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**Mechanisms underlying higher order interactions: from quantitative definitions to ecological processes**

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# Abstract

When species simultaneously compete with two or more competitors, higher order interactions (HOIs) can invalidate the application of classical models of species competition. In order to extend ecological theory to multi-species communities, it is critical to develop a practical and general definition for HOIs that can be applied to a wide range of competition models. In this paper we discuss the concept of HOIs and how they have been defined by ecologists in the literature. We then derive a new definition for HOIs that distinguishes HOIs from non-linear density dependence and emphasizes the consequence of HOIs for multi-species competition. In order to demonstrate how our definition can be applied to empirical data we simulate resource competition between three annual plant species differing in their phenology and functional response to resource depletion. We then fit a phenomenological competition model to the outcome of simulated competition and use it to test for the presence of HOIs. In our simulations, we find the strength of HOIs varies with phenology: species that grow later experience stronger HOIs than earlier growing species. We conclude that stronger HOIs are likely to occur in phenomenological models are used to summarize competition in ecosystems where resource availability and plant size change rapidly throughout the course of the growing season.

# Introduction

Almost all organisms interact with a diversity of predators, pathogens and competitors. Despite this, classical models in community ecology summarize species interactions in a pairwise fashion, assuming that the per capita effects of each species on each other are not dependent on the densities of any other species in the system. The implication of this assumption is that we can predict the dynamics of multispecies communities once we have an accurate model of the interactions pairs of species (Chesson 2000, Levine et al. 2017). 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).

Higher order interactions (HOIs) between species invalidate the core assumption of pairwise interactions and could have profound implications for predicting ecological dynamics (Neill 1974, Mayfield and Stouffer 2017, Levine et al. 2017, Grilli et al. 2017). If HOIs are strong, even a perfect understanding of competition between each and every pair of species may not be sufficient to describe the dynamics when those competitors are together (Neill 1974, Billick and Case 1994, Levine et al. 2017). A specific example of where HOIs can impact our understanding of community dynamics is in the application of the mutual invasibility criterion for determining the stability of coexistence (Levine et al. 2017). In theory, strong HOIs can allow three competitor species to coexist even if not all competitors can invade monocultures of one another (Grilli et al. 2017).

While HOIs could profoundly alter our understanding of multi-species communities research in this area has suffered from inconsistent definitions of HOIs and few investigations of the processes that give rise to HOIs. Moreover, older discussions of HOIs were developed within the context of only a small range of commonly used competition models. Improvements in statistical software now allow ecologists to fit a much wider range of functions for interactions between species and this more flexible approach to modeling competition requires a more general definition for HOIs. In this paper we first review previous discussions of HOIs and define a new quantitative definition for HOIs that can be applied to a wide range of phenomenological models of species competition. In the second part of the paper, we use a simulation model to illustrate our definition and to investigate the mechanisms that may generate HOIs.

## The consequences of higher order interactions for ecological understanding

The issue of HOIs is fundamentally a question about the complexity of ecological communities—how much do we need to know in order to understand a community? For the sake of clarity, our discussion of understanding is aimed at modeling a focal species’ performance (usually per capita population growth rate) as a function of competitor population density. This is expressed in a general form as,

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|  |  | (1) |

where the left-hand side is the per capita growth rate of the focal species *i,* and *Fi* is a function of competitor densities denoted by the vector **n**. In most widely used models of species interactions each species has one effect on each other species in the community, including itself. We refer to this as a pairwise model because each interaction is specified by the pair of species involved. A pairwise model of a community of *m* species requires understanding *m*2 interactions.

In contrast, a community with HOIs requires more information than a pairwise model can hold. A truly general consequence of this is that HOIs make it impossible to predict how a focal species responds to two competitor species together from a model that only includes information on how focal species respond to each competitor separately (Figure 1). While this may sound mysterious, this can be interpreted as resulting from interaction modification (IM) (Adler and Morris 1994). For instance, in a classical Lotka-Volterra (LV) model for two species affecting a focal species,

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|  |  | (2) |

pairwise effects (denoted with ‘’) are independent of the density of any *other* species in the system and there are no HOIs. As shown by Billick and Case (1994) and others, we can introduce multispecies HOIs by making any per capita effect itself a function of some other competitor’s density. For instance, if we make the a density dependent function of species two such that , then the new model would be,

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|  |  | (3) |

We can no longer describe the effect of the two competitors together by observing their separate effects only. We require a new parameter, , that we can only measure by observing the effect of competitor one across a range of densities of competitor two. Alternatively, we can say that competitor two modifies the interaction between competitor one and the focal species or vice versa.

## The problem of defining HOIs

Describing the consequences of HOIs for multispecies communities is not the same as defining HOIs. While most ecologists seem to have the same phenomenon in mind when discussing HOIs, previous attempts to define HOIs have been problematic. For instance, the fact that higher order interaction includes the phrase ‘higher order’ might suggest that any higher order terms of competitor density in a competition model are HOIs. This is the definition was used recently by Letten and Stouffer (2019) and Mayfield and Letten (2017). Starting from the standard LV model, this definition makes sense: the LV model can be viewed as a first order approximation of density dependence (Alfred J.Lotka 1925, Neill 1974). Adding higher order terms to the model is analogous to expanding a Taylor series in order to approximate a non-linear function.

However, a consequence of this definition is that it includes higher-order single species terms, such as , as HOIs. This does not fit with the multispecies nature of HOIs emphasized in the literature. The first empirical studies of HOIs defined them as a non-additive effect of *two or more* competitor species on one focal species (Hairston et al. 1968, Vandermeer 1969, Neill 1974). Or equivalently, that the “nature of density dependent competition between two species is influenced by additional species” (Morin et al. 1988). The question of whether single species terms should or should not count as HOIs may seem esoteric, but in fact it gets to the heart of why HOIs matter. Single species higher order terms do not lead to emergent properties in multispecies communities. HOIs by contrast do. HOIs therefore limit our ability to understand multispecies communities by observing only subsets of the species in them.

