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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 lead to emergent properties not present when species interact in isolated pairs. In order to extend ecological theory to multi-competitor 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 propose a new general definition for HOIs that distinguishes HOIs from non-linear density dependence and emphasizes the consequence of HOIs for modeling multi-species communities. 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 growth rates and 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 HOIs may be more likely to occur in ecosystems where resource availability and individual 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 assume that the per capita effects of each species on each other is 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 from a model that only quantifies the interaction between each 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 fixed per capita interactions between species and this could have profound consequences for modeling community dynamics and species coexistence (Neill 1974, Mayfield and Stouffer 2017, Levine et al. 2017, Grilli et al. 2017). If HOIs are strong, even a perfect understanding of the interaction between each and every pair of species would not be sufficient to describe the dynamics when all the species are present 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).

Progress in measuring HOIs in nature has suffered from inconsistent definitions of 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 to describe the density dependent effects between species. This more flexible approach to modeling species interactions such as competition requires a more general definition for HOIs that can be applied to any density dependent model of population dynamics. Here, we provide a general definition for HOIs that we believe is both practical and that accurately distinguishes HOIs from related phenomena such as non-linear density dependence and indirect effects. In the second part of the paper, we use a simulation model to illustrate how our definition can be applied to empirical data and to investigate the mechanisms that may commonly generate HOIs in nature.

## 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 rate of growth for the focal species *i* and is the per capita effect of competitor species *j* on the growth rate of the focal species. 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 introduces the product of competitors one and two as new term in the model,

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|  |  | (4) |

IM implies a meaningful change in the nature of an interaction between species: in this example, that the interaction between species one and the focal species changes depending on the density of *n2* suggests the behavior or traits of these competitors are different when they are separate compared to when they are together.

## A general definition of HOIs

While the basic outline of how IM produces HOIs 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 Hassel model (Hassell and Comins 1976),

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|  |  | (6) |

has the partial derivative . Thus, the effect of competitor *j* on the focal species is given by a function which includes the density of all other competitor species. Nevertheless, as in the LV model, the Hassel model does not imply hard HOIs as we define because it can be decomposed into a set of pairwise interactions without loss of any information. For instance, for two competitor species:

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|  | (the response to competitor one)  , (the response to competitor two). | (7) |

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 Hassel 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 is implicit in the form of the model.

Adler and Morris (1994) describe another example where different species of plants 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 its canopy. 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 Hassel 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 the presence of any other species. By contrast, hard HOIs as we define them require distinct IM between competitors.

A related issue that arises in equating simple non-linearity with HOIs is that this would treat as 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 a kind of 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 they 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 criteria for determining whether a model had HOIs, that like ours, made a distinction between hard HOIs and simple non-linearity. To apply their criteria, one must first find the partial derivative of the population growth model with respect to competitor density as discussed above. Next one attempts to express this partial derivative as a function of the population growth model itself, the function *Fi*. If the partial derivative could be expressed this way and 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). For example, for the Hassel model in (6), the partial derivative can be expressed as , so there are no HOIs per the Adler and Morris criteria. While this achieves a practical goal, why *Fi* is allowed in the expression for the partial derivative is not entirely clear. Moreover, while their criterion works for many competition models, it does not work in multi-competitor models in which there are different forms of density dependence for different competitor species. The Alder and Morris test would indicate HOIs in such models, but not our definition of HOIs.

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 growth 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 plants in a Mediterranean climate. These systems are characterized by 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 nutrients. This pool is not resupplied during the season and is depleted overtime. As the resource concentration declines, plant growth slows and eventually stops. We make the assumption that when net plant growth is zero, the plants will convert a fraction of their standing biomass into seeds that will then remain dormant until the next growing season (Cohen 1976). These seeds are the only individuals that survive to the next growing season.

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

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|  |  | (8) |

where is the resource availability at time , is the resource supply rate, and the final term is the sum of resource uptake over 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*(*b­i*) converts per capita biomass into surface area of fine roots. Total resource uptake rate is the product of 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.

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

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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 an exponent that scales root volume to root surface area (similar to Kooijmans (1986)). The rate of resource uptake per unit root surface area is dependent on resource concentration following Michaelis-Menton kinetics:

The equations above describe growth in biomass, *Bi*, over the course of days within a single growing 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 population density into biomass we assume that individuals start the growing season as seeds with a fixed size. Thus, 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.

