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**Detecting Higher Order Competitive Interactions**

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I think this is a great start. What I think we need are clearer expectations or hypotheses from the outset about what will cause a higher order interaction (which to me is trait change in response to competitors) so that when we present our modeling results they support a hypothesis, and help to refine that hypothesis. Otherwise someone might think that this paper builds a quirky model and finds some HOIs, but does not get at general issues. This is just a matter of framing that we should talk about.

Running Title: Higher Order Interactions

Word Count:

# Abstract

Almost every species on earth interacts with more than one competitor. When species simultaneously interact with two or more competitors, higher order interactions (HOIs) can invalidate the application of classical theories of species competition based on pairwise interactions. HOIs occur when the strength of competition between two species depends on the density of other species in the community. It is therefore critical to understand how often and by what mechanisms HOIs arise in order to extend pairwise ecological theory to multi-species communities. In this paper we use simple competition models to illustrate potential causes of HOIs and their interpretation in a community context. We quantify the higher order interactions emerging in a system of annual plants differing in their growth phenology and competing for a single shared resource. We find that higher order interactions emerge most strongly for late season competitors- species that experience a competitive environment strongly modified by earlier growing competitors. We use these results to discuss possible pitfalls in detecting HOIs in empirical datasets. We conclude that HOIs are likely to arise when competitive effects arise over time periods in which competition or competitor densities are not constant. Clarifying the source of HOIs in simple analytical and simulation models may help us better understand the true nature of competition and stability in multi-species communities.

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

# Introduction

Almost every species on earth interacts with a diversity of predators, pathogens and competitors. And the densities of each of these species are themselves determined by interactions with yet other species in the community. Despite this reality, most classical models in community ecology summarize species interactions assuming that the per capita effect of one species on another is independent of the densities of other species in the system. In particular, models with such fixed per capita competitive effects have been critical to the development of modern coexistence theory (Chesson 2000, Levine et al. 2017), and imply that the dynamics of multi-species species competition can be predicted by understanding competition between all competitive pairs (Grilli et al. 2017a). This idea is also foundational to recent efforts to relate species’ functional traits and phylogenetic relationships to the outcome of their competitive dynamic (Adler et al. 2013, Godoy et al. 2014, Kraft et al. 2015).

The potential for higher order interactions (HOIs) between species challenges the core assumption of many classical models in ecology (Billick and Case 1994, Mayfield and Stouffer 2017, Levine et al. 2017, Grilli et al. 2017b). By definition, HOIs mean that our understanding of competition between pairs of species is not sufficient on its own to describe the interactions of more than two species (Abrams 1983, Billick and Case 1994). For these reasons, predicting community assembly and composition in natural communities with information on all possible pairwise competitive interactions may not be possible (e.g. Kraft et al. 2015). In addition, the presence of HOIs also challenges classical definitions of coexistence and niche differences that rest on a comparison of pairwise intraspecific vs. interspecific limitation (Adler et al. 2007, Levine et al. 2017, Grilli et al. 2017b). In the extreme, HOIs may permit coexistence in multi-species communities impossible in simpler systems (Grilli et al. 2017b).

Although ecologists are beginning to appreciate the implications of higher order interactions for our understanding of how communities assemble, what is generally not understood are the mechanistic processes that generate higher order interactions in the first place. do knowprocesses Understanding these processes is particularly important to generate expectations about which systems are likely to show HOIs, and therefore worthy of further examination, and which might be enable to more classical descriptions of pairwise competitive dynamics.

which are often made based on measurements over discrete time that could be applied to understanding HOIs

In this paper we attempt to demystify HOIs by exploring the processes by which they may emerge in nature. To do so, w, . We conduct a virtual experiment where the mechanistic model is used to project the demographic fate of individuals growing with varying densities of neighbors of either a single or two other species. We then analyze the results of the this experiment by fitting phenomenological models of competition with and without a higher order term. Before presenting the model, we first clarify the definition of HOIs.

