statistically fitting a phenomenological model to observed or simulated effects of competition is that this approach can help us understand pairwise competition even in such complex cases. However, our work here shows that this advantage may come at the cost of ignoring important HOIs in multispecies communities.

# Are HOIs Common in Nature?

One way to view HOIs in this system is to consider it a specific instance of a more general case in which the trait that determines each species’ impact on and sensitivity to resource availability is itself governed by resource availability over time (Meszéna et al. 2006). In this case, the trait in question is the average rate of resource uptake, which shifts in response to resource availability and thus the activity of competitors. More generally, we believe a general recipe for HOIs will be systems in which 1) some species can cause large resource fluctuations, 2) the rate of resource uptake by other species shifts in response to resource availability, and 3) the strength of this response varies across species. Among plants, plastic changes in traits such as height, specific leaf area, and phenology, have been shown in response to competition and changes in resource availability (e.g. (Aronson et al. 1992, Bennett et al. 2016, Conti et al. 2018)). In theory, these traits should also determine each individual’s impact and sensitivity to competition. So, are HOIs inevitable? And if so why are so few documented examples among competing plants (but see Mayfield and Stouffer 2017)?

One hypothesis is while HOIs are common, they are often weak. A key factor in producing HOIs in our simulation is that each species has a uniquely shaped resource uptake curve. Additional simulations show that the weaker the trade-off between resource uptake rates at high versus low resource availability—or the more similar species resource uptake curves are to one another—the weaker the HOIs are in this system (Appendix A). In nature, such strong trade-offs may be rare.

The large changes in resource availability and plant biomass in our simulation also contribute to the strength of HOIs. Because resource availability fluctuates widely in our simulation, it means that species interactions change dramatically over the course of the season. Without the extreme fluctuation in the resource environment, species would have relatively constant competitive effects on one another and no HOIs would emerge. For instance, compare our system to an idealized version of resource competition experienced by competing perennial plants (Dybzinski and Tilman 2007). Due to their large size, perennial plants can be assumed to quickly draw resources down to a dynamic equilibrium close to the environmental resource supply rate. Thus, even if species have different non-linear responses to resource concentration the fact that resource concentration is relatively fixed eliminates the possibility of strong higher order interactions. Because of their resource dynamics, seasonally forced systems, such as annual plant communities in a Mediterranean climate, may be a good place to look for strong HOIs (Mayfield and Stouffer 2017).

Our definition of HOIs does lead to some peculiar properties where species contribution to change non-linearly with density. In our simulation for example, we found a model with non-linear terms for each species’ effect best fit the data for the mid and late-season species. These terms are required to fit the single species data because the densities of each competitor have different non-linear effects (Figure 3). To see how this creates issues for defining HOIs, consider two species, one and two, that have identical effects on shared resources and therefore identical effects on a third competitor, species three. Our definition of HOIs suggests that if there are no HOIs, the true combined effect of one and two together will be the sum of their separate effects:, where is a linear or non-linear function of species density. However, since we have assumed that individuals of one and two are identical we know that their true effect on three must in fact be equal to If is a non-linear function then . Hence the sum of the separate species effects will not be equal to the true effect, even when we do not assume any explicit interaction modification. This problem hints that any system in which competition depends non-linearly on the effects of density, even single species density, will produce HOIs.

# Conclusion

We have sought to clarify the definition of HOI’s and explain how they could arise from relatively simple competitive dynamics. We propose that the most robust method to detect HOIs is to compare the observed strength of multispecies competition to the sum of individual species effects. We illustrate our definition of HOIs and our proposed method for detecting HOIs with a simple mechanistic model of species competition for a single resource. Defining HOIs in this way requires that the focal species’ response to single species competition is accurately modeled first. Our analysis also reveals a potential difficulty in formulating a truly general way of measuring HOIs—it may be that HOIs are only defined in cases where per capita interspecific competition is constant. While we believe that HOIs should be common in nature this does not mean that they will be strong or strong enough to detect statistically in empirical settings. Our work suggests that environments in which resource availability and competitor size change rapidly during a single growing season may be a likely place for HOIs to emerge.

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# References

Abrams, P. A. 1983. Arguments in Favor of Higher Order Interactions. The American Naturalist 121:887–891.

Adler, F. R., and W. F. Morris. 1994. A General Test for Interaction Modification. Ecology 75:1552–1559.

