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

Andrew R. Kleinhesselink1, Nathan J.B. Kraft1, Jonathan M. Levine2,

1Department of Ecology and Evolutionary Biology, University of California, Los Angeles 621 Charles E. Young Drive South, Los Angeles, USA

2Institute of Integrative Biology, ETH Zurich, Switzerland

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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 species interact with a diversity of predators, pathogens and competitors. Despite this, most 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 between 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 provide a general conceptual definition for HOIs that we believe captures the key consequences of HOIs for the empiricist hoping to model multispecies communities. We then review and classify several alternative way HOIs have been defined by ecologists. 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.

## Higher order interactions result from interaction modification

For the purpose of defining HOIs we focus on modeling a focal species’ performance (usually per capita population growth rate) phenomenologically as a function of competitor population density. This can be expressed generally 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 competitor has one effect on each other species in the community, including itself. The simplest example of such a pairwise competition model is the Lotka-Volterra (LV) model,

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|  |  | (2) |

where, *ri* is the intrinsic growth rate of the focal species *i* and is the per capita effect of each competitor species *j* on the growth rate. This model is pairwise because each interaction can be specified by the pair of species involved, *i* and *j*. A key property of any pairwise model, such as the LV model, is that the effect of each competitor species is independent of the density of all *other* competitor species.

HOIs occur when the effect of one competitor species is modified by the density of another competitor species, also known as an interaction modification (IM) (Adler and Morris 1994). We can introduce an IM in the LV model by replacing any of the terms with a function that is dependent on another competitor’s density (Billick and Case 1994). For instance, in a pairwise model with two competitor species,

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|  |  | (3) |

replacing the term with the function makes the per capita effect of *n*1 dependent on the density of another competitor, *n*2. Substituting this into the model and expanding yields a new term in the model which involves the product of competitors one and two,

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|  |  | (4) |

This model can imply biological hypotheses: the fact that the interaction between species one and the focal species changes depending on the density of *n2* suggests that there is some species-specific change in the behavior or traits of the competitors when they are together that could explain the change in their per capita effect on the focal species.

## A general definition of HOIs

While the basic outline of how IM and HOIs are related has been understood by ecologists for years, devising a clear definition that can be applied generally to competition models has proven difficult and definitions are inconsistent (Hairston et al. 1968, Billick and Case 1994, Grilli et al. 2017, Letten and Stouffer 2019). Here we offer our own general definition of HOIs and compare it with previous definitions. We hope our definition is practically useful for empirical ecologists in need of clarity when discussing HOIs in empirical data. We define a model with HOIs as *a multispecies competition model that cannot be entirely broken down into separate density dependent models for each species of competitor*. By contrast, a model is *pairwise* and there are no HOIs if it can be broken down into a set of single competitor models without any loss of information. For instance, in the case of the modified LV model in (3), we can break it down into two separate single competitor models:

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|  | (the response to competitor one)  , (the response to competitor two) | (5) |

This decomposition of the multi-competitor model results in the loss of the term The empirical significance of this is that there is no way to measure the coefficient from observations of separate single competitor gradients. By our definition this is an HOI resulting from an IM between species one and two.

We refer to the above as *hard HOIs* and contrast them with the more general phenomenon of non-linear density dependence which produce what we term *soft HOI*s. A general test for soft HOIs is to take the partial derivative of the competition function, *F­i* in (1), with respect to the density of a single competitor species, *nj*. The partial derivative is the mathematical definition of a single competitor species’ effect on the focal species. If this partial derivative is itself a function of competitor density, then there is some form of non-linear density dependence either within or between competitor species. This definition of HOIs is similar to that used in many earlier discussions of HOIs (Case and Bender 1981, Letten and Stouffer 2019). However, if this definition would indicate HOIs in all competition models except the linear LV model (Pomerantz 1981, Adler and Morris 1994). For instance, the multispecies Beverton-Holt model,

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|  |  | (6) |

has the partial derivative . Thus, the effect of the competitor *j* on the focal species is given by a function which includes the density of all other competitor species. Nevertheless, the Beverton-Holt form does not contain hard HOIs as we define them because it can be decomposed into a set of models containing only the density of a single competitor without loss of any information.

In addition to the practical question of whether a model can be parameterized from observing each competitor’s effects separately, there is an important ecological distinction between soft HOIs, as found in the Beverton-Holt model, and hard HOIs. For instance, soft HOIs between species can arise over discrete time intervals when the interaction between competitors is linear in continuous time (Hassell and Comins 1976, O’Dwyer 2018). In the case of the discrete time Beverton-Holt model, the lifetime competitive effect of each additional individual declines with competitor density: as density increases each individual competitor is smaller and thus has less of a per capita effect on the focal species. Thus, while the effects of competition are non-linear, there is no ecologically meaningful IM between competitors other than their change in size—and this implicit in the form of the model.