Given this objection, one might propose narrowing the above definition to include as HOIs any terms involving the densities of more than one species. However, one can imagine models involving such terms that do not have HOI-like consequences for communities. For instance, the hypothetical model,

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|  |  | (4) |

involves only one competition coefficient per pair of competitor species, i.e. it is pairwise. However, we can rewrite the model in a way that includes higher order terms: for example, for two competitor species,

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|  |  | (5) |

This clearly looks like a model with IM—the effect of species one appears to be modified by the presence of species two, and vice versa, just as in equation (2). On the other hand, all the same parameters are present when two competitors are together as when they are separate which validates the pairwise approach.

The above example shows the issue of building a general definition that is true to the functional consequences of HOIs but that does not implicate all non-linear responses to competition as HOIs. Adler and Morris (1994) argued that a non-linear response to competition is not necessarily the same thing as an IM or an HOI. They proposed a definition for HOIs aimed at this problem. With reference to our general model in equation (1), their definition involves taking the partial derivative of the function with respect to the density of each competitor, . These partial derivatives isolate the effects of each competitor species on the focal species. It would be intuitive to expect that HOIs occur when such a partial derivative is a function of more than one competitor species. However, Adler and Morris showed that this definition would lead to HOIs being present in standard multispecies competition models. For instance, consider a discrete time model for competition and population growth, such as the multispecies Beverton-Holt model:

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|  |  | (6) |

This model has the partial derivative . Thus, the effect of the competitor *j* on the focal species depends on all other competitors in the community!

Again this may appear to be an HOI, but as in the simple LV model, the behavior of the multispecies system can be understood entirely by pairwise interactions. In order to exclude such models from including HOIs, Adler and Morris proposed expressing the partial derivative as a function of the original population growth rate, *Fi*. Once the partial derivative was expressed this way, if any other competitors densities appeared outside of *Fi*, then there were HOIs (we have simplified the Adler and Morris’s definition slightly for the sake of this discussion). In the case of the Beverton-Holt model, the partial derivative can be expressed as , so there are no HOIs. While this definition achieves a practical goal, the underlying logic behind it is not clear, in particular why *Fi* is allowed in the expression for the partial derivative. Their paper also dealt with HOIs in the context of models with both trophic and competitive interactions further complicating their criteria. In the following section, we build on their insight and propose a simpler definition of HOIs for competitive systems.

## A general definition of HOIs

We propose that competition models that can be expressed in the following general form do not contain HOIs,

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| --- | --- | --- |
| No HOIs |  | (7) |

where, *li*, is a function that transforms the RHS of equation (1) into the sum of *m* separate functions, *gij*, each one being dependent on the density of only a single competitor species’. By contrast, models with HOIs, require additional terms on the RHS which are functions of more than one competitor’s density,

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| With HOIs |  | (8) |

where *Hi* is a stand-in for any function of two or more competitor species’ densities. Our definition stems from the observation that in many non-linear models, such as the Beverton-Holt model, per capita growth rate can be transformed by a function, *li*, so that the RHS is a sum terms as in the LV model. As an example, for the Beverton-Holt model we divide both sides by , take the inverse and subtract one:

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|  |  | (9) |

where, .

This definition is general enough to be applied to a wide range of models and has a straightforward interpretation: in models without HOIs, each competitor species has an independent effect on the focal species’ per capita growth rate, albeit an effect that is transformed by an overarching function which is the inverse of *li*. Our definition is in fact a more basic formulation of the Adler and Morris definition: if we take the partial derivative of the per capita population growth rate in equation (7) with respect to a specific competitor species *j*, we find that it can be expressed in the following way,

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| --- | --- | --- |
|  |  | (7) |

matching the Adler and Morris criteria for a model without HOIs.























































## The phenomenological nature of higher order interactions

Neither our definition, nor previous definitions can determine whether there are HOIs in raw data on species interactions. The definition we propose offers a way to determine whether a model includes HOIs, but it can only be applied once we have decided on a phenomenological model of species competition that fits the data. Competition occurs when individuals consume the same limiting resource, such that increases in population density reduces the availability of resources, which in turn changes the population growth rate of the consumers (Meszéna et al. 2006). A phenomenological model of competition simplifies the representation of this interaction by tracking only the population density of the competitors without tracking fluctuations in the resources (Chesson 2000).

Nevertheless, HOIs may emerge in phenomenological models precisely because they leave out mechanistic details and do not explicitly model resource (or shared predator) dynamics (Abrams 1983, O’Dwyer 2018, Letten and Stouffer 2019). Given this, one might argue that HOIs are an artifact of incomplete understanding in phenomenological models. Our response is that the concept of competitors *interacting* at all is inherently phenomenological; competitors do not directly interact in most cases but indirectly influence each other through a shared environment. One could instead do away with the notion of interaction entirely and just model populations and their influence on the environment. But modeling community interactions requires confronting the issue of HOIs.

Moreover, if mechanistic models of resource competition frequently generate HOIs (Abrams 1983, O’Dwyer 2018) this also begs the question of why there have been few rigorous demonstrations of HOIs among competitors in nature—the logistical challenge of studying multispecies competition notwithstanding. We believe our definition above will help ecologists tackle this important gap in our knowledge. While Adler and Morris, applied their definition to a handful of competition models, we believe that our definition can more generally be applied to a wide range of competition models. This is critical because new statistical software makes it much easier today to fit a wide array of phenomenological models to data (Kraft et al. 2015, Mayfield and Stouffer 2017). In the next part of the paper we show how an ecologist could apply our definition to test for the presence of HOIs in empirical data.

# HOIs in a mechanistic resource competition model

To illustrate how we might detect 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 attempt to fit species’ responses to interspecific competition using phenomenological competition models. Using our definition of HOIs above, we evaluate which species’ responses require models with HOIs. By considering when HOIs emerge in this simple simulation we shed some light on how HOIs can be detected in empirical data and the processes that generate HOIs.