Aronson, J., J. Kigel, A. Shmida, and J. Klein. 1992. Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. Oecologia 89:17–26.

Bennett, J. A., K. Riibak, R. Tamme, R. J. Lewis, and M. Pärtel. 2016. The reciprocal relationship between competition and intraspecific trait variation. Journal of Ecology 104:1410–1420.

Billick, I., and T. J. Case. 1994. Higher Order Interactions in Ecological Communities: What Are They and How Can They be Detected? Ecology 75:1530–1543.

Case, T. J., and E. A. Bender. 1981. Testing for Higher Order Interactions. The American Naturalist 118:920–929.

Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics 31:343–366.

Cohen, D. 1976. The Optimal Timing of Reproduction. The American Naturalist 110:801–807.

Conti, L., S. Block, M. Parepa, T. Münkemüller, W. Thuiller, A. T. R. Acosta, M. van Kleunen, S. Dullinger, F. Essl, I. Dullinger, D. Moser, G. Klonner, O. Bossdorf, and M. Carboni. 2018. Functional trait differences and trait plasticity mediate biotic resistance to potential plant invaders. Journal of Ecology 106:1607–1620.

Dybzinski, R., and D. Tilman. 2007. Resource Use Patterns Predict Long‐Term Outcomes of Plant Competition for Nutrients and Light. The American Naturalist 170:305–318.

Godoy, O., and J. M. Levine. 2013. Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. Ecology 95:726–736.

Grilli, J., G. Barabás, M. J. Michalska-Smith, and S. Allesina. 2017. Higher-order interactions stabilize dynamics in competitive network models. Nature 548:210–213.

Hassell, M. P., and H. N. Comins. 1976. Discrete time models for two-species competition. Theoretical Population Biology 9:202–221.

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences of the United States of America 112:797–802.

Letten, A. D., P.-J. Ke, and T. Fukami. 2017. Linking modern coexistence theory and contemporary niche theory. Ecological Monographs 87:161–177.

Levine, J. M., J. Bascompte, P. B. Adler, and S. Allesina. 2017. Beyond pairwise mechanisms of species coexistence in complex communities. Nature 546:56–64.

Mayfield, M. M., and D. B. Stouffer. 2017. Higher-order interactions capture unexplained complexity in diverse communities. Nature Ecology & Evolution 1:0062.

Meszéna, G., M. Gyllenberg, L. Pásztor, and J. A. J. Metz. 2006. Competitive exclusion and limiting similarity: A unified theory. Theoretical Population Biology 69:68–87.

Miller, E. T., and C. A. Klausmeier. 2017. Evolutionary stability of coexistence due to the storage effect in a two-season model. Theoretical Ecology 10:91–103.

Neill, W. E. 1974. The Community Matrix and Interdependence of the Competition Coefficients. The American Naturalist 108:399–408.

O’Dwyer, J. P. 2018. Whence Lotka-Volterra?: Conservation laws and integrable systems in ecology. Theoretical Ecology.

Pomerantz, M. J. 1981. Do “Higher Order Interactions” in Competition Systems Really Exist? The American Naturalist 117:583–591.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Tilman, D. 1977. Resource Competition between Plankton Algae: An Experimental and Theoretical Approach. Ecology 58:338–348.

Vandermeer, J. H. 1969. The Competitive Structure of Communities: An Experimental Approach with Protozoa. Ecology 50:362–371.

# Figures



Figure 1. Three species competitive network. Inter- and intraspecific competition between species is depicted with the blue arrows. The effect of species two on one can be described by the per capita effect α12. An HOI, β1(23), is depicted as arrows from species two and three converging on one. The added effect of the HOI indicates that net effect of two and three on species one is non-additive.