Adler and Morris (1994) describe another example where different species of plants of compete for light with taller species reducing the amount of light shorter species receive. The nature of the interaction between a tall species and a shorter one is independent of all other competitor species—each species simply blocks a proportion of the light that passes through the canopy of taller species. Nevertheless, the effect of a taller species on a shorter species depends multiplicatively on the density of competitors of intermediate height between the two. As in the Beverton-Holt model, per capita competition is non-linear, but arguably there is no ecologically meaningful IM between different competitors—they simply reduce the fraction of light received regardless of its amount. By contrast, hard HOIs as we define them require distinct IM between competitors, i.e. the IM is not implicit in the nature of the shared resource.

A separate issue with equating simple non-linearity with HOIs is that this would treat as an HOIs non-linear responses to single competitor densities. For instance, recent papers by Letten and Stouffer (2019) and Mayfield and Letten (2017) defined HOIs as any higher order terms of competitor density, including single species terms, such as . This does not fit with the conception most ecologists have when discussing HOIs which is that of an IM between two or more *different species* of competitor (Hairston et al. 1968, Vandermeer 1969, Neill 1974, Morin et al. 1988). Single species higher order terms can be interpreted as the result of an IM between individuals of the same species, i.e. the effect of each additional individual is modified by all other individuals. However, these single species higher order terms can be fully measured and parameterized by observing density gradients of a single species, thus these do not qualify as hard HOIs by our definition. More importantly, they do not on their own lead to any emergent properties in communities with two or more competitors that are not present in the set of single competitor communities.

Adler and Morris (1994) proposed a general definition for HOIs, that like ours, made a distinction between hard HOIs and simple non-linearity. They 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 terms for competitor density 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 in (6), the partial derivative can be expressed as , so there are no HOIs per their definition. While this achieves a practical goal, why *Fi* is allowed in the expression for the partial derivative in non-HOI models is not particularly clear. Moreover, while their criterion works in many realistic competition models, it would detect HOIs in a multi-competitor model with different forms of density dependence for different competitor species, even when the model can be decomposed into a set of separate single species models without loss of information.

In the second half of the paper we show how an ecologist could apply our definition to test for the presence of HOIs in empirical data. We use a mechanistic model to simulate resource competition among three annual plant species. We then attempt to fit species’ responses to interspecific competition using phenomenological competition models. Using our definition for HOIs above, we evaluate which species’ responses require models with HOIs and which do not. By considering when HOIs emerge in this simple simulation we show the steps required to detect HOIs in empirical data and shed light on the processes that could generate HOIs in nature.

# HOIs in a mechanistic resource competition model

Our mechanistic competition model is intended to simulate the growth dynamics of annual plant communities in a Mediterranean climate. These systems are characterized annual plants that germinate in the winter and grow, flower, and produce seeds by the early summer (Godoy and Levine 2013). In our model, we track a single pool of soil resources, most easily thought of as water or water-soluble mineral nutrients. This pool is not resupplied during the season and is gradually depleted. As the resource is depleted, plant growth slows and eventually stops. We make the assumption that when net plant growth is zero, the plants will convert their standing biomass into seeds that will then remain dormant until the next growing season (Cohen 1976).

Resource dynamics in the model are given by the differential equation,

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where is the resource availability at time , is the resource supply rate, and the final term is the resource uptake by all*m*, species in the community. Biomass per individual of each species at time is given by and the number of individuals in the population is given by *ni*. The function *gi* converts per capita biomass into per capita fine root surface area. Total resource uptake rate is the product of total root surface area and the rate of resource flow into roots per unit root surface area, which is a function of soil resource concentration, . We simulate a Mediterranean climate by setting initial resource availability high, , and setting the resource supply rate to zero (Figure 2 a).

Growth of each species is given by a piecewise differential equation,

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|  |  | (8) |

where, *q* is the rate of resource conversion into biomass and is the rate of biomass loss and respiration. The inequalities indicate that when net growth of each species is less than or equal to zero, growth and resource consumption stops (i.e. is set to zero). Per capita biomass of each species, *bi*, is converted into per capita root surface area via the function , where *p* is the proportion of growth allocated to roots, *di* is root tissue density in g cm­-3 and is a scaling exponent between zero and one (Kooijman 1986). The rate of resource uptake per unit root surface area follows Michaelis-Menton kinetics

The equations above describe growth dynamics with units of biomass, *Bi*, within a single season. In contrast, a phenomenological model of competition for annual plants would track the total population density, *ni*, over annual time steps, . In order to convert between population density and biomass we assume that individuals start the growing season as seeds, such that the initial biomass is, where is the mass per seed and is the number of seeds in the population in year *t*. The population density in the following year is equal to the number of seeds produced during the course of a simulation, which is proportional to the final biomass of each species,

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where max is the final accumulated biomass of species *i* and *c* gives the proportion of total biomass converted to seeds.