## Defining higher order interactions

Competition occurs when individuals consume the same limiting resource, such that increases in consumer densities reduce the availability of resources, which in turn changes the population growth rate of the consumers (Meszéna et al. 2006). Thus, resource competition can be considered an indirect effect of individuals on one another mediated by shared resources. The commonly used phenomenological definition of competition simplifies the representation of the interaction by focusing on the net effect of the indirect interaction without tracking the status of shared resources. Phenomenological competition is typically measured as the reduction in a per-capita population growth rate due to an increase in density of individuals of the same trophic level (Chesson 2000). This perspective on competition is powerful because it includes all shared resources and other environmental feedbacks into one effect that can be measured empirically.

The advantages of phenomenological models, however, come with a complication. In particular, they often make the simplifying assumption that each species per capita competitive effect is independent of each other species’ per capita effect. This assumption may not necessarily be valid for competition in nature or even for many mechanistic competition models (Abrams 1983). When species competitive effects change depending on the presence of other species this is an interaction modification or higher order interaction (HOIs) (Billick and Case 1994, Adler and Morris 1994).

HOIs have important practical and theoretical implications for ecologists working to understand biological communities. In the most general sense, a HOI means that the interactions between multiple species could not be predicted with knowledge of how each competes in a pairwise manner. The challenge is developing a precise mathematic form for this definition. Following Billick and Case (1994), we argue that HOIs can be defined as non-additive competitive interactions (Box 1 “Defining HOIs”). This has both a technical mathematical definition as well as an intuitive ecological meaning: when competition between species is additive, then competition between species can be studied separately as a set of pairwise interactions that when summed predict the population growth rates of the focal species in a community. Importantly, the summing can occur on a transformed (e.g. log or inverse) scale such that even interactions that are multiplicative or nonlinear in their effect in the linear scale do not necessarily generate HOIs (Adler and Morris 1994). Figure 1

The definition of higher order interactions developed here follows closely from Billick and Case (1994), with the added qualifier that additivity can be assessed on a transformed scale. As pointed out by Billick and Case (1994), such non-additivity can also emerge in a pairwise interactions if for example, intraspecific interaction strengths are altered by the presence of interspecific competitors. Whether one treats these types of pairwise interactions as higher order interactions depends on the study goals, but such pairwise “HOI”s do not necessarily cause an understanding of pairwise interactions to poorly predict dynamics in more diverse contexts.

Resolving the mathematical definition of HOIs is a necessary first step for understanding these interactions, but does not clarify the processes generating these interactions in nature. Addressing these processes is the subject of the remainder of this paper.

**Box: Mathematical definition of HOIs ------------------**

A mathematical definition of HOIs starts with a general phenomenological model of species competition in discrete time,

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|  |  | (1) |

where is the density of species at time , is a function that gives the per capita population growth rate as a function of the densities of species , and . A Beverton-Holt model of density dependent competition, for example, is a specific case of this general functional form in which the per capita population growth rate declines in proportion to the inverse of the sum of competitor densities,

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|  |  | (2) |

where is the per capita population growth rate in the absence of all competition and gives the per capita competitive effect of each individual of species *j*.

Despite the fact that the functional relationship between population growth rate and competition is non-linear in the Beverton-Holt model, it is possible to transform population growth by some function, such that the effects of competition are additive on this scale. In this case, we transform population growth rate by dividing by , then taking the inverse and subtracting one,

On this transformed scale we can still predict the overall effects of competition in multi-species community by adding up the separate pairwise competitive interactions and applying the appropriate transformation—competition is additive on the transformed scale and there are no HOI’s.

In contrast, consider the case with a higher order interaction where, . The coefficient captures an HOI between species *j* and *k*. So long as , there are no transformations of the population growth rate that will allow us to assess the effects of species *j* and *k* as a linear combination of their effects. By extension, we also cannot predict the population growth rate of species *i* in a multi-species community from just the pairwise interaction coefficients. From this definition, even a two species community can include non-additivity and HOIs, as might describe the effects of species *j* and on the effect species *i* has on itself (Billick and Case 1994, Mayfield and Stouffer 2017). [ end box ]

# HOIs arise from unmeasured population states

Theoretical discussions of HOIs have often focused on differential equations where competition operates as a function of continuously changing species densities or individual sizes (Billick and Case 1994). Yet, except for work in laboratory microcosms and studies of plankton, ecologists rarely quantify competition using models that are explicitly continuous in time. Population-level effects of competition are most often measured by observing per-capita population growth rates over some discrete period of time, typically one year. Competitor density and individual performance can also be measured over a period shorter than a single growing season yet still model population growth rate on an annual time scale if all demographic rates are measured e.g. (Kraft et al. 2015, Mayfield and Stouffer 2017). Importantly, measuring the effects of competition over a discrete time interval opens the possibility for HOIs to emerge as a result of unmeasured states within the population (Adler and Morris 1994, Levine et al. 2017, Grilli et al. 2017b).