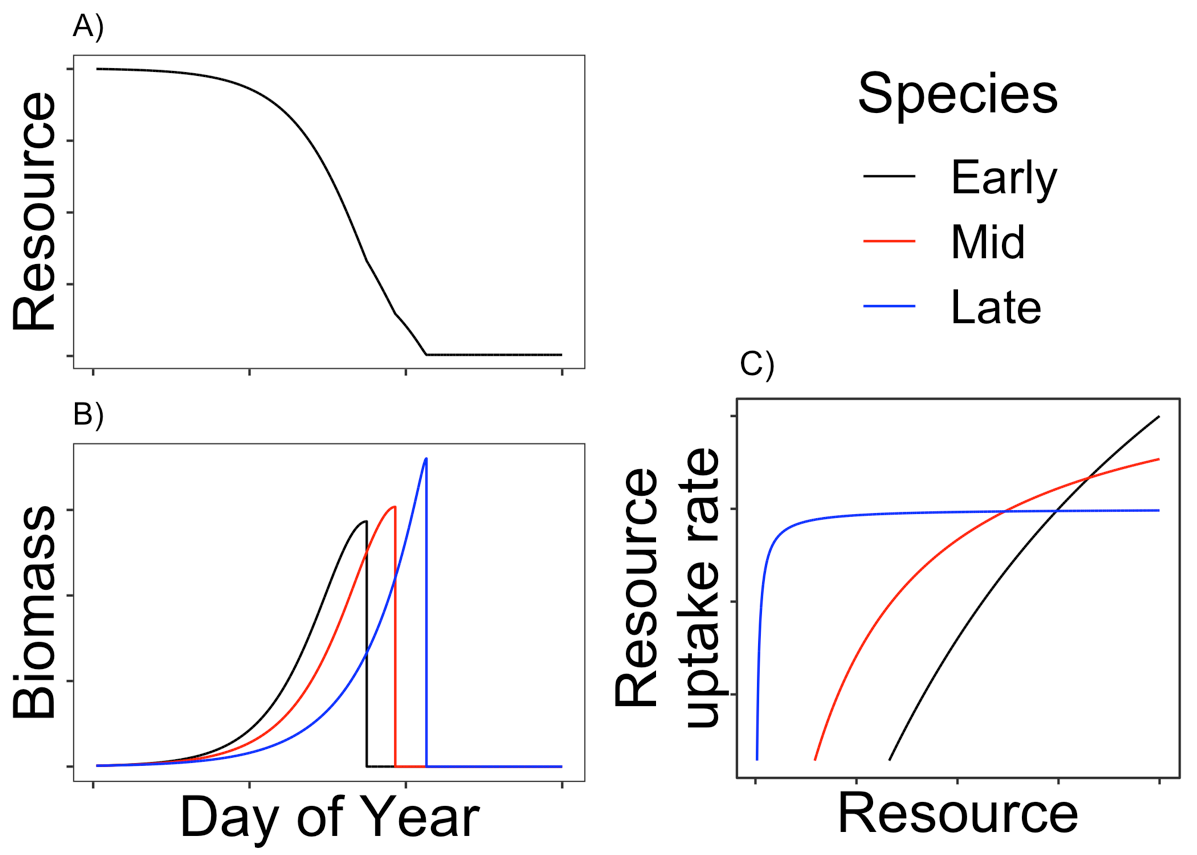


Figure 2. Example time series showing a) the drawdown of the resource during the course of the simulated growing season, b) the growth of each of species shown with colored lines and c) the dependence of resource uptake rates on resource concentration. The early season species grows rapidly when resource availability is high and senesces early. By contrast, the late season species grows slower than species one and two when resource availability is high but it is able to maintain higher rates of resource uptake at lower resource concentrations. This allows it to grow later into the season and senesce last. The middle season species lies between these extremes.