We simulate the dynamics of three virtual species of annual plant that differ in only two parameters: 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). Phenological difference, i.e. their growth over time, between the species naturally emerge from the differences in these traits (Figure 2). 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. 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. Thus, we refer to the three species in our simulations as ‘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 annual plant species is grown with a range of competitor densities. Each simulation lasts one growing season (200 days). After the simulation ends, we find the per capita seed output of each species and save this as a measure of performance. We quantified each species performance across densities of 0, 1, 2, 3, 4, 9, 16, 25 or 36 individual competitors. Each species is tested against each other species including itself and all possible combinations of two competitor species in an orthogonal design. We excluded scenarios in which all three species have densities greater than one to avoid the possibility of three-way HOIs. This design allows us to measure the pairwise effects between competitors as well as the presence of IMs between species.

We chose parameters that produced growth and phenology patterns qualitatively similar to growth curves observed in annual plant communities (Godoy and Levine 2013). A table of parameter values for the simulations can be found in the supporting information (Table S 1). We simulate growth and resource dynamics by solving (7) and (8) using the package desolve in the statistical program R (R Core Team 2015).

## Phenomenological annual plant model

In order to investigate whether this simulation produces HOIs between the competitors, we fit three phenomenological competition models to the simulated per capita seed production of each species. The first model is a multispecies version of the Hassell model (Equation 6), where is the maximum per capita seed production, is the per capita competitive effect of species on and the denominator in the model is raised to species-specific exponent where We specified an HOI version of the Hassel model as follows,

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|  |  | (12) |

where two-species HOI effects on the focal species *i* are terms involving the coefficients (Mayfield and Stouffer 2017). By our definition, represents a hard HOI that can only be evaluated by measuring the per capita seed production of the focal species in cases where 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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|  |  | (13) |

This model does not have HOIs per our definition. However, when there are two or more competitors the denominator becomes a polynomial with multiplicative terms of competitor density. Thus, contrasting this model with the HOI model allows us to test whether hard HOIs are truly required.

We first fit the Hassel model to only the pairwise cases and checked the model fit graphically. We then fit all three models to the full set of competitor densities. The response of each focal species was modeled separately. For each model we calculated root mean squared error (RMSE) as a measure of goodness of fit. We evaluated the strength and direction of HOIs by examining the HOI coefficients . To fit the models, we used the non-linear least squares (“nls”) modeling function in R. Code to run the simulations, fit the models and produce the figures is given in the online supporting information.

# Results

For all three species we found that the Hassel model fit the simulated pairwise data accurately (Figure 3). We next compared the three phenomenological models fit to the full range of competitor densities (Figure 4). For the early season species, the Hassel model and the HOI model showed more or less equivalent fits to the data with only a slight decrease in RMSE for the HOI model (Figure 4 A&G). For the mid-season species, we found that the HOI model fit the data better than the Hassel model (Figure 4 B&H). For this species, the RMSE of the HOI model was less than half that of the Hassel model. The HOI model also fit the late season species per capita seed production better than the Hassel model (Figure 4 C&I). The inability of the Hassel model to fit the per capita seed output of the mid and late-season species can be seen by plotting the observed and per capita seed production against competitor density (Figure S1). The fitted HOI coefficients also showed stronger HOIs for the mid and late season species but not for the early season species (Figure 5). In all cases, the fitted HOI coefficients, the , were of smaller magnitude than the fitted pairwise effects, the (Figure 5). The multiplicative model “model 2”, did not fit the multi-competitor dynamics as well as the Hassel or the HOI models (Figure 4 D,E,F).

# Discussion

*Evidence for higher order interactions*

Our simulation shows clear evidence for HOIs affecting two of the three virtual species in our simulations (Figure 4 and Figure 5). For the mid-season and late season species, the strength of per capita competition changed depending on the presence of other interspecific competitors. Specifically, both early season and mid-season species increased the per capita effects of competition on the late-season species (Figure 5 F). Likewise, the early season species increased the per capita effects of competition on the mid-season species (Figure 5 E). For the early season species, no clear HOIs were detected: the Hassel model fit the data nearly as well as the HOI model (Figure 4) and the magnitudes of HOI coefficients were very small (Figure 5D).