Our mechanistic model is inspired by annual plant communities growing in a Mediterranean climate. In this system, rainfall starts in the early winter and gradually declines through the spring while temperature and potential evapotranspiration increase. Annual plants germinate in the winter or early spring, grow, flower, produce seeds and die by the early summer (Godoy and Levine 2013). 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 and plants eventually use up the pool of stored soil resources. As resources are depleted, plant growth slows and eventually stops. We make the assumption that when net plant growth stops, the plants stop producing vegetative biomass and start producing seeds (Cohen 1976).

The model is expressed as a set of differential equations,

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|  |  | (24) |

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 , *m* 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 (Figure 3 a).

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

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|  |  | (25) |

where, is the total biomass of species , is a resource conversion factor, is the rate of respiration and biomass loss. The growth of each species stops when meaning that the rate of biomass gain is equal to biomass loss. At this time in the season the plant stops growing we set growth and resource uptake rates to zero.

Different species are likely to have different rates of resource uptake. 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 3c). This means that species which grow rapidly early in the season when resource concentration is high will stop growing and produce seeds earlier (Figure 3b). In contrast, species that grow slowly early in the growing season will persist later into the season when resource concentration is low.

The resource uptake rate of each species throughout the season is given by a Monod model (Miller and Klausmeier 2017),

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|  |  | (26) |

where, is the maximum rate of resource capture and is the half-saturation constant of resource capture. We impose a trade-off among the three species between the maximum resource uptake rate and the half-saturation constant . Thus, the species with the fastest max uptake rate has the highest half-saturation constant and the species with the slowest max uptake rate has lowest half-saturation constant (Table S1). This trade-off results in species-specific phenology for the three species and so we refer to these as ‘early’, ‘mid’ and ‘late’ (Figure 3). The differences in the timing of growth recreates a patterns of phenology similar to patterns observed in natural annual plant communities (Godoy and Levine 2013).

So far, we have described a of growth dynamics in continuous time, *u*, within a single season and with units of total biomass, *B*(*u*). In contrast, a phenomenological model of competition that might realistically be parameterized from field data would track the total population density, , over annual time steps, . In order to convert between population density and biomass we assume that individuals start the season as seeds, such that the initial biomass is, where is the mass of an individual seed and is the population density in number of seeds. The population density in the following year is equal to the number of seeds produced during the course of a simulation and we assume this is proportional to the biomass at the time of flowering,

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|  |  | (27) |

where max is equal to the total accumulated biomass of species *i* and *c* gives the proportion of total biomass that is converted to seeds. We assume that all species have the same values for and *c* (Table S 1). We simulate the within season growth dynamics by solving (24) and (25) using the differential equation solvers package desolve in the statistical program R (R Core Team 2015). Code to run the simulations are given in the supporting information.

We used the model to simulate plant growth of each species when faced with a range of densities of one or two other interspecific competitors. To characterize these interspecific interactions, each species was grown as a single “focal” individual in each simulation. In each replicate simulation, the focal individual faced either or both of its interspecific competitors at densities of 0, 1, 2, 3, 4, 5, 6, 7, 8 or 16 individuals. This orthogonal design allows us to assess the independent effects of each species on every other species.

## Phenomenological annual plant model

In order to investigate whether this simulation entails HOIs, we fit phenomenological competition models to the annual population dynamics. We fit a custom phenomenological model of the form,

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|  |  | (15) |



where denotes maximum per capita reproductive output, is the per capita competitive effect of species on and each competitor term is raised to a separate where When all = 1, our model becomes identical to the more widely used Beverton-Holt form (Kraft et al. 2015). The competitor-specific exponents, , increases the flexibility of the model and allows the shape of density dependence to change depending on the competitor species. This flexibility is warranted as we seek to isolate HOIs once the effect of each specific competitor is modeled accurately. We created an HOI version of the model by adding a two-species HOI term to the denominator,

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|  |  | (16) |

Each HOI term includes the densities of two species and one new parameter, .

In order to evaluate the presence of HOIs and measure their strength we fit the simpler non-HOI model first to scenarios where each focal species was grown with only one competitor species (details in the preceding section). Once we were satisfied that phenomenological model could fit the single competitor cases, we fit the HOI model to the entire range of species densities, including cases where there were two competitor species. When there are not HOIs, the HOI term .

In order to fit the models we first added a small amount of noise to the simulated population densities and then fit the non-HOI phenomenological competition model (15) using the Bayesian software Stan in R (Stan Development Team 2018).

# 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 (Figure 4), whereas the standard model (equation 6) only fit the data for the early species (Figure S 1). When we tested how well models fit to single species competition 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 5). In other words, for the early species, the observed effect of two species together was close to the sum of the two species’ individual effects (Figure 6). However, assuming additive competitor effects underpredicted the total strength of competition on the mid-season species (Figure 6 b), and overpredicted the strength of competition on the late species (Figure 6 c). This shows that competitors’ effects changed depending on the density of other competing species, and by our definition this is a HOI. Using the first phenomenological model, equation 6, which was less accurate in fitting the fecundity of single species, we also found evidence of HOIs (Figure S 2) but these were different in direction and magnitude than those detected with equation 7, indicating that HOIs are by definition dependent on what form of phenomenological model is fit to single species effects.

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 3 c). This means that as species use resources they not only affect the growth rates of their competitors, but they can also affect the interactions between those competitors. For instance, the early species has the most rapid growth and resource uptake rate early in the season. This shifts the resource uptake rates of the mid and late season species towards the left along their resource uptake curves (Figure 7a). 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 it does the late season species during the period of time when both species are active, that is until the mid-season species stops growing (vertical lines Figure 7 a). Thus the average resource uptake rate of the mid-season species declines more than that of the late season species in response to the presence of the early season species (Figure 7 b).