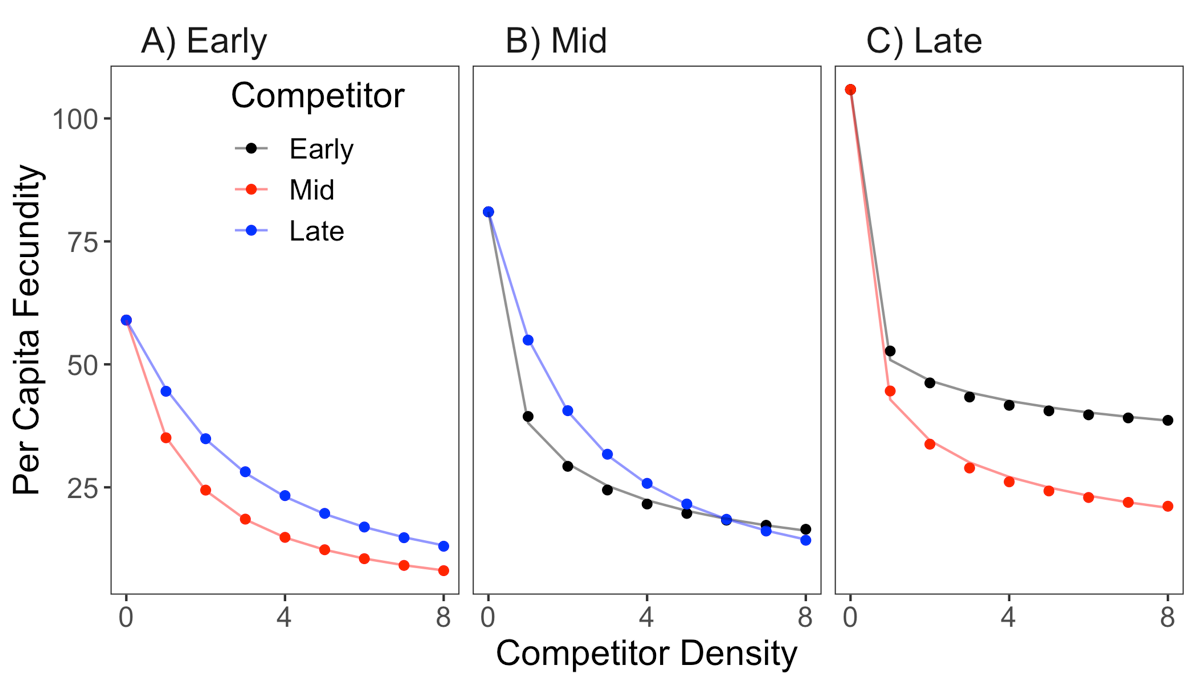


Figure 3. Simulated per capita seed production of the a) early, b) middle and c) late season species in response to increasing inter-specific density on the x-axis. Colors correspond to the identity of the competitor species. The solid line shows best fit line from the model with varying exponents on each competitor’s effect (equation 7).