We observe competition in our simulations because of a feedback between individual density and resource concentration. As individuals grow, they draw down resource concentrations (Figure 2) and this slows the growth of other individuals in the community. The magnitudes of pairwise interactions between species is easily understood from this perspective. For instance, the late season species has a weak per capita effect on the early season species, because while the early species is active, roughly the first 30 days of the simulation, the late-season species is growing slowly and remains small (Figures 2 & 5). In contrast, the mid-season species has a stronger effect on the early season species because it grows faster during the same period (Figure 5). On the other hand, for the late-season species, the early season species has the weakest per capita effect because it stops growing so early in the season (Figure 5).

The simplicity of the simulation makes it possible to understand how HOIs emerge in this system as well. The HOIs that affect individuals of the mid and late season species are essentially an indirect effect of resource uptake on competitor size over time. For instance, in a scenario with one individual of each species the early season species slows the growth of both the mid-season and the late-season species, this keeps them smaller later into the season and makes them both more sensitive to competition as the season progresses (Figure 2). This is reflected in the HOI coefficients for the mid and late-season species (Figure 5). In contrast, the early season species grows fast and exerts the dominant effect on resources while it is active, this makes any indirect effects on it mediated by changes in the size of its interspecific competitors negligible by comparison (Figure 5).

While the HOIs in this system are similar to competition mediated indirect effects (Levine et al. 2017) there are two important differences between the HOIs we observed and indirect effects. First, indirect effects are not emergent properties of a multi-competitor system, rather they are the natural result of pairwise per capita competition coefficients. Second, indirect effects emerge because of changes in the density of competitors over time, not because of changes in per capita competition coefficients. For example, one species may have an indirect effect on its competitor by changing the density of a second competitor over the course of several years. In contrast, the HOIs in our simulation are emerge over the course of a single growing season with a fixed population densities. Thus, these HOIs represent real IMs, i.e. a real change in the per capita effect of one species on another. Our example can be contrasted with a recent simulation of forest dynamics that demonstrated how HOIs could affect species coexistence (Grilli et al. 2017). In that simulation, unlike ours, there were fixed per capita interactions between species. What the authors called HOIs in that model, were not due to changes in the per capita effects of competition, but were caused by changes in competitor density over time that were not explicitly tracked by the model.

*The phenomenological nature of HOIs*

HOIs can only be discussed, defined and quantified within phenomenological models of competition. Phenomenological models simplify dynamics by only tracking population densities and not the resources 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 dynamics (Abrams 1983, O’Dwyer 2018, Letten and Stouffer 2019). Given this, one might argue that HOIs are an artifact of the inadequacy of phenomenological models. However, we argue that any concept of species *interactions* is almost always phenomenological in nature; in most cases, competing individuals do not directly interact, rather they influence each other’s growth or survival indirectly through changes in shared resources. One could do away with interactions entirely and model populations and the resources they compete for (e.g. Dybzinski and Tilman (2007)), but measuring competitive interactions requires a phenomenological model, and thus requires confronting the issue of HOIs.

By assuming that resources concentrations are near a fixed equilibrium, phenomenological competition coefficients can sometimes be derived analytically from mechanistic competition models (Tilman 1977, Meszéna et al. 2006, Letten et al. 2017). However, in many natural systems, such as such as those involving annual plants, resource concentrations and individual size fluctuate rapidly over the course of a single growing season or generation. This makes deriving competition coefficients directly from the resource dynamics much more difficult, perhaps impossible (O’Dwyer 2018). Thus even in cases in which we actually know which resources species compete for, fitting a phenomenological model statistically to population dynamics may be the only way we can describe species interactions. Our work shows the importance of considering HOIs when moving beyond pairwise dynamics to multi-competitor settings.

*Are HOIs widespread?*

In our simulation model, HOIs can be seen to arise because individual size, the trait that determines each species’ impact on and sensitivity to resource availability, is itself governed by resource availability and also changes over time (Meszéna et al. 2006). More generally, changes in individual size and corresponding changes in resource uptake rate may be a common cause of HOIs in nature. We predict that HOIs will likely be common in systems in which 1) some species can cause large resource fluctuations, 2) the per capita rate of resource uptake changes in response to resource availability, and 3) the strength of this response varies across species. Instead of changes in individual size, another mechanism that could generate HOIs would be density-dependent changes in resource acquisition traits. For example traits, such as height, specific leaf area, and phenology, have been shown to change in response to competition and resource availability (e.g. Aronson et al. 1992, Bennett et al. 2016, Conti et al. 2018). If per capita competition coefficients are a function of these traits, then it would not be surprising if changes in these traits led to HOIs. If changes in in individual size or trait plasticity can be so easily imagined to cause HOIs, this begs the question of why there have been so few documented examples of HOIs in natural communities (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. In additional simulations, we found that as species became more similar in their traits HOIs became weaker (Appendix A). In nature, such large functional differences in the shape of resource uptake curves with or growth curves may be rare.