In principle, the issue of HOIs arising from unmeasured population states at intermediate time steps has an easy resolution. By measuring those population states and the effects of competition on those states, a strictly pairwise model can still capture community dynamics—no HOI terms are required in the model. This situation is exactly equivalent to interaction chains or competition-mediated indirect effects that propagate over more than one timestep. However, with noisy data in nature, it may not always be easy to identify whether HOIs emerge due to the application of an incomplete demographic model or whether they arise for more fundamental changes in the environment, or species phenotypes.

# HOIs in a mechanistic resource competition model

Theoretical discussions of HOIs have often focused on differential equations where competition operates as a function of continuously changing species densities or individual sizes (Billick and Case 1994). Yet, except for work in laboratory microcosms and studies of plankton, ecologists rarely quantify competition using models that are explicitly continuous in time, making these theoretical studies an awkward match to the way we study natural systems. Population-level effects of competition in empirical studies are most often measured by observing per-capita population growth rates over some discrete period of time, typically one year. Importantly, because we measure the effects of competition over a discrete time interval, HOIs can emerge as a result of the unmeasured states within the population that change over the time interval (Adler and Morris 1994, Levine et al. 2017, Grilli et al. 2017b). We know that these states can include changes to the size or morphology of individuals, or even their density, in response to their competitive environment. But we lack hypotheses about which state changes will most strongly generate HOIs.

To explore these processes, we simulate competition among annual plants for a single shared resource over continuous time using a mechanistic resource competition model. We then describe competition in the system using a simple phenomenological competition model. By comparing the cases in which higher order interactions emerge or fail to emerge in this phenomenological description of the system, we can address the processes causing these interactions develop.

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

The model is expressed as a set of differential equations,

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where gives the resource availability at time , and gives the resource supply rate. The final term expresses the loss of resources due to uptake by plants. Plant biomass of species at time is given by , *s* is the number of species in the community and is the resource dependent uptake function for species *i*. We simulate a Mediterranean climate by setting initial resource availability high, , and setting the resource supply rate to zero. This means that resource availability starts out high and is gradually depleted without being resupplied (Figure 2 a).

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

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|  |  | (4) |

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

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

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

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|  |  | (5) |

where, is the maximum rate of resource capture and is the half-saturation constant of resource capture. The unique resource uptake curves result in unique growth and phenology for the three species we model here, and term ‘early’, ‘mid’ and ‘late’ (Figure 2).

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

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|  |  | (6) |

where is the number of seeds produced at the end of the growing season, and therefore available to start the next years population growth. We assume that there is no seed mortality between years and all seeds germinate.

We simulate these dynamics using the ordinary differential equation solvers package desolve in the statistical program R (R Core Team 2015). Simulation parameters and code to run the simulations are given in the supporting information.

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

## Phenomenological annual plant model

We model annual plant competition in terms of the decline in per capita reproductive output with increasing density of competitors at the start of the growing season (). We tested two different phenomenological competition models. The first has been used in a number of empirical studies of annual plant competition (Rees et al. 1996, Freckleton et al. 2000, Kraft et al. 2015),

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

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

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|  |  | (8) |

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

In order to detect HOIs emerging from these simple dynamics and measure their strength we first fit the phenomenological models to cases where each focal species faced increasing densities of one other competitor species at a time- the pairwise case. Once we had shown that phenomenological models fit these pairwise dynamics adequately we used the best fitting model to predict species fecundity in the case where the focal species simultaneously faces two interspecific competitor species. This approach provides a direct and concise test of the assumption of additive species effects in this simulation. If species effects are additive, then our model fit to density gradients of a single competitor species should be able to predict the joint effect of competition from two competitor species together. The average deviation between the fecundity of each species predicted by the additive phenomenological model and the fecundity observed in the simulations is a measure of the effect of the HOIs between the competitors. Importantly, this approach does not require that we specify the functional form of the higher order term- i.e. whether a function that includes an or term best describes the data.