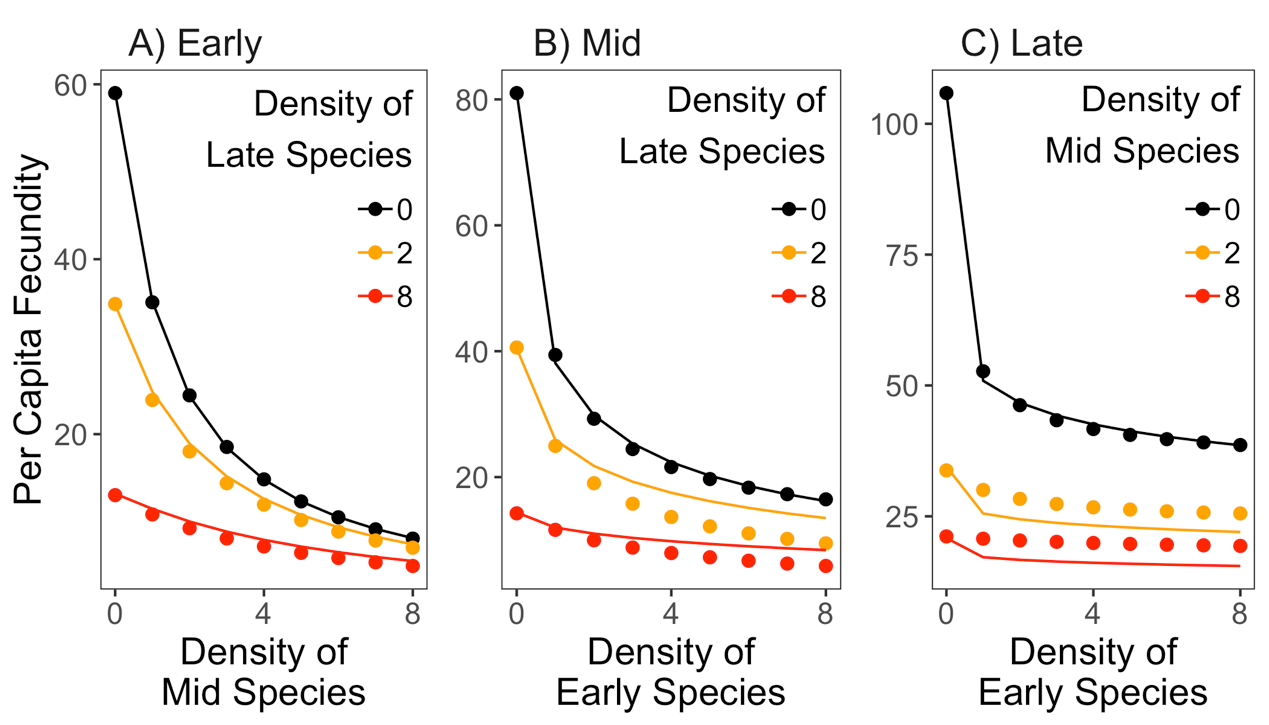


Figure 4. Simulated per capita seed production of the a) early, b) mid and c) late season species in response to increasing competition from two species at once. Increasing densities of one competitor species are shown on the x-axis and increasing density of a second competitor are shown with the varying colors. The lines show the predicted per capita fecundity from the competition model with varying exponents (equation 7). The predictions are generated assuming that species’ competitive effects are additive. Deviations between the predictions (lines) and the observations (points) indicate the presence of non-additive species’ effects and therefore higher order interactions.

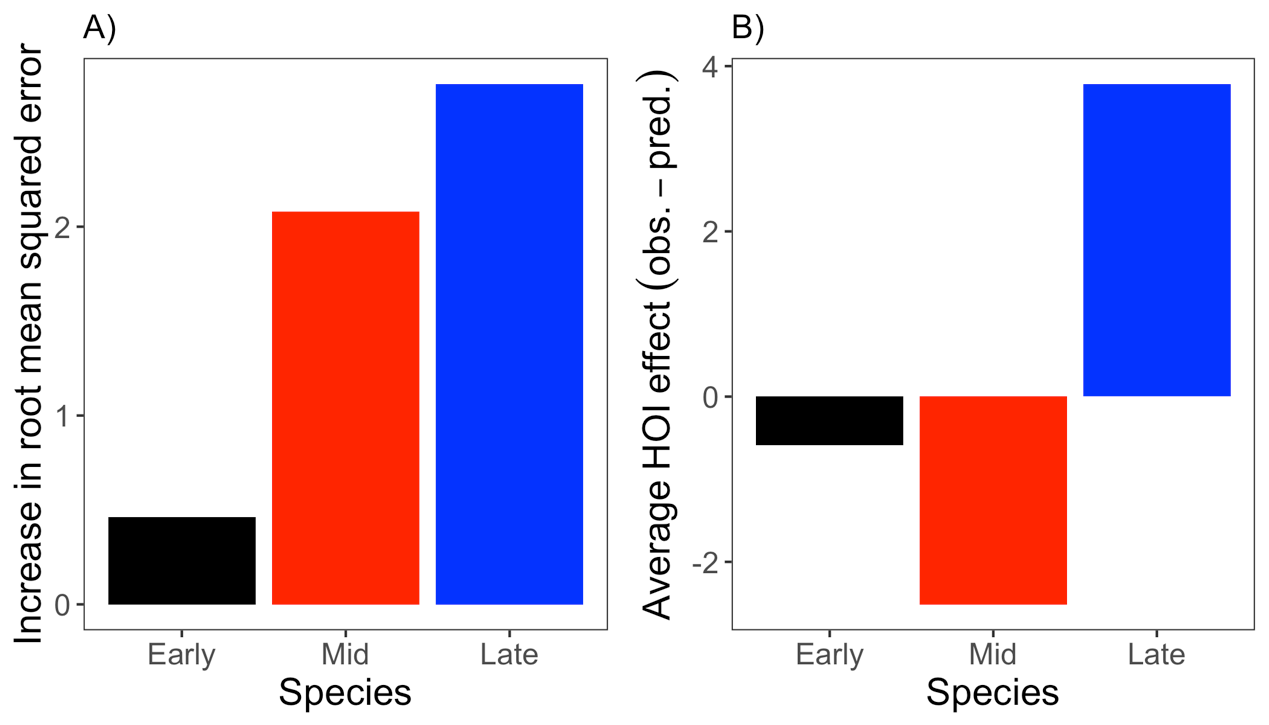


Figure 5. Deviation from additivity of two-species competition for each species in the community. A) The deviation from additive competitor effects is shown as the increase in root mean squared error of the phenomenological model (equation 7) in multispecies competition compared to single species competition. B) The average deviation from additive competitor effects, positive values show that multispecies competition was weaker than predicted, negative values show where competition was greater than predicted.