Differences between species in how much their resource uptake rates change with the presence of the early competitor explain the direction of the HOI effects on the late season species: the presence of the early species, puts the mid-season species at a slight disadvantage relative to the late species; thus the joint effect of the early and mid-season species together is less than their additive effect (Figure 5 c; Figure 6 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 5 b; Figure 6 b).

By contrast, the early species is only weakly affected by HOIs (Figure 6). 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 weak because the late season species grows much more slowly early in the season than its competitors 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 3).

The origin of HOIs in this system are therefore 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 3c). 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 3 a). Deriving phenomenological 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 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 also 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 them instances 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 (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 earlier activity of competitors. More generally, we believe HOIs will be inevitable in 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 significant HOIs inevitable? And if so, why are there 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 more similar species resource uptake curves are to one another the weaker the HOIs are in this system (Appendix A). In nature, such large differences in the shape of resource uptake curves may be rare.

In addition, the large changes in resource availability and plant biomass in our simulation contribute to the magnitude of HOIs. Because resource availability fluctuates widely from the beginning to the end of the growth period 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. 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. For this reason, seasonally forced systems, such as annual plant communities in Mediterranean climates, may be a good place to look for strong HOIs (Mayfield and Stouffer 2017).

Finally, our analysis that even though we restrict our definition of HOIs to only involve interaction modification between heterospecific and not conspecific individuals (in their total competitive effects), HOIs are virtually guaranteed when species’ individual contributions to change non-linearly with density. Such non-linearity would arise when individuals alter the competitive effects of other individuals within the same species. In our simulated experiment for example, we found that a model with non-linear terms for each competitor species’ effect best fit the simulated data for the mid and late-season species. These species-specific non-linear terms were required to fit the single species data because the densities of each competitor had different non-linear effects (Figure 4).

To see how these non-linear effects of competitor density within species almost guarantee an HOI (between species), 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 function of species density. In the case where individuals of one and two are identical, we know that their true effect on three must in fact be equal to yet if is a non-linear function, . Just because we label the individuals of species one and two as belonging to different species, the sum of their separate effects will not equal their combined effect. This example illustrates why any system in which competition, *C*, depends non-linearly on the density of individual species will likely result in HOIs between species.

# Conclusion

Higher order interactions have profound implications for how we understand multispecies communities. We have sought to clarify the definition of HOI’s and explain how they could arise from simple resource 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 simulation of species competition for a single resource. Defining HOIs in this way requires first finding a phenomenological model that accurately describes the focal species’ response to single species competition. While we believe that HOIs should be common in nature this does not mean that they will be 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.

# Acknowledgments

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# Figures

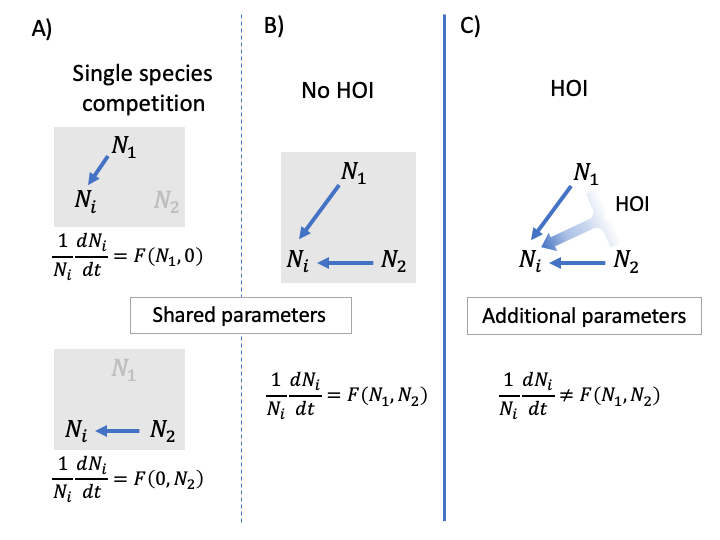


Figure 2. Conceptual definition of HOIs. In A, the competitive effects (blue arrows) of species 1 and 2 on the focal species are observed separately. The per capita growth rate of the focal species, *i,* is modeled as a function, *F*, of the density of competitor species 1 and 2. Importantly, all the information in *F* can be obtained by observing each competitor’s effects separately, as in A. In the communities in B and C, two competitor species are present together (i.e. *N*1 > 0 & *N*2 > 0). In B, the function *F* characterizes multispecies dynamics and there are no HOIs. In C, the function *F* does not characterize the multispecies case; specifically, additional parameters are required to model the HOI that arises when competitor species one and two are present together.