In our simulation, species differ in only two ways, 1) root tissue density, *di* and 2) the rate of tissue loss and respiration, . We assume a trade-off between these parameters such that the rank of root density *di* among species is inverse to the rank of tissue respiration and loss rate, (Tjoelker et al. 2005, Birouste et al. 2014) (Figure 2c). Differences between species in phenology, i.e. the time at which species stop growing, naturally emerge from this trade-off between root density and biomass loss rate. Species with lower root density convert each gram of biomass into more root surface area and this allows them to grow faster early in the season when resource concentrations are high (Figure 2b). In contrast, species with denser roots but lower rates of tissue loss and respiration, will grow more slowly but will continue growing later into the season as resource availability declines (Figure 2). Thus, we refer to the three species in our simulations ‘early’, ‘mid’ and ‘late’, depending on when they stop growing during the simulation (Figure 2).

We used the model to simulate a virtual experiment in which each species is grown across a range of starting competitor densities. From each simulation, we find the per capita seed output of each species and save this as a density dependent measure of performance. We quantified each species performance across competitor densities of 0, 1, 2, 3, 4, 9, 16, 25 or 36 individuals in an orthogonal design. We excluded scenarios in which all three species have densities greater than one, thereby excluding the possibility of three-way HOIs. This design allows us to measure both the effect of each competitor separately and with one other competitor species.

A table of parameters for the simulations can be found in the supporting information (Table S 1). We chose parameters that led to patterns of growth and phenology that qualitatively match species-specific growth curves observed in Mediterranean annual communities (Godoy and Levine 2013) We simulate growth and resource dynamics by solving (7) and (8) using the package desolve in the statistical program R (R Core Team 2015). Code to run the simulations are given in the supporting information.

## Phenomenological annual plant model

In order to investigate whether this simulation entails HOIs, we fit three phenomenological competition models to the simulated per capita seed production of each species in the simulated field experiment. The first model is a multispecies version of the Hassell model (Hassell and Comins 1976),

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where is the maximum per capita seed production, is the per capita competitive effect of species on and each competitor term is raised to a separate where Importantly, the Hassel model does not contain HOIs per our definition: there is only one parameter, , per pair of species and this can be fitted from only the pairwise scenarios. We specified an HOI version of the Hassel model as follows,

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where two-species HOI effects on the focal species *i* are given by the parameter (Mayfield and Stouffer 2017). By our definition, represents a hard HOI that can only be evaluated from measuring the response of the focal species to scenarios in which two competitor species are present (i.e. *nj* > 0 and ­*n­k* > 0).

Finally, we also considered a pairwise multiplicative model of the form,

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|  |  | (12) |

This model does not have HOIs per our definition, and in fact is identical to the Hassel form when only one competitor species is present at a time. However, when there are two or more competitors the denominator becomes a polynomial with multiplicative terms of competitor density.

We first fit the Hassel model to only the pairwise cases and checked graphically whether the model captured pairwise dynamics (Fig). We then fit all three models to the full range of full set of combinations of competitor density, both those with only one competitor species and also those with two competitor species present. For each focal species we determined how well each model fit by examining the sum of squared error and plotting the observed per capita population growth rate of the focal species against predicted per capita growth. We evaluated the strength and direction of HOIs in the HOI model by examining the HOI coefficients . In order to fit the models we first added a small amount of noise to the simulated population densities and then fit each model with the non-linear least squares model “nls” function in R.

# Evidence for HOIs

For all three species we found that the Hassel model fit the fit the simulated pairwise data accurately (Figure 3). The early season species competed more strongly with the 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 4). 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 5). However, assuming additive competitor effects underpredicted 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). 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 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 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 6a). 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 6 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 6 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 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 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 2).

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 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 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?

HOIs can only be discussed, defined and quantified in the context of phenomenological competition models. Phenomenological models simplify ecological dynamics by only tracking population densities and not the physical resources that for which species compete (Chesson 2000). 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. However, one must keep in mind that the concept of *interactions* between competing species or individuals is inherently phenomenological; competiting individuals do not directly interact in most cases but indirectly influence each other’s growth or survival through shared resources. One could do away with interactions entirely and just model populations and their influence on shared resources. But modeling community interactions requires confronting the issue of HOIs.