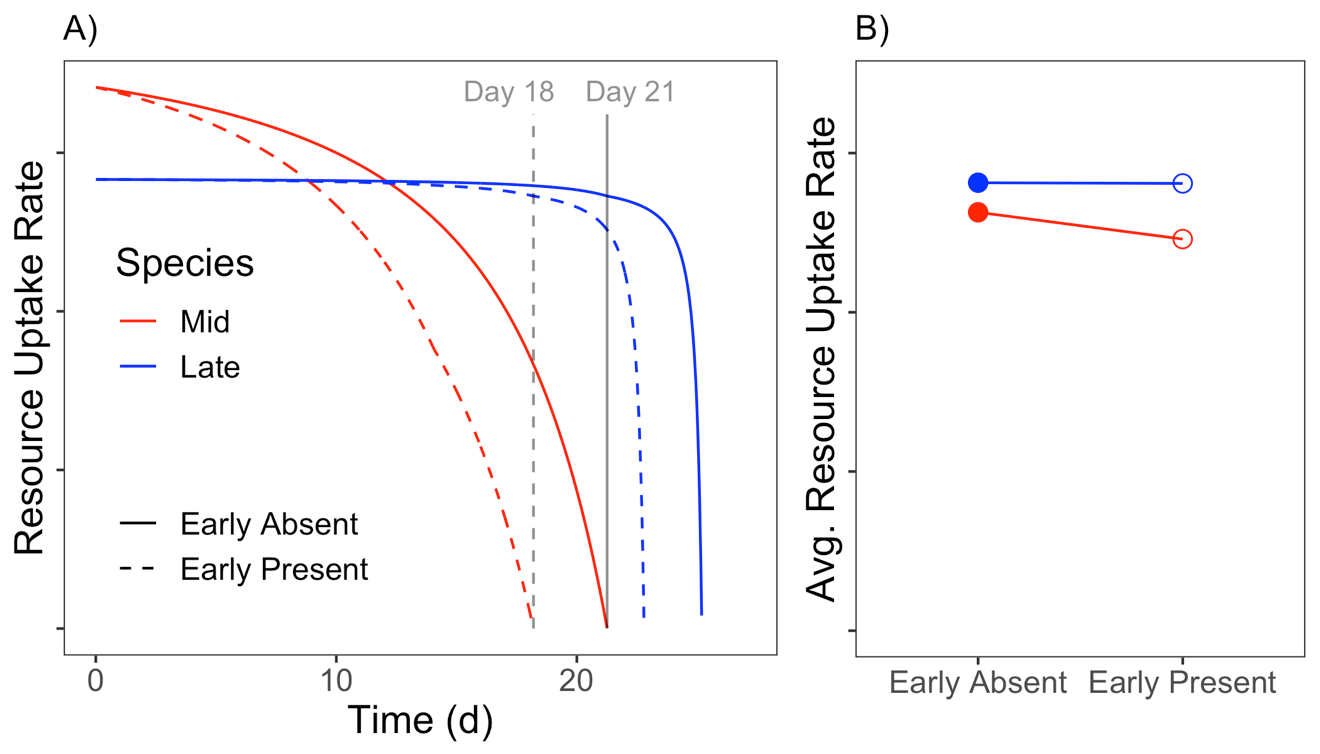


Figure 6. Mechanistic explanation for higher-order interactions. A) The resource uptake rates of the mid and late season species over the course of a growing season, with and without the early species. Gray vertical lines show the day at which the mid-season species stops growing with and without the early species. B) The average resource uptake rates of the mid and late season species in the absence and presence of the early season species.

# Supporting Information – Additional Figures

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Figure S Simulated per capita seed production of the A) early, B) middle and C) late season species in response to increasing inter-specific density on the x-axis. Points show the simulated response from the mechanistic model. Lines show best fit from the basic Beverton-Holt phenomenological model (“model 1”; equation 6) and the modified model with varying exponents for each species’ effect (“model 2”; equation 7).