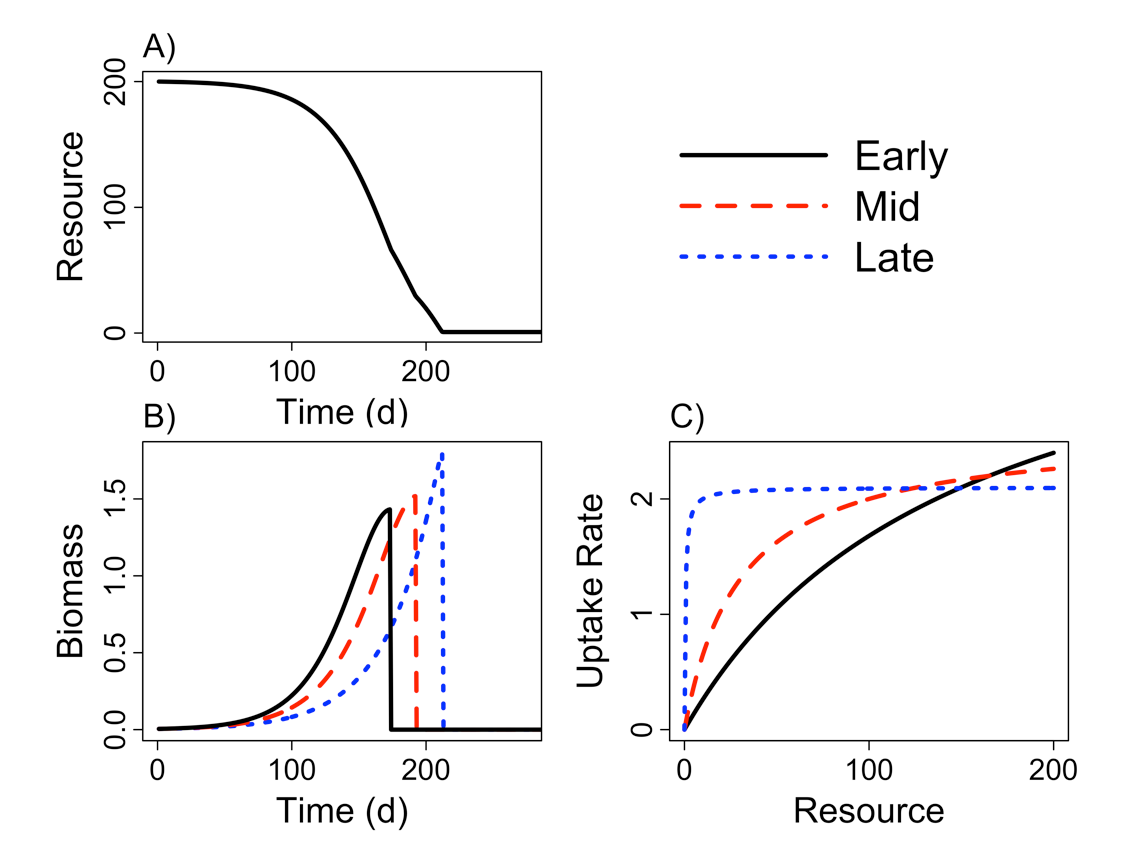


Figure 3. Example time series showing A) the drawdown of the resource during the course of the simulated growing season with starting densities of one individual of each species, B) the growth of each of species shown with colored lines and C) the dependence of resource uptake rates on resource concentration. 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 mid season species lies between these extremes.

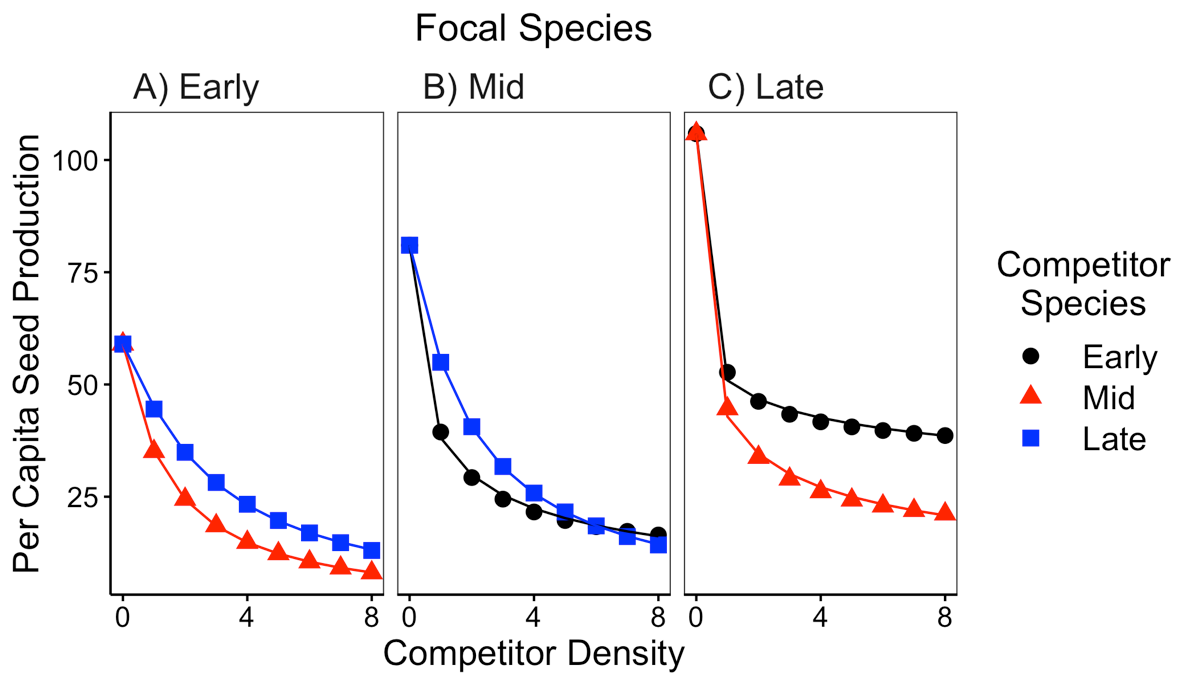


Figure 4. Simulated per capita seed production of the A) early, B) middle and C) late season species in response to increasing inter-specific density on the x-axis. Colors correspond to the identity of the competitor species. The solid line shows the best fit from the model with varying exponents on each competitor’s effect (equation 7).