In our simulation, HOIs can be seen to arise because 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 individual size. 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 growth curve and thus resource uptake rates. 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, and plant size changes over time as well, it means that species interactions can change over the course of the season. Without the extreme fluctuation in resources, 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. 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).

If mechanistic models of resource competition frequently generate HOIs (Abrams 1983, O’Dwyer 2018) this 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. Advances in statistical software make it increasingly easy to fit a wide array of phenomenological models to data (Kraft et al. 2015, Mayfield and Stouffer 2017). A key feature of our definition is its generality, allowing it to be applied to a wide range of multi-competitor models.

# 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

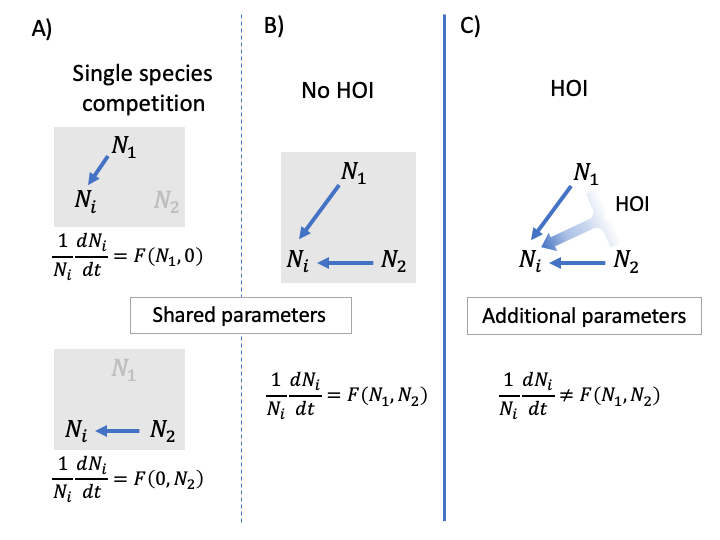


Figure 1. Conceptual definition of HOIs. In A, the competitive effects (blue arrows) of species 1 and 2 on the focal species are observed separately. The per capita growth rate of the focal species, *i,* is modeled as a function, *F*, of the density of competitor species 1 and 2. Importantly, all the 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.