In addition, our simulation produces rapid changes in resource availability and average plant size. These changes cause changes in species interactions over the course of the season; without these changes species would have relatively constant per capita 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. By contrast, 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).

# Conclusion

Higher order interactions have profound implications for how we understand multispecies communities. We have provided a more rigorous general definition of HOIs that will be useful as more ecologists seek empirical evidence for HOIs in nature. In addition, by fitting HOIs to simulated resource competition we show how an empiricist could go about measuring and discussing HOIs. This simulation also sheds light on the environmental conditions and life-history traits that may be more likely to generate HOIs. 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

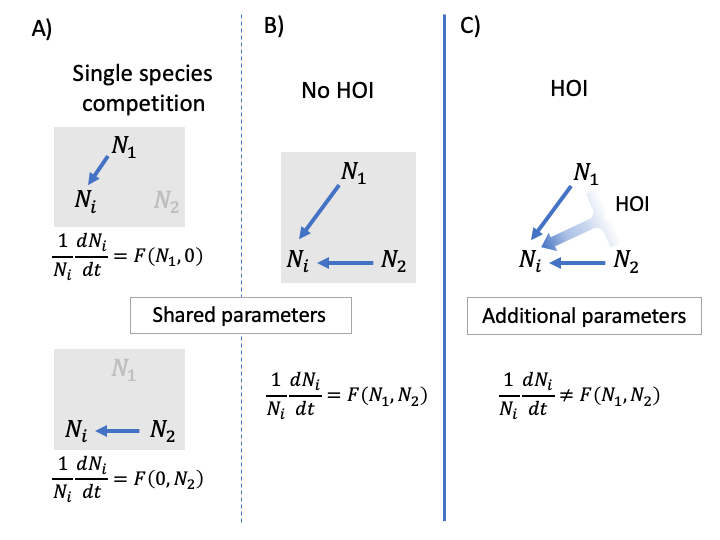


Figure 1. Conceptual definition of HOIs. In A, the competitive effects (blue arrows) of species 1 and 2 on the focal species are observed separately. The per capita growth rate of the focal species, *i,* is modeled as a function, *F*, of the density of competitor species 1 and 2. Importantly, all the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