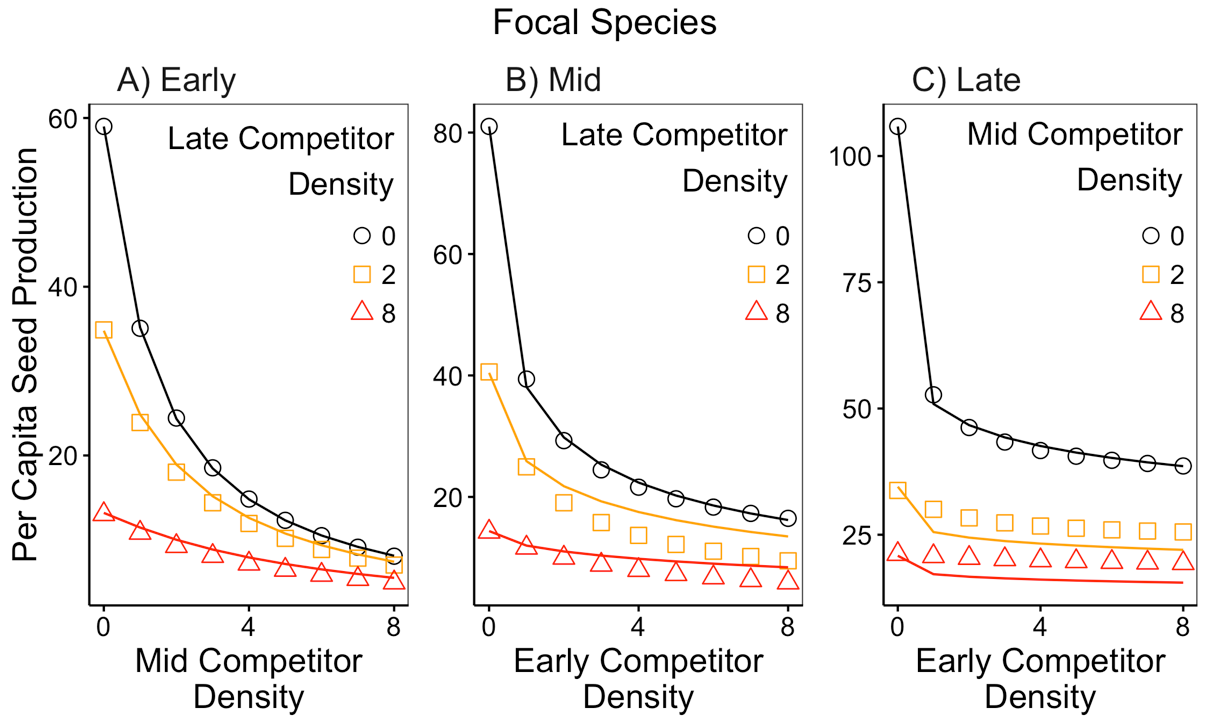


Figure 5. Simulated per capita seed production of the A) early, B) mid and C) late season species in response to increasing simultaneous competition from two species. Increasing densities of one competitor species are shown on the x-axis and increasing density of a second competitor are shown with the varying colors. The lines show the predicted per capita fecundity from the competition model with varying exponents (equation 7). The predicted per capita seed production assumes 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.

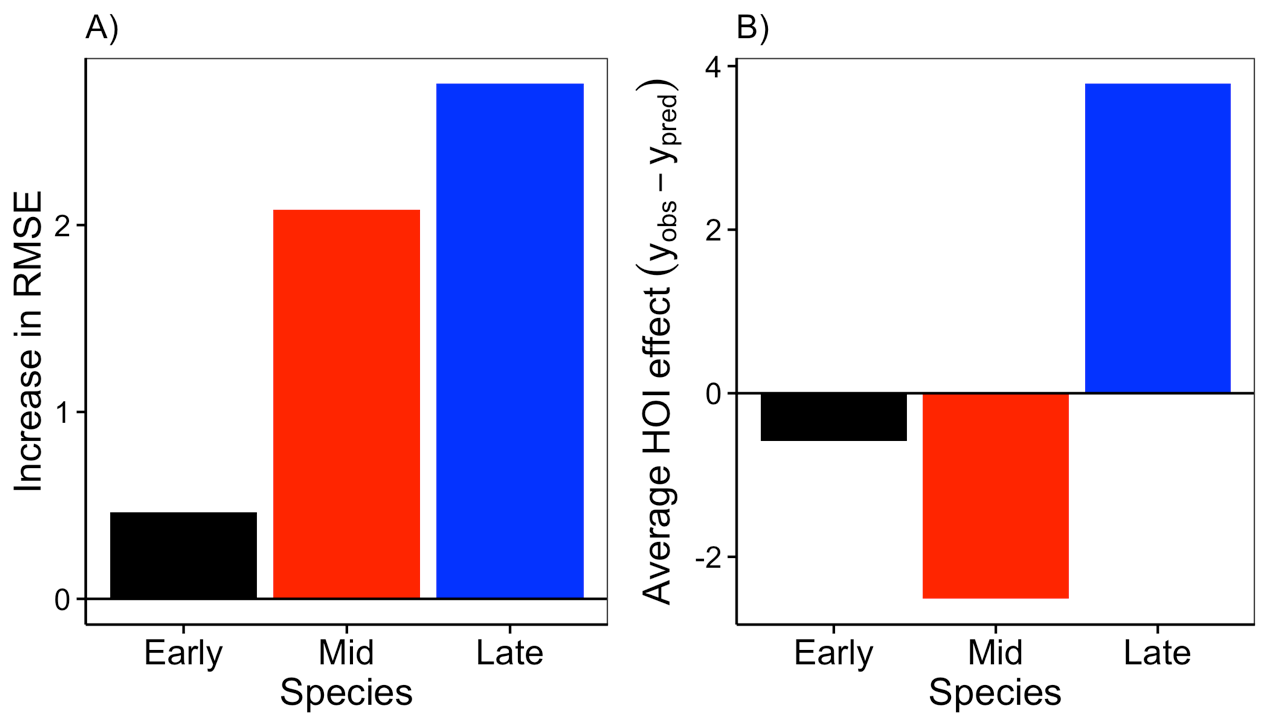


Figure 6. Deviation from additivity of two-species competition for each species in the community. A) The deviation from additive competitor effects is shown as the increase in root mean squared error of the second phenomenological model (equation 7) in multispecies competition compared to single species 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.