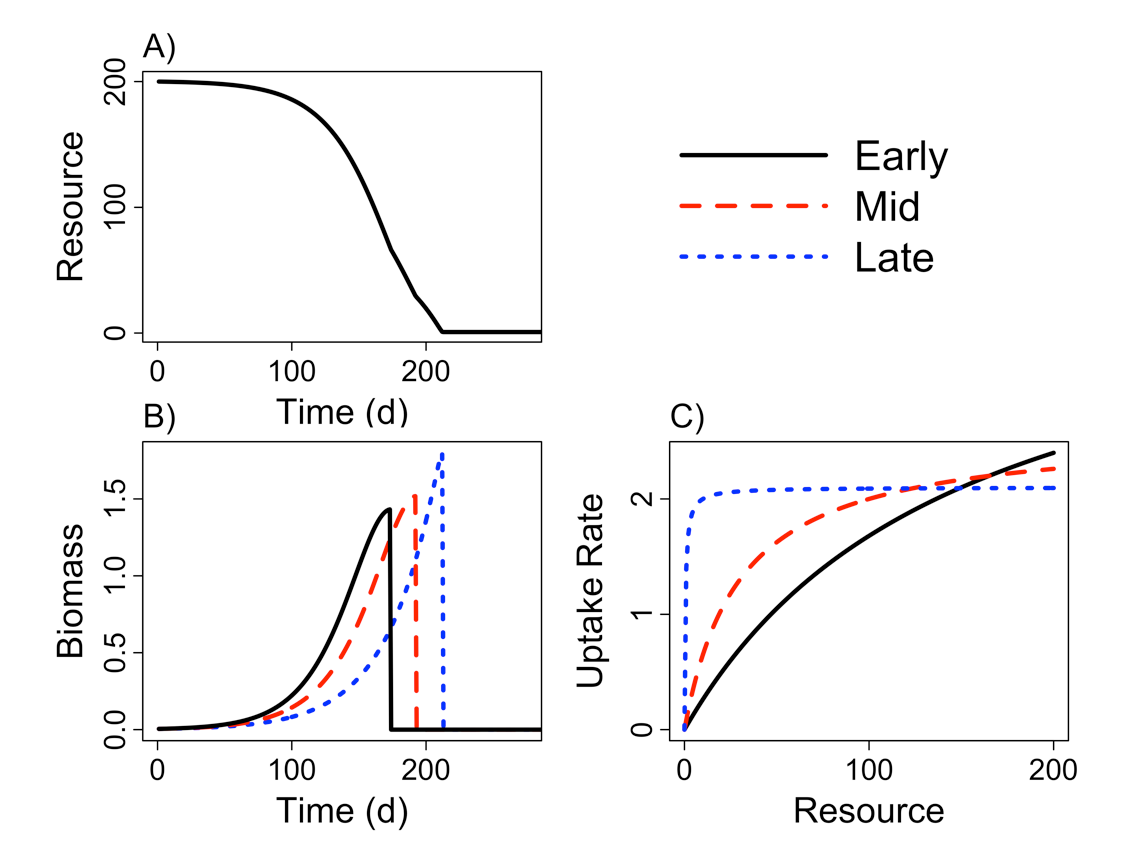


Figure 2. Example time series showing A) the drawdown of the resource during the course of the simulated growing season with starting densities of one individual of each species, B) the growth of each of species shown with colored lines and C) the dependence of resource uptake rates on resource concentration. 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.

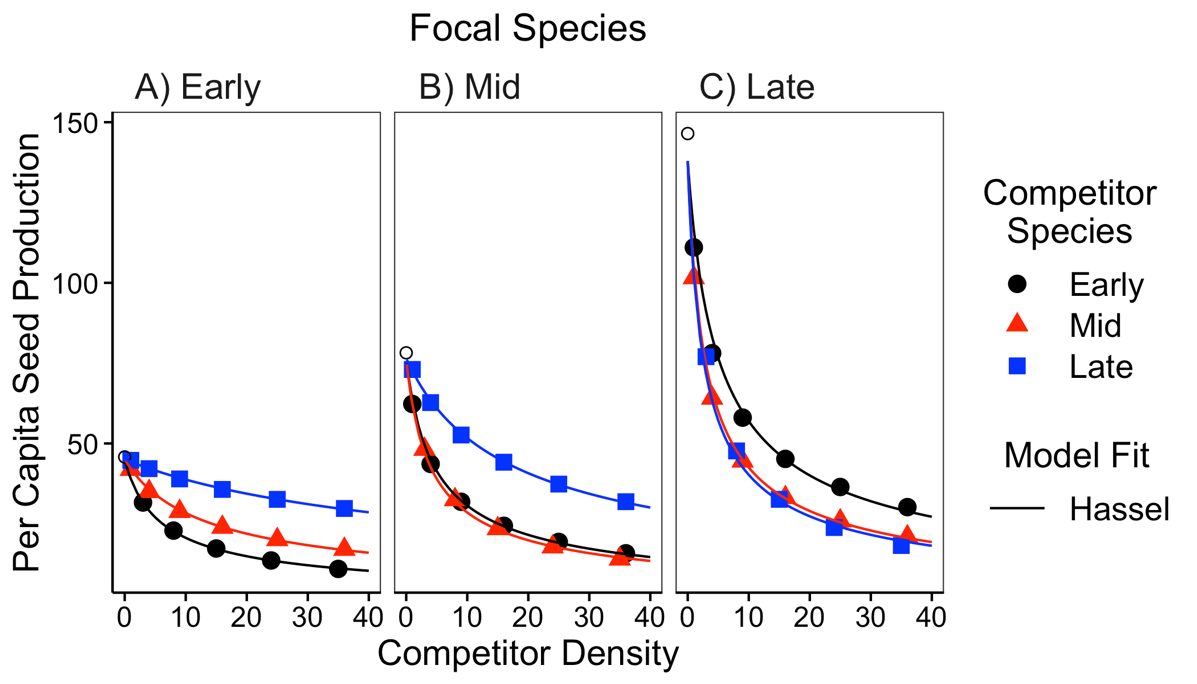


Figure 3. Simulated per capita seed production of the A) early, B) middle and C) late season species in response to increasing competitor density on the x-axis. Colors and shapes correspond to the identity of the competitor species. The solid line shows the best fit from the Hassel model fit to only the pairwise data (equation 10).