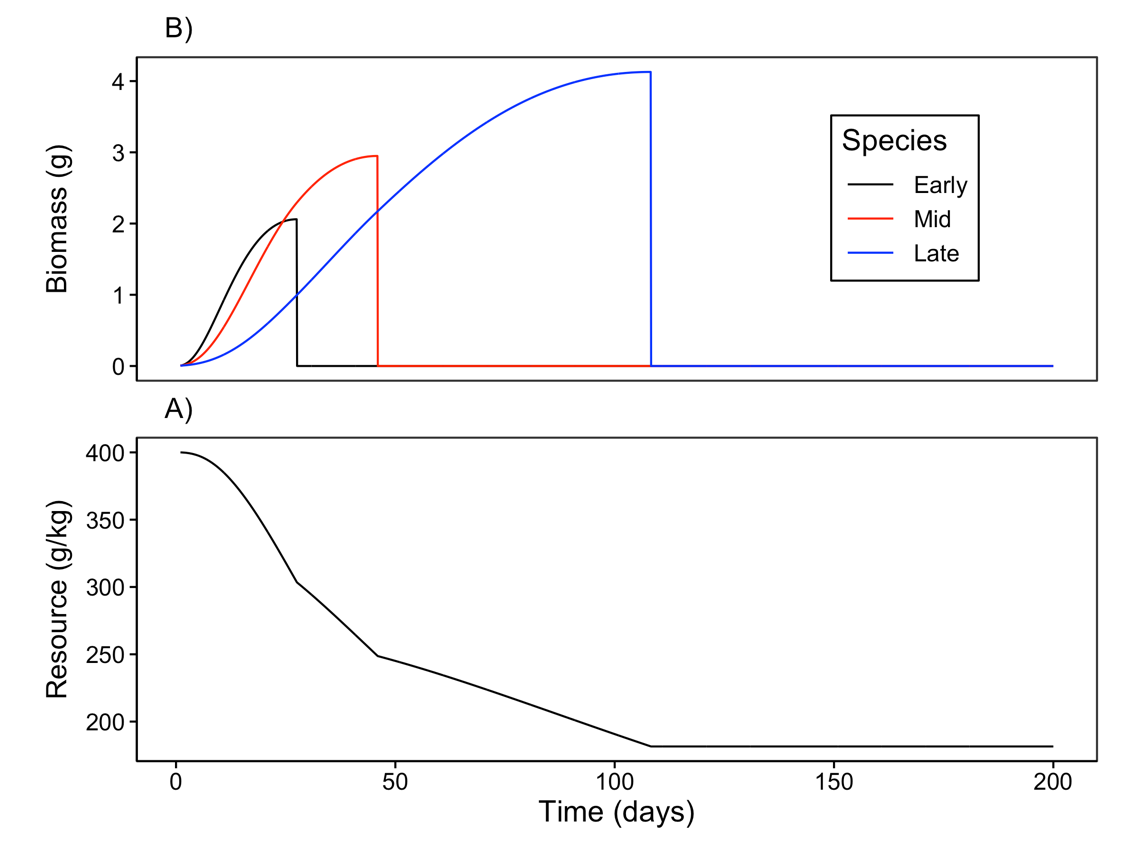


Figure 2. Example time course of A) annual plant growth and B) resource concentration during a single simulated growing season. In this example, each species was initiated with one individual (one seed). The early season species (black) grows rapidly when resource availability is high and senesces early. By contrast, the late season species (blue) grows more slowly but grows later into the season as resource availability declines. The growth curve for the mid-season species (red) lies between these extremes.