# Evidence for HOIs

For all three species we found that the modified phenomenological competition model with varying exponents on species effects fit the simulated data accurately (, whereas the standard model with one coefficient per recipient of competition did not fit the data as well (Figure 3). When we tested how well the pairwise competition model fits predict species’ response to simultaneous competition from two other species, we found the emergence of HOIs depended on the focal species’ phenology (Figure 4). For the early species, the observed effect of the two other competitors on its growth was close to that predicted by each of their pairwise effects (Figure 5). For the mid and late season species, the predicted fecundity based on pairwise interactions did not match the observed fecundity when the focal species faced the two other competitors at once (Figure 5). Specifically, the additive model underpredicted the strength of competition on the mid-season species (Figure 5 b), and overpredicted the strength of competition on the late species (Figure 5 c). The difference between the predicted and observed effects of competition on the mid and late season species indicate the presence of HOIs: in other words, competitors’ effects change depending on the presence of other competing species.

In sum, our example shows that even in a relatively simple resource competition model, the effects of multi-species competition may not match the additive effects of pairwise species competition. Our method of comparing the effects of competition assuming additivity to the observed effects of multispecies competition is a useful way to determine the presence of HOIs without assuming a specific functional form for the HOIs. This makes it a diagnostic tool, not a way to predict multispecies community dynamics.

*What Causes Higher Order Interactions?*

In this model, HOIs emerge because species growth and resource uptake rates are dependent on the current availability of resources in the system (Figure 2 c). This means that as species use resources they not only affect the growth rates of their competitors, but they can also affect the net interaction between their competitors. For instance, the early species has the most rapid growth and resource uptake rate early in the season when resource concentrations are high and it has a strong impact on early season resource availability. This shifts the resource uptake rates of the mid and late season species left along their resource uptake curves. Because these curves are shaped differently, this reduces the uptake rate of the mid-season species more than the late season species and effectively weakens the effect of the mid-season species on the late species. Thus, we find that when the late species faces competition from the mid and early season species at once the competitive effect is less than expected (Figure 4 c; Figure 5 b). The same dynamics mean that the mid-season species experiences competition from the early and late species that is stronger than the sum of the single species effects (Figure 4 b; Figure 5 b).

By contrast, the early species is only weakly affected by HOIs (Figure 5). This is because it dominates early season resource competition and senesces before its competitors grow large (Figure 2). In principle, the reduced growth of the mid species could modify the effect of late species on the early one. However, the early species senesces before the slower growing mid or late season species can have

strong effects on resource availability in the system. This reduces its exposure to potential HOIs involving the mid and late competitors.

The origin of HOIs in this system are consistent with the arguments in favor of HOIs put forward by Abrams (1983). Abrams argued that HOIs should occur when competing species show 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). They also stop competing at different resource availabilities. This means that competition between pairs of species depends upon the level of resources available. Since all 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). Classically, deriving competition coefficients from a mechanistic resource competition model involves solving stable resource equilibriua 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, Abrams 1983, Meszéna et al. 2006). 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. The great advantage of statistically fitting a phenomenological model to observed or simulated effects of competition is that this approach can help us understand pairwise competition even in such complex cases. However, our work here shows that this advantage may come at the cost of ignoring important HOIs in multispecies communities.

# Are HOIs Common in Nature?

One way to view HOIs in this system is to consider it a specific instance of a more general case in which the trait that determines each species’ impact on and sensitivity to resource availability is itself governed by resource availability. In this case, the trait in question is the temporal dynamic of resource uptake by each species, which shifts in response to resource availability and thus the activity of competitors. More generally, we believe that whenever the functional traits that govern the impact or the sensitivity of species to resources change in response to competition this is a recipe for HOIs. Among competing plants, changes in height, biomass, and root to shoot allocation in response to competition are widespread. In theory, these traits should also determine each individual’s impact and sensitivity to competition. So, are HOIs inevitable? And if so why are so few documented examples among competing plants (but see Mayfield and Stouffer 2017)?