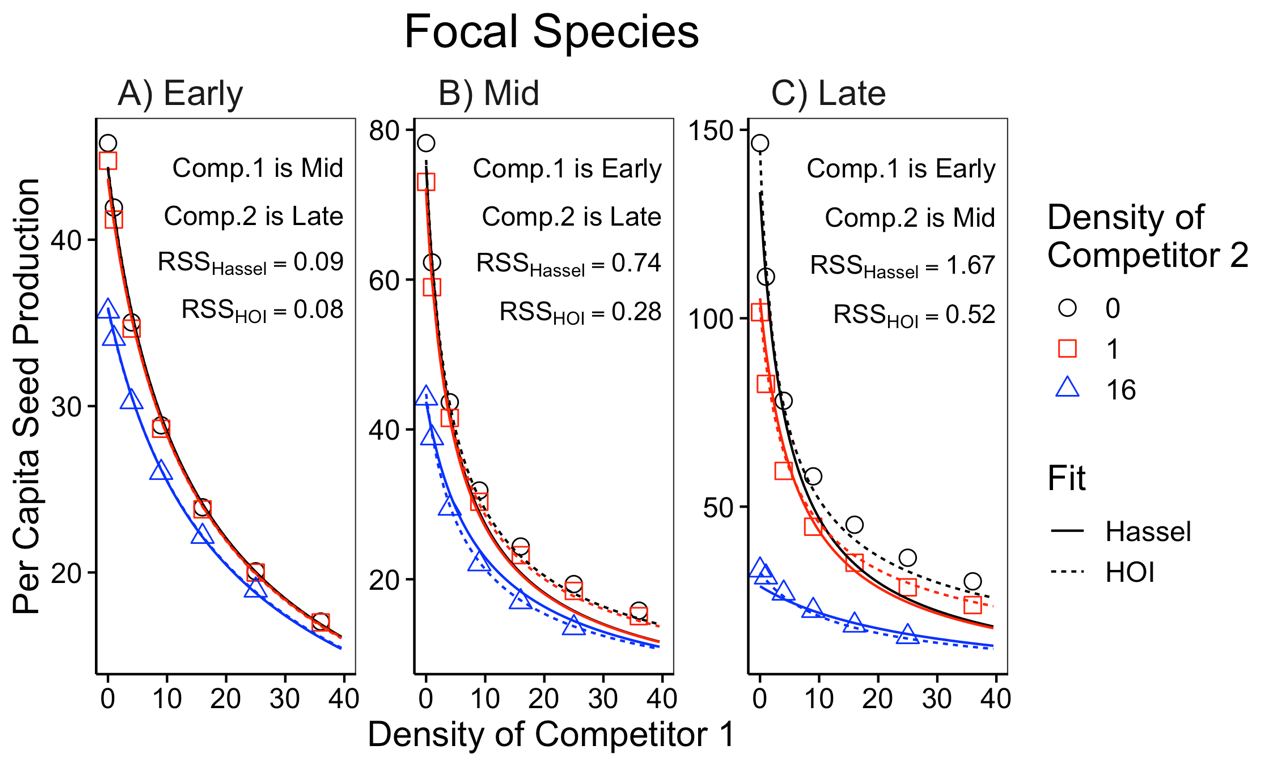


Figure 4. Simulated per capita seed production of the A) early, B) mid and C) late season species in response to increasing density of two competitor species. Increasing densities of the first competitor are shown on the x-axis and increasing density of a second competitor are shown with the varying colors and shapes. The identities of the first and second competitors are listed in each panel. The lines show the predicted per capita fecundity from Hassel and HOI models. Residual sum of squares are given for each model and species are listed on each panel.