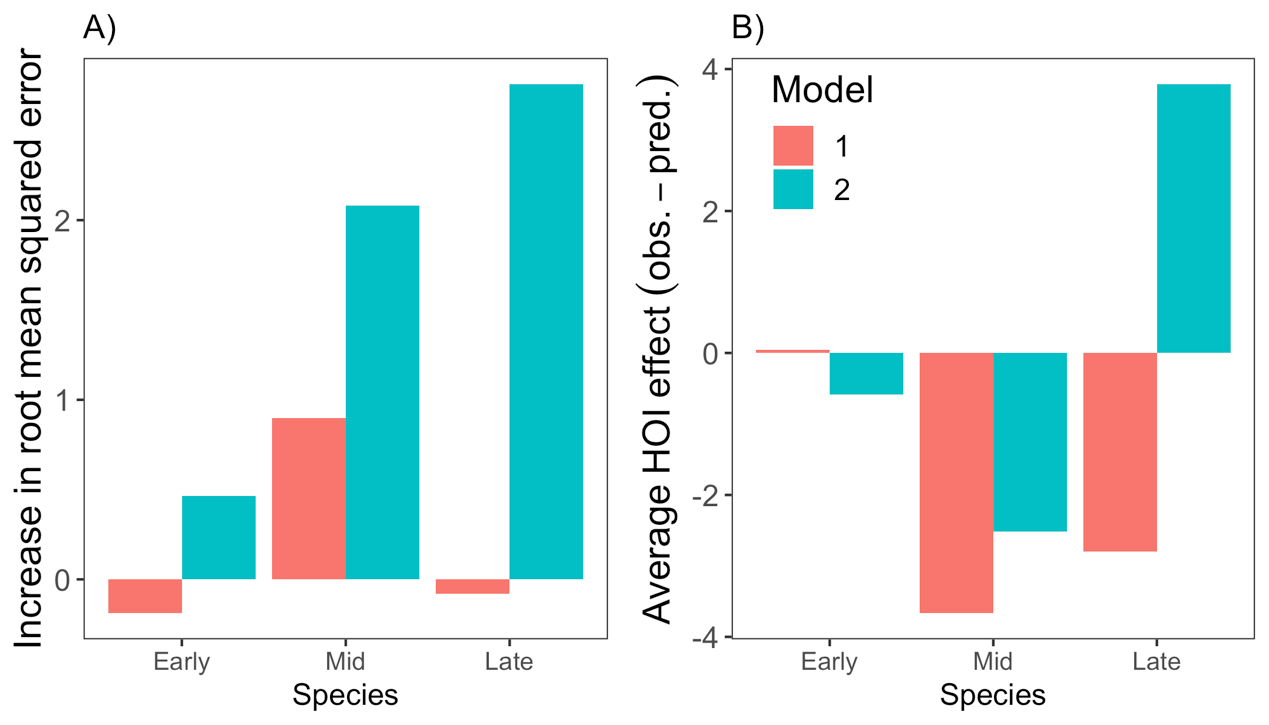


Figure S Deviation from additivity of two-species competition for each species in the community. A) The deviation from additive competitor effects is shown as the increase in root mean squared error of the phenomenological models in multispecies competition compared to single species competition. B) The average deviation from additive competitor effects, positive values show that multispecies competition was weaker than predicted, negative values show where competition was greater than predicted. Deviations from additivity are shown for both phenomenological models—the standard Beverton-Holt model (“model 1”, equation 6) and the model with separate exponents on each competitor (“model 2”, equation 7).

# Appendix A – The effect of relative non-linearity in resource uptake curves on higher order interactions

In order to test whether the strength of higher order interactions was associated with the strength of the trade-off in the competitors’ resource uptake curves, we simulated an additional five communities in which we varied the degree of relative non-linearity between species resource uptake curves. We did this by starting with a scenario in which each species was given a resource uptake curve close to that of the mid-season species in the main text (Figure 2 b). In this first scenario there is very little difference between species in their resource uptake curves. Then we parameterized four additional scenarios by gradually increasing the maximum uptake rate and half-saturation constant of the early season species, and gradually decreasing the maximum uptake rate and half-saturation constant of the late season species (Table A1). We then simulated competition, fit phenomenological competition models, and compared the predicted effects of competition assuming additivity, to the observed effects of competition as in the main text. Our simulations show that as the relative non-linearity between species is increased, the error between the additive phenomenological model and the simulated observations grows (Figure A 1).