One hypothesis is while HOIs are common, they are often weak. A key factor in producing HOIs in our simulation is that each species differs in the relative non-linearity of its resource uptake curve. The weaker the trade-off between resource uptake rates at high versus low resource availability, the weaker the HOIs in this system. In nature, such strong trade-offs may be rare.

The very large changes in resource availability and plant biomass in our simulation also contribute to the strength of HOIs. Because resource availability fluctuates widely in our simulation it means that species interactions change dramatically over the course of the season. Without this 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 in a temperate climate (Dybzinski and Tilman 2007). Due to their large size, perennial plants can be assumed to quickly draw resources down to a dynamic equilibrium close to the environmental resource supply rate. Thus, even if species have different non-linear responses to resource concentration the fact that resource concentration is relatively fixed eliminates the possibility of strong higher order interactions. Because of their resource dynamics, seasonally forced systems, such as annual plant communities in a Mediterranean climate, may be a good place to look for strong HOIs (Mayfield and Stouffer 2017).

# Conclusion

We have sought to clarify the definition of HOI’s and explain how they could arise from relatively simple competitive dynamics. We illustrate this point with a simple mechanistic model of species competition for a single resource. Separating cases where non-additive competition is due to indirect effects mediated by intermediate population states, and those where competition is fundamentally irreducible to pairwise competition will be an important challenge for future empirical studies of HOIs. While we believe that HOIs should be common in nature this does not mean that they will be strong or strong enough to detect statistically in empirical settings. Our work suggests that environments in which resource availability varies strongly throughout the season may  
be a likely place for HOIs to emerge.