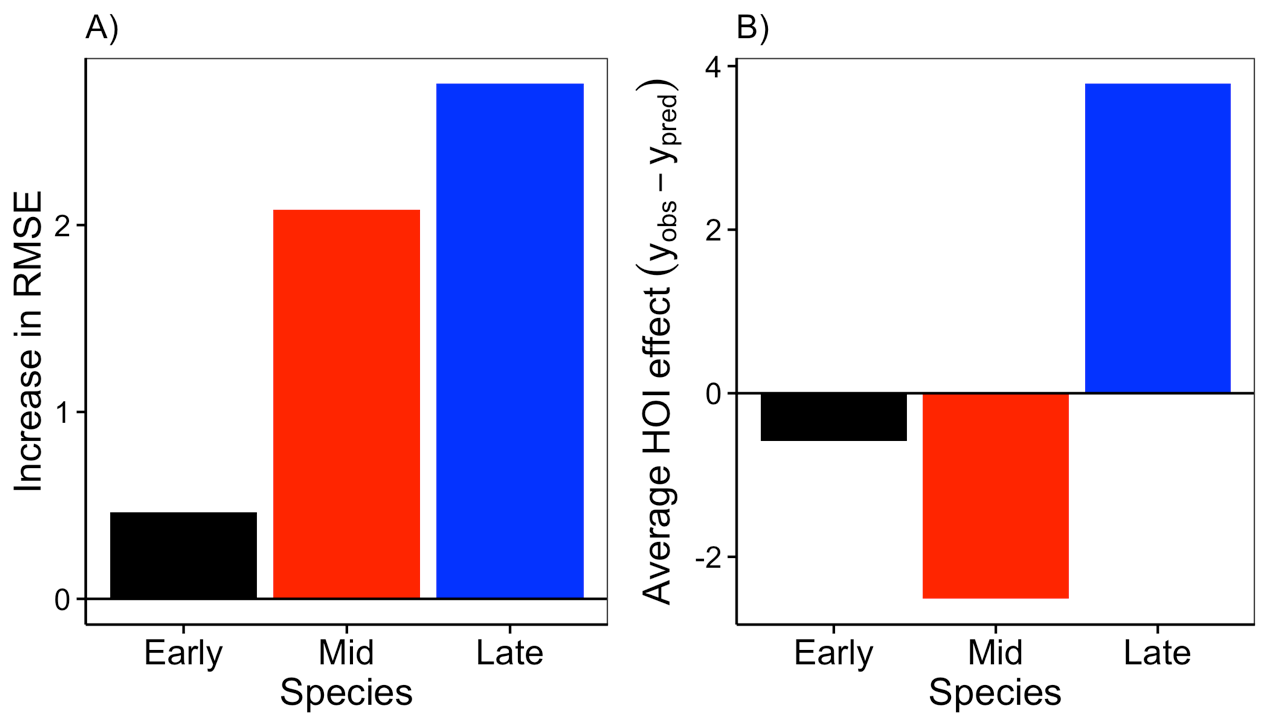


Figure 5. Deviation from additivity of two-species competition for each species in the community. A) The deviation from additive competitor effects is shown as the increase in root mean squared error of the second phenomenological model (equation 7) in multispecies competition compared to single species 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.

# 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* | 400 | Duration of growth simulation in days |
| *I* | 0 | Environmental resource supply rate |
| *R(0)* | 200 | Initial resource concentration |
| *d1* | 0.6 | Early competitor root density |
| *d2* | 0.12 | Mid competitor root density |
| *d3* | 0.36 | Late competitor root density |
| *Delta1* |  | Early competitor loss and respiration rate |
| *Delta2* |  | Mid competitor loss and respiration rate |
| *Delta3* |  | Late competitor loss and respiration rate |
| *K* | 350 | Resource half-saturation constant |
| *Vmax* | 1 | Maximum resource conductance |
| *p* | 0.5 | Root to total biomass ratio |
| *nu* | 0.66 | Scaling exponent |
| *q* | 0.2 | 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).