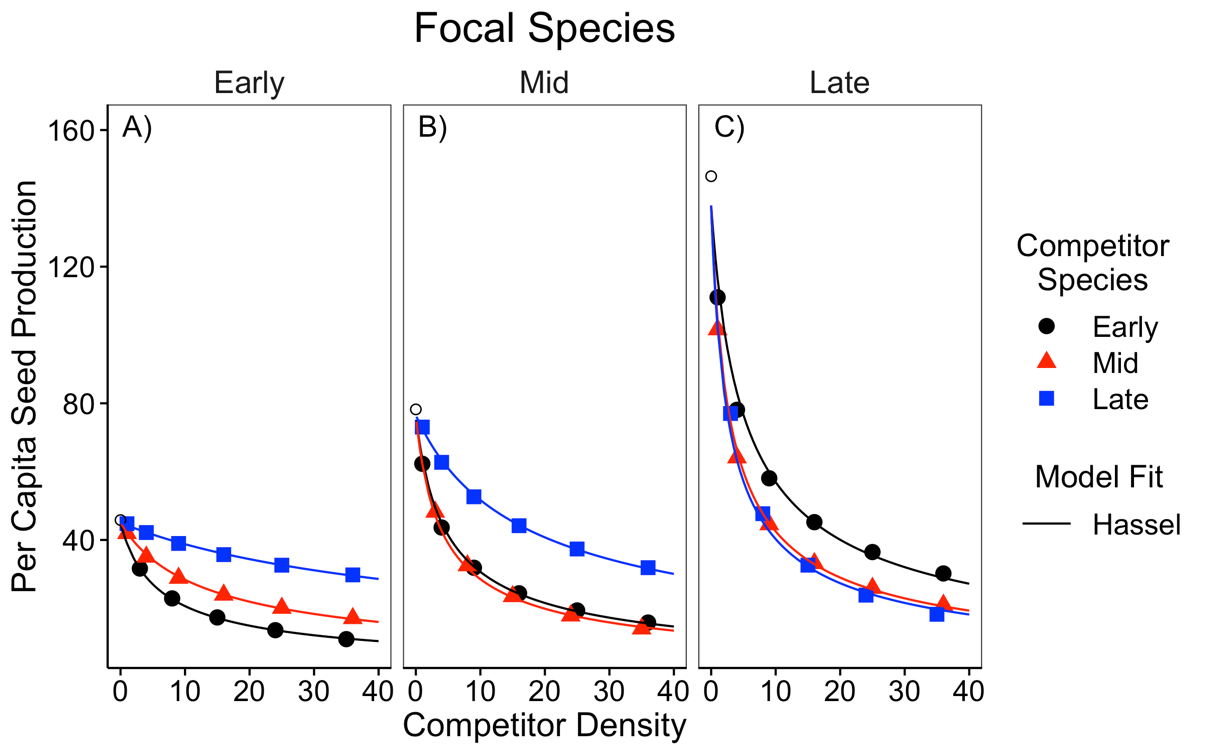


Figure 3. Simulated per capita seed production of the A) early, B) middle and C) late season species with competitor density on the x-axis. Colors and shapes indicate the identity of the competitor species. Open circles show the per capita seed production of each focal species in the absence of competitors. The solid line shows the fit of the Hassel model fit to the pairwise data only.

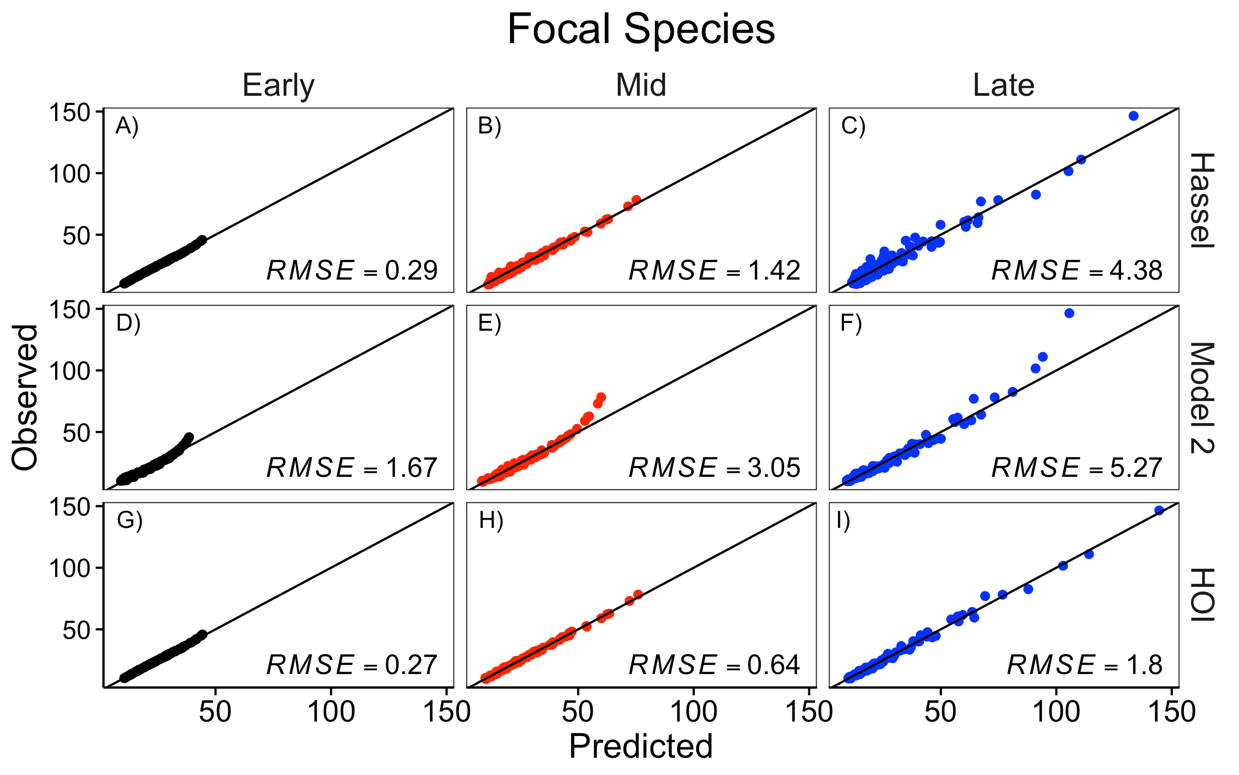


Figure 4. Comparison of model fits for each focal species. The y-axis shows the simulated per capita seed production of the focal species. The x-axis shows the per capita seed production predicted by each of the phenomenological models. The top row, A-C, shows the prediction for the Hassel model; the middle row, D-F, shows the prediction from the multiplicative model; and the bottom row, G-I, shows the prediction from the HOI model. One-to-one line and root-mean-squared error (RMSE) for each model are shown on each panel.