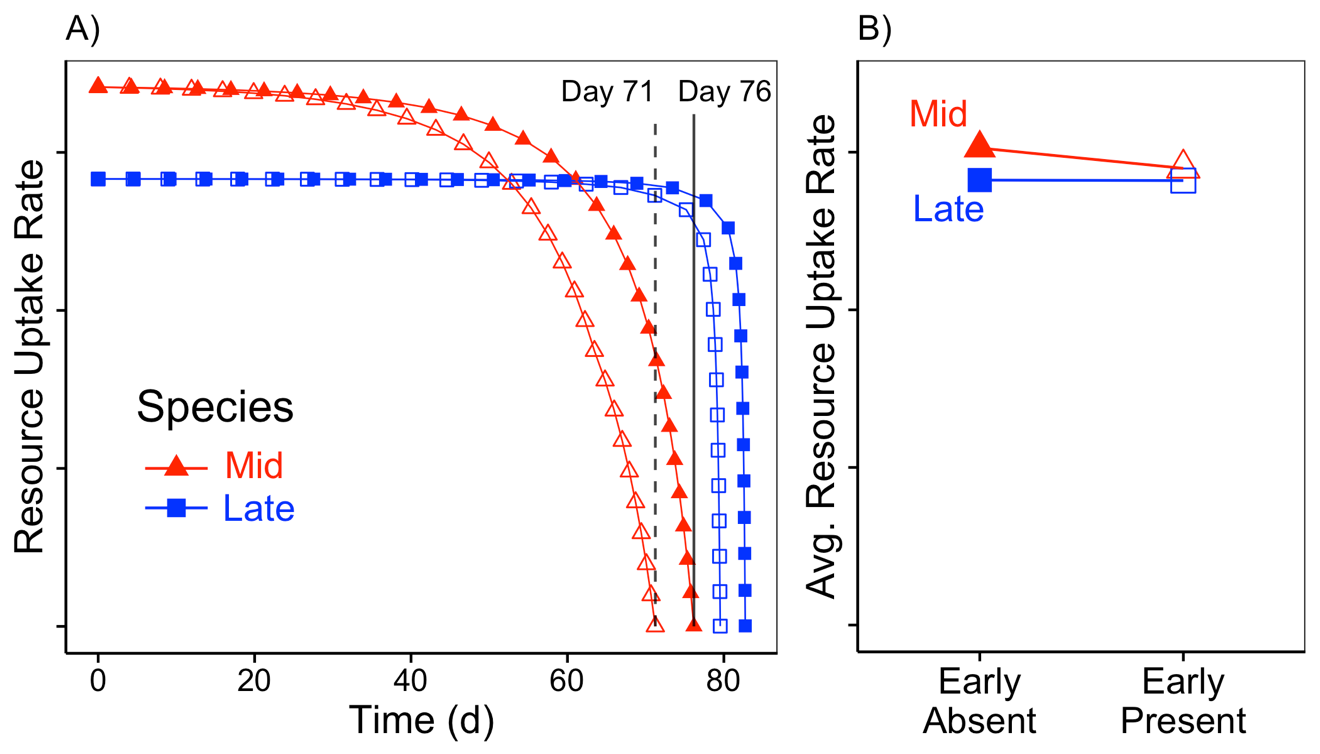


Figure 7. Mechanistic explanation for higher-order interactions. A) The resource uptake rates of the mid and late season species plotted over the course of a growing season, with (open symbols) and without (filled symbols) the early species. Vertical lines show the day at which the mid-season species stops growing with (dashed) and without (solid) the early species. B) The time-averaged resource uptake rates of the mid and late season species in the absence and presence of the early season species.

# Supporting Information – Additional Tables

Table S 1 Table of parameter values used in the growth simulation experiment in the main text.

|  |  |  |
| --- | --- | --- |
| Parameter | Value | Definition |
| *U* | 200 | Duration of growth simulation in days |
| *I* | 0 | Environmental resource supply rate |
| *R(0)* | 200 | Initial resource concentration |
| *r1* | 4.2 | Early competitor maximum resource uptake rate |
| *r2* | 2.6 | Mid competitor maximum resource uptake rate |
| *r3* | 2.1 | Late competitor maximum resource uptake rate |
| *K1* | 150 | Early competitor half-saturation constant |
| *K2* | 30 | Mid competitor half-saturation constant |
| *K3* | 0.5 | Late competitor half-saturation constant |
| *m* | 0.09 | Respiration/Loss rate |
| *q* | 0.07 | Biomass assimilation rate |
|  | 0.005 | Seed mass |
| *c* | 0.1 | Conversion rate of total biomass to seed mass |

# Supporting Information – Additional figures

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Figure S 1 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. Solid lines show best fit from the standard Beverton-Holt phenomenological model (equation 6) and the dashed line shows the best fit from the modified model with varying exponents for each species’ effect (equation 7).