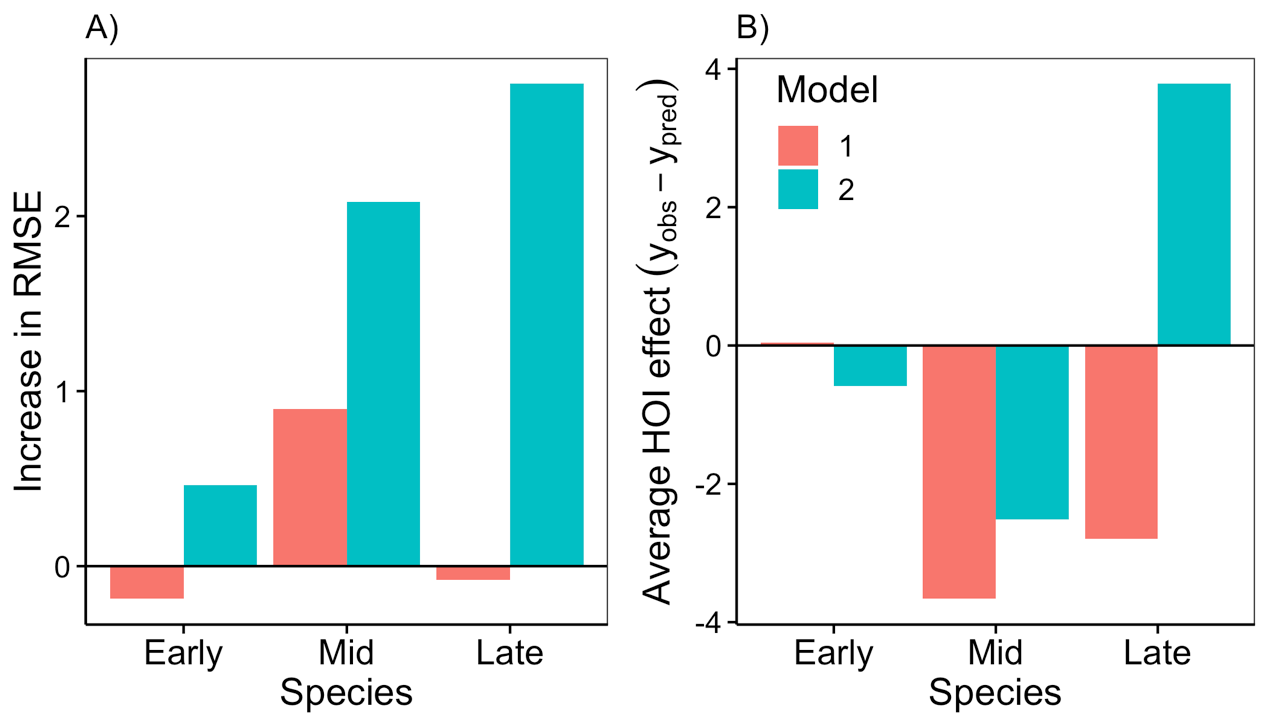


Figure S 2 Deviation from additivity of two-species competition for each species in the community. A) The deviation from additive competitor effects is shown as the increase in root mean squared error of the phenomenological models in multispecies competition compared to single species competition. B) 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 2 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 |

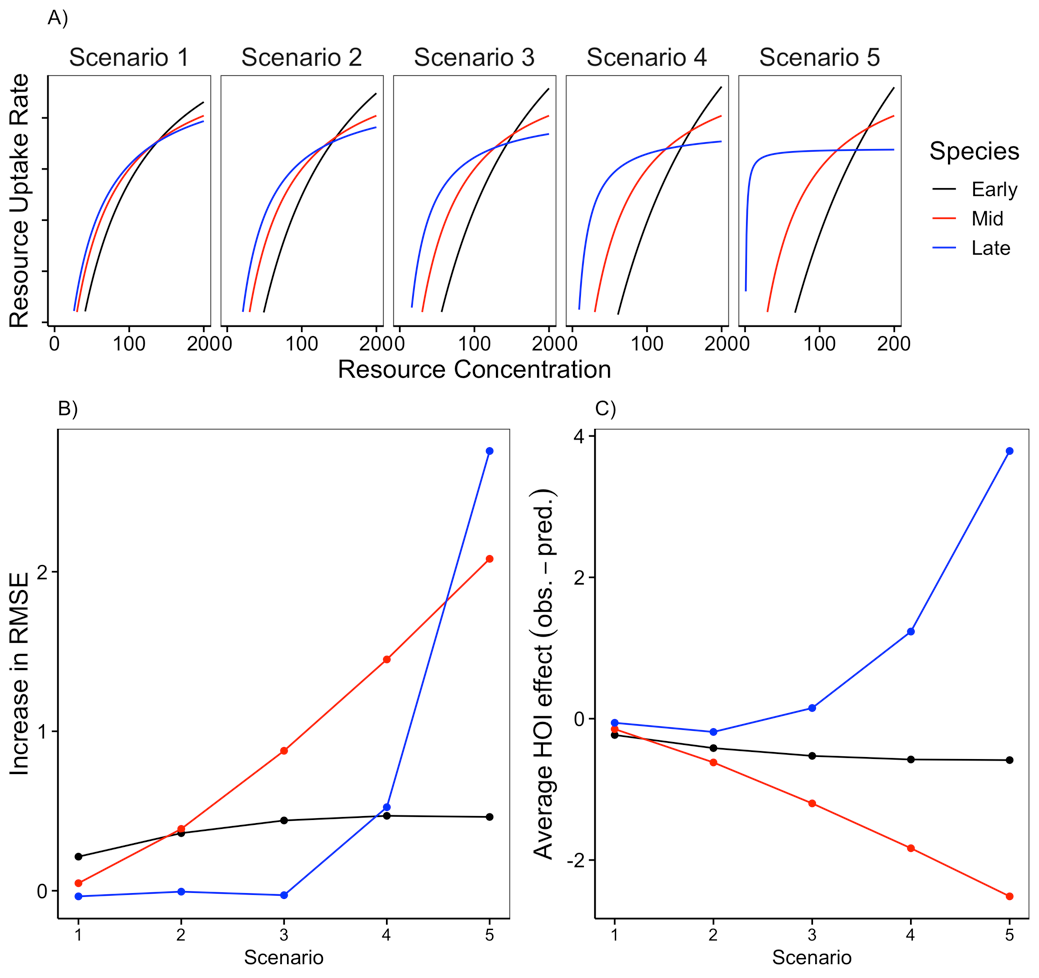


Figure A 1 Increasing the strength of the resource uptake trade-off between the early and late season species increases the magnitude of higher order interactions. A) Shows increasing relative non-linearity between species’ resource uptake curves in five scenarios. B) The deviation from additive competitor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