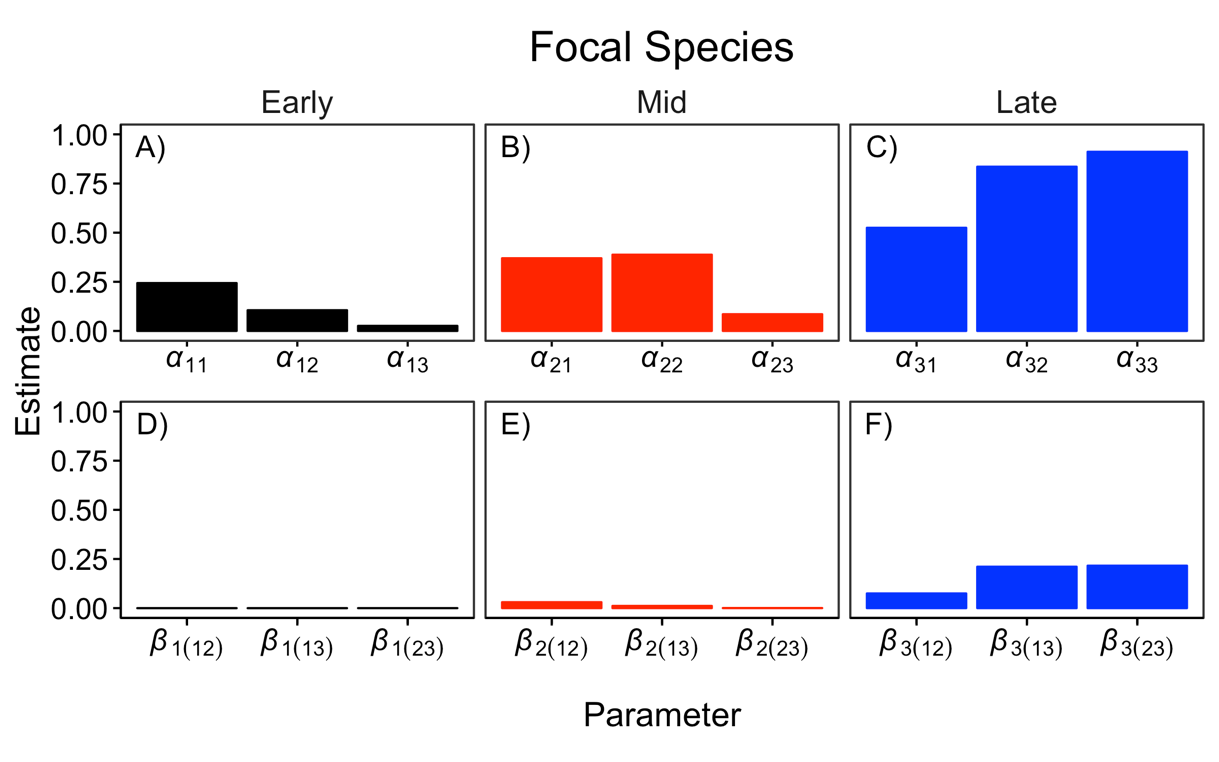


Figure 5. Interaction coefficients for each of focal species from the HOI model. The top row, A-C, shows the pairwise competition coefficients for the focal species and each competitor. The bottom row, D-F, shows the two-species HOI coefficients. Coefficient subscripts indicate which focal species and competitor species are involved, 1 = Early, 2 = Mid, 3 = Late.

# 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 (days) |
| *I* | 0 | Resource supply rate (g day-1) |
| *R(0)* | 400 | Initial resource concentration (g kg-1) |
| *d1* | 0.06 | Early competitor root density (g cm-3) |
| *d2* | 0.12 | Mid competitor root density (g cm-3) |
| *d3* | 0.36 | Late competitor root density (g cm-3) |
|  | 0.3 | Early competitor loss and respiration rate (g/g) |
|  | 0.15 | Mid competitor loss and respiration rate (g/g) |
|  | 0.053 | Late competitor loss and respiration rate (g/g) |
| *K* | 350 | Resource half-saturation constant (g kg-1) |
| *Vmax* | 1 | Maximum resource conductance (g d-1cm-2) |
| *p* | 0.5 | Ratio of root to total biomass |
| *nu* | 0.66 | Scaling exponent (unitless) |
| *q* | 0.2 | Biomass assimilation rate (g/g) |
|  | 0.005 | Seed mass (g/seed) |
| *c* | 0.1 | Conversion of final biomass to seed mass (g/g) |