# Acknowledgments

# References

# Figures



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

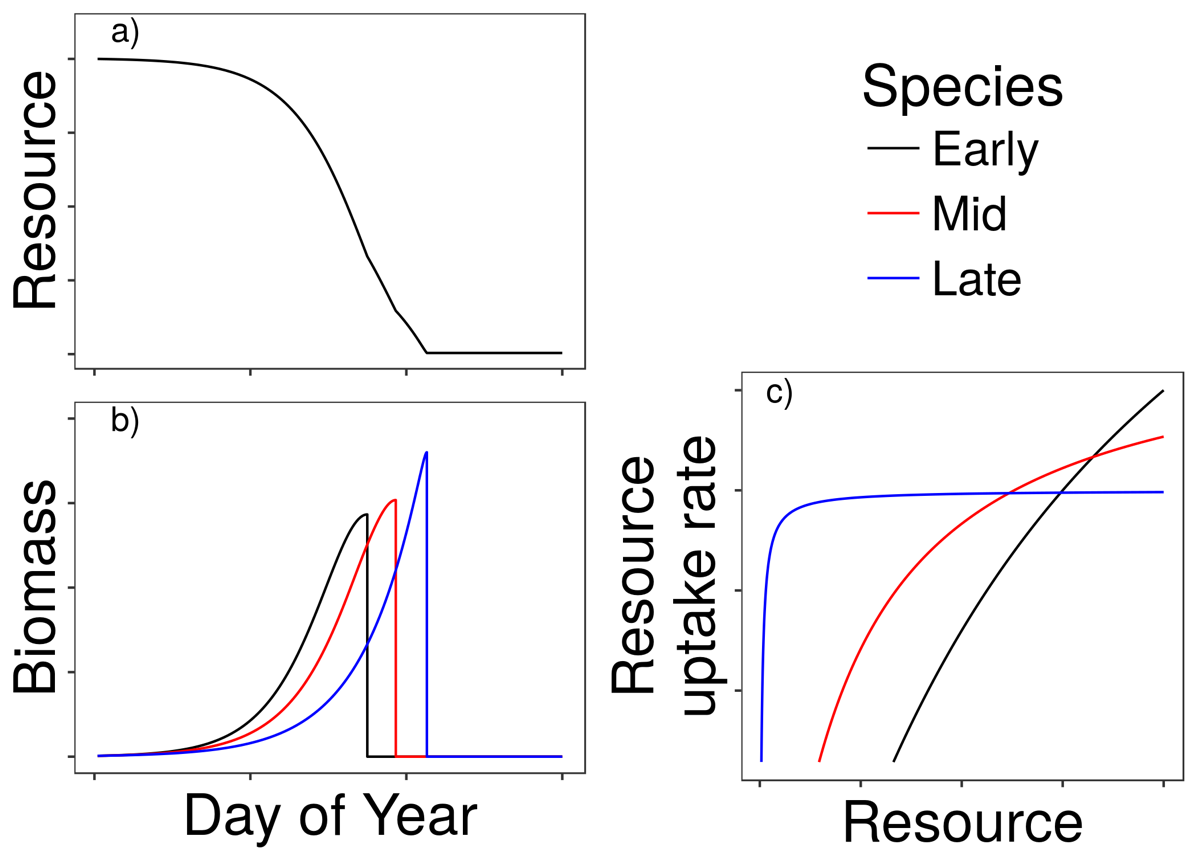


Figure 2. Example time series showing a) the drawdown of the resource during the course of the simulated growing season, b) the growth of each of species shown with colored lines and c) the dependence of resource uptake rates on resource concentration. The early season species grows rapidly when resource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

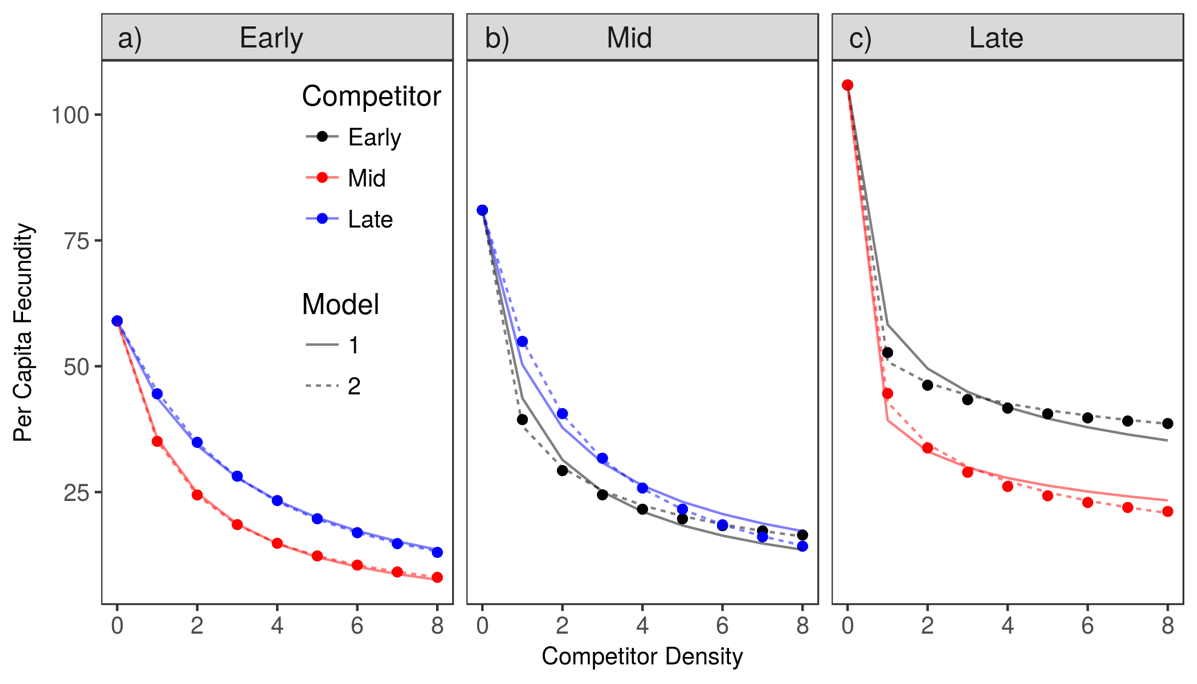


Figure 3. Simulated per capita seed production of the a) early, b) middle and c) late season species in response to increasing inter-specific density on the x-axis. Colors correspond to the identity of the competitor species. The solid line shows best fit line from the standard competition model (eq. 7) and the dashed line shows the best fit line from the model with varying exponents on each competitors effects (eq. 8).