Table A . Parameter values for five simulations with gradually increasing strength of the trade-off between the early season and late season species resource uptake curves.

|  |  |  |  |
| --- | --- | --- | --- |
| Scenario | Species | Max Uptake Rate (r) | Half Saturation Constant (K) |
| 1 | Early | 2.92 | 50.88 |
| Mid | 2.60 | 30.00 |
| Late | 2.50 | 23.79 |
| 2 | Early | 3.24 | 73.32 |
| Mid | 2.60 | 30.00 |
| Late | 2.40 | 17.74 |
| 3 | Early | 3.56 | 97.32 |
| Mid | 2.60 | 30.00 |
| Late | 2.30 | 11.84 |
| 4 | Early | 3.88 | 122.88 |
| Mid | 2.60 | 30.00 |
| Late | 2.20 | 6.09 |
| 5 | Early | 4.20 | 150.00 |
| Mid | 2.60 | 30.00 |
| Late | 2.10 | 0.50 |

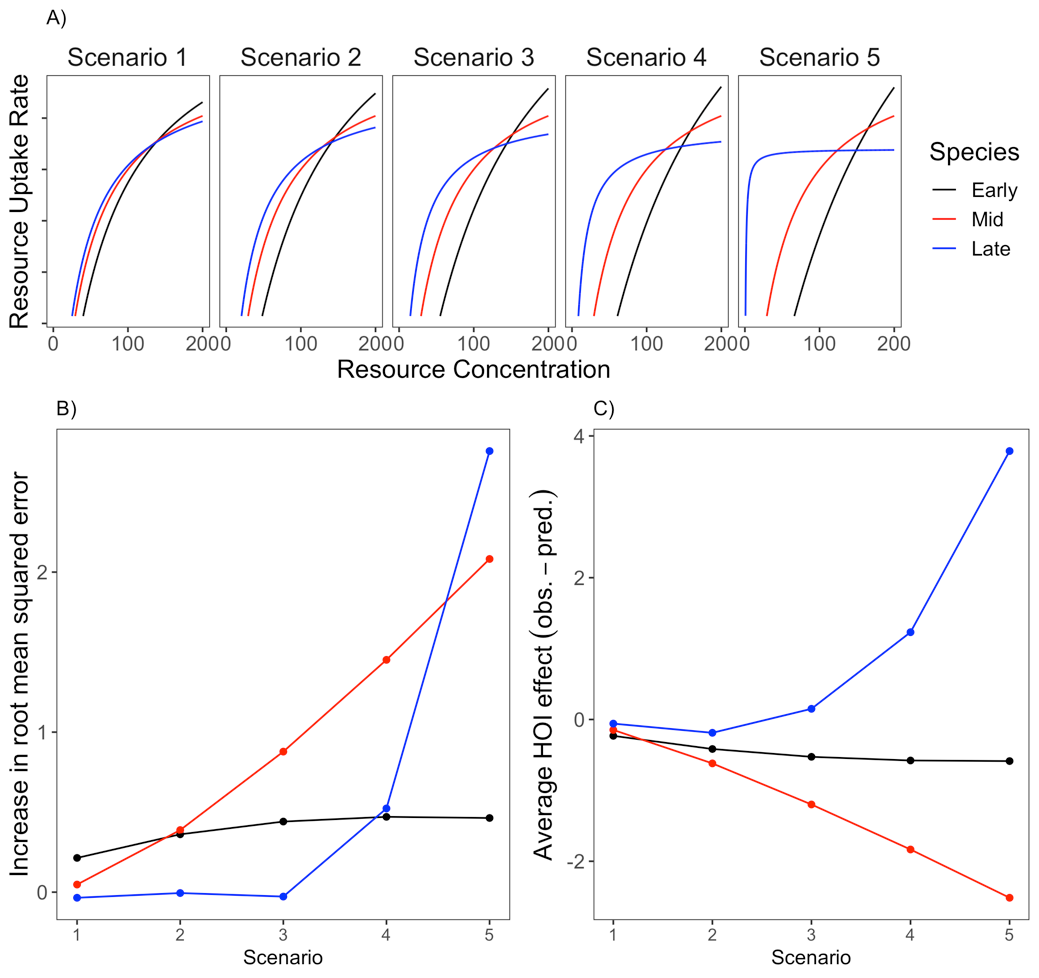


Figure A Increasing the strength of the resource uptake trade-off between the early and late season species increases the deviations from additivity of two species competition. A) Shows increasing relative non-linearity between species’ resource uptake curves in five scenarios. B) The deviation from additive competitor effects is shown as the increase in root mean squared error of the phenomenological model (equation 7) in multispecies competition compared to single species competition. C) The average deviation from additive competitor effects, positive values show that multispecies competition was weaker than predicted, negative values show where competition was greater than predicted. In B and C, the x-axis refers to the different scenarios depicted in A.