# Supporting Information – Additional figures

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Figure S 1 Simulated per capita seed production of the A) early, B) mid and C) late season species in response to density of two interspecific competitors. Density of competitor species one is shown on the x-axis and density of competitor species two is shown with colors and shapes. Text in each panel lists the identities of competitor one and two (early, mid or late). Lines show best fit from the phenomenological models fit to the simulations. Residual sum of squared error is shown for each model and focal species.

# 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 |

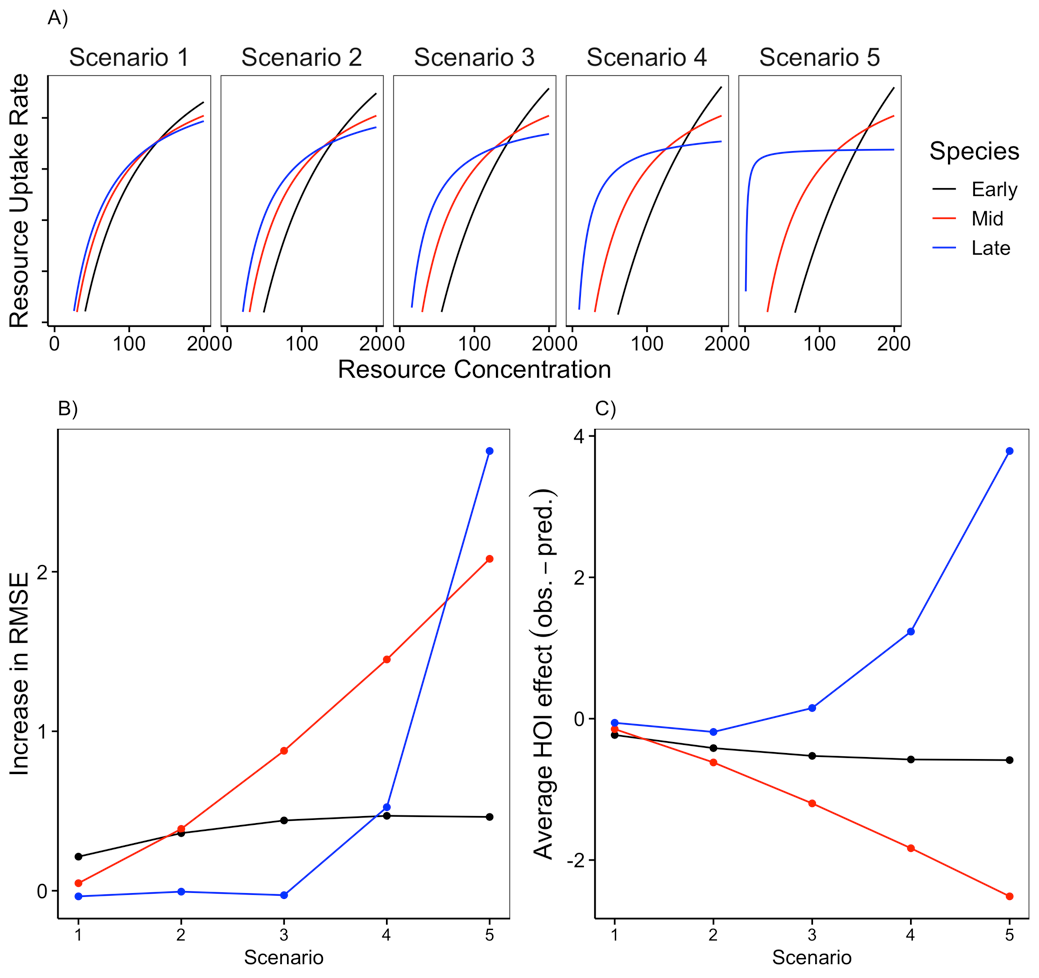


Figure A 1 Increasing the strength of the resource uptake trade-off between the early and late season species increases the magnitude of higher order interactions. A) Shows increasing relative non-linearity between species’ resource uptake curves in five scenarios. B) The deviation from additive competitor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