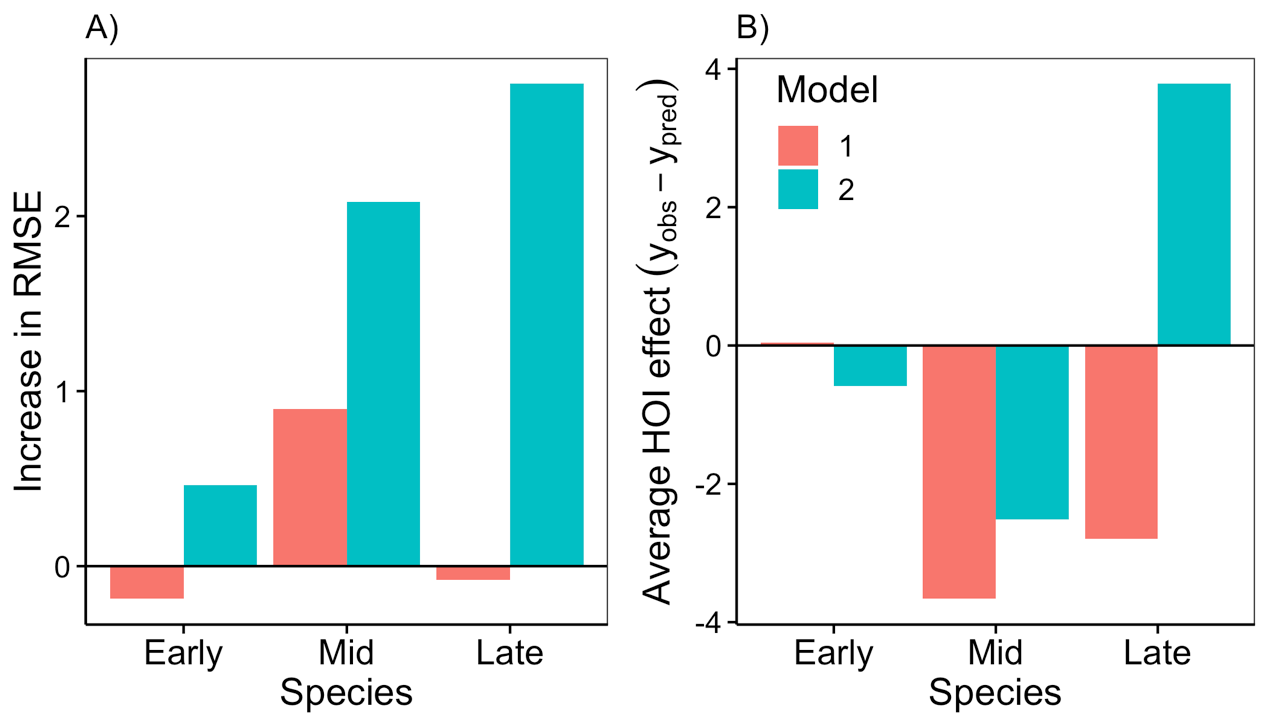


Figure S 2 Deviation from additivity of two-species competition for each species in the community. A) The deviation from additive competitor effects is shown as the increase in root mean squared error of the phenomenological models in multispecies competition compared to single species competition. B) 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 3 b). In this first scenario there is very little difference between species in their resource uptake curves (see top of Figure A1). 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 1. Parameter values for five simulations with gradually increasing strength of the trade-off between the early season and late season species resource uptake curves.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Tradeoff | Scenario | Species | Max Uptake Rate (r) | Half Saturation Constant (K) |
|  | 1 | Early | 2.92 | 50.88 |
| Weak | 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 |
| Strong | Mid | 2.60 | 30.00 |
|  | Late | 2.10 | 0.50 |

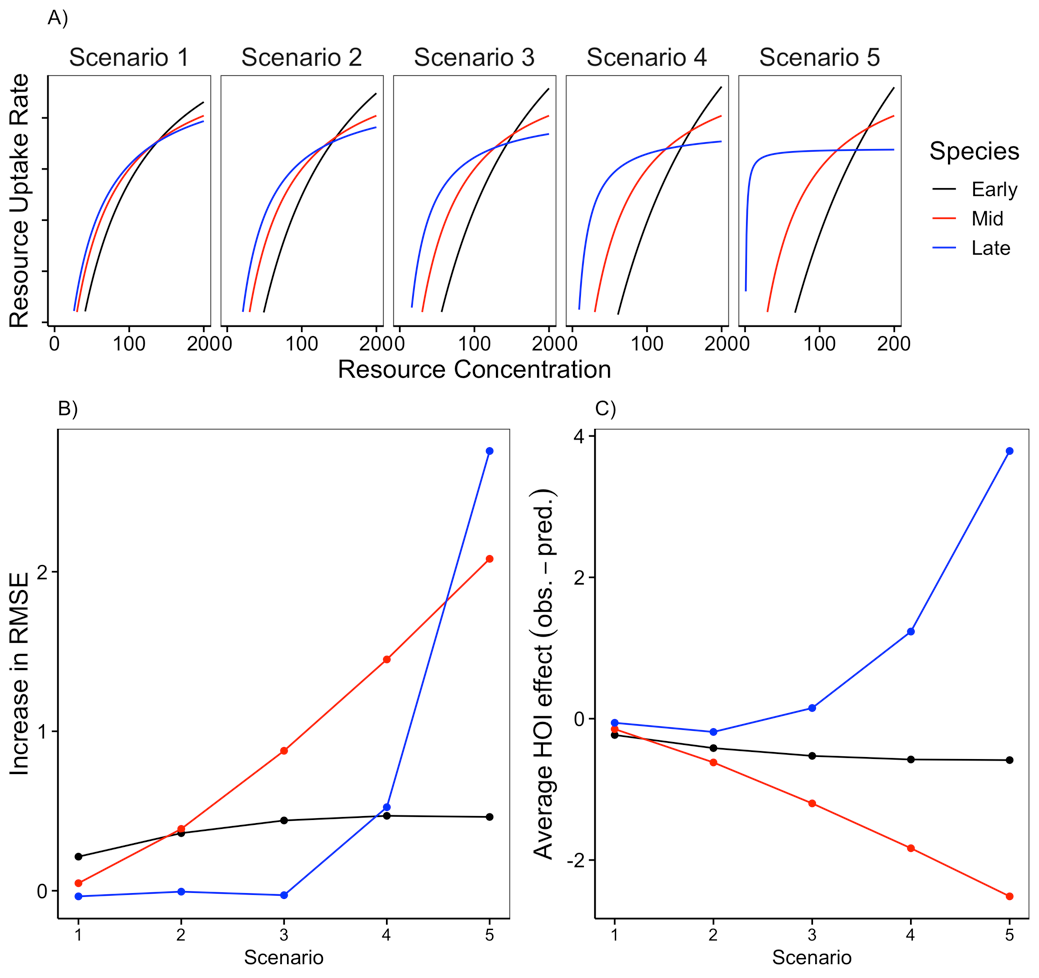


Figure A 1 Increasing the strength of the resource uptake trade-off between the early and late season species increases the magnitude of higher order interactions. A) Shows increasing relative non-linearity between species’ resource uptake curves in five scenarios. B) The deviation from additive competitor 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.