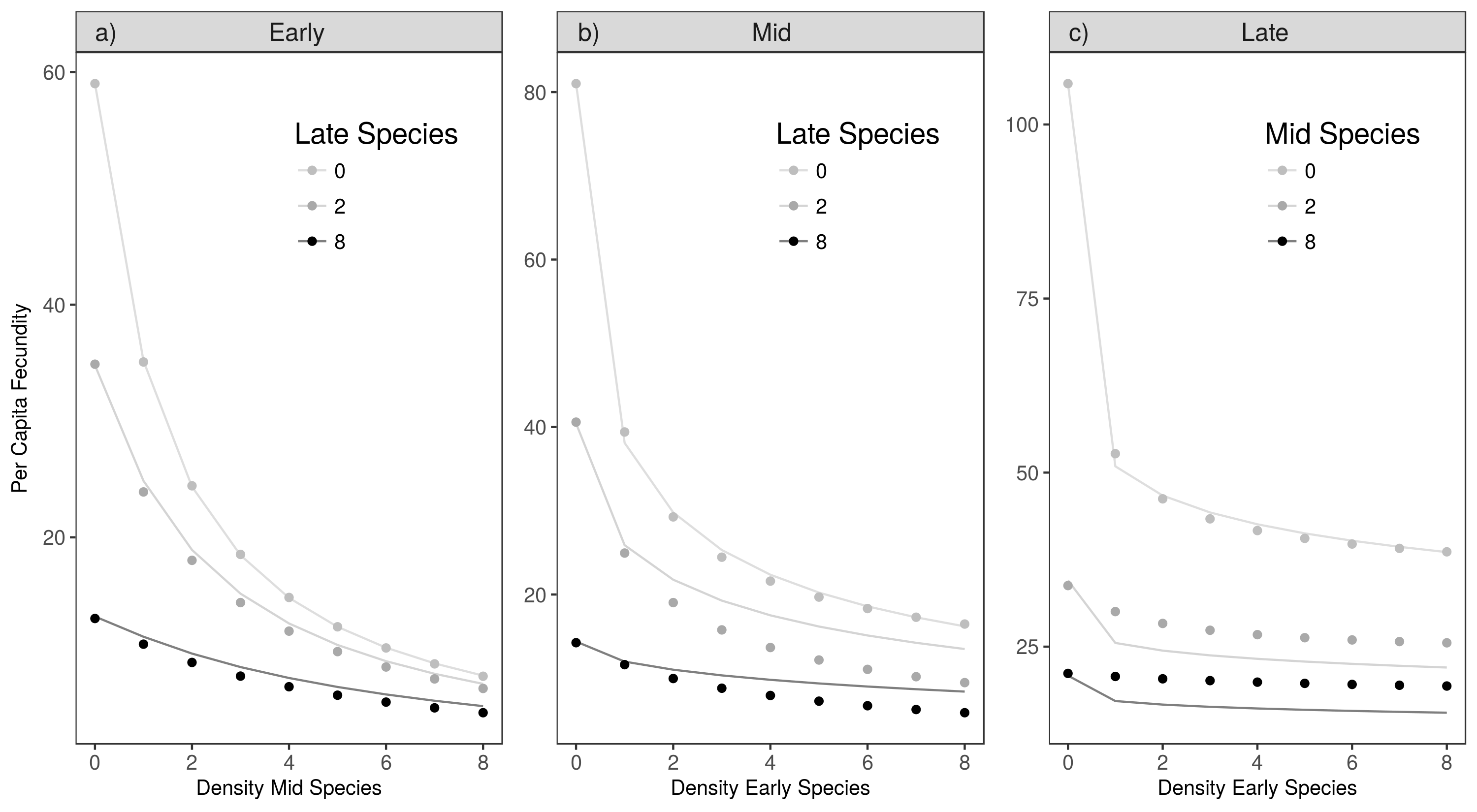


Figure 4. Simulated per capita seed production of the a) early, b) middle and c) late season species in response to increasing competition from two species at once. Increasing densities of one competitor species are shown on the x-axis and three different levels of density from another competitor are shown with the varying shades of gray points. Only the response to interspecific competition is shown. The lines show the predicted per capita fecundity from the competition model with varying exponents (eq. 8). The predictions are generated assuming that single species competitive effects are additive. Deviations between the observed (simulated) fecundity and the predicted fecundity (lines) indicated that competition is non-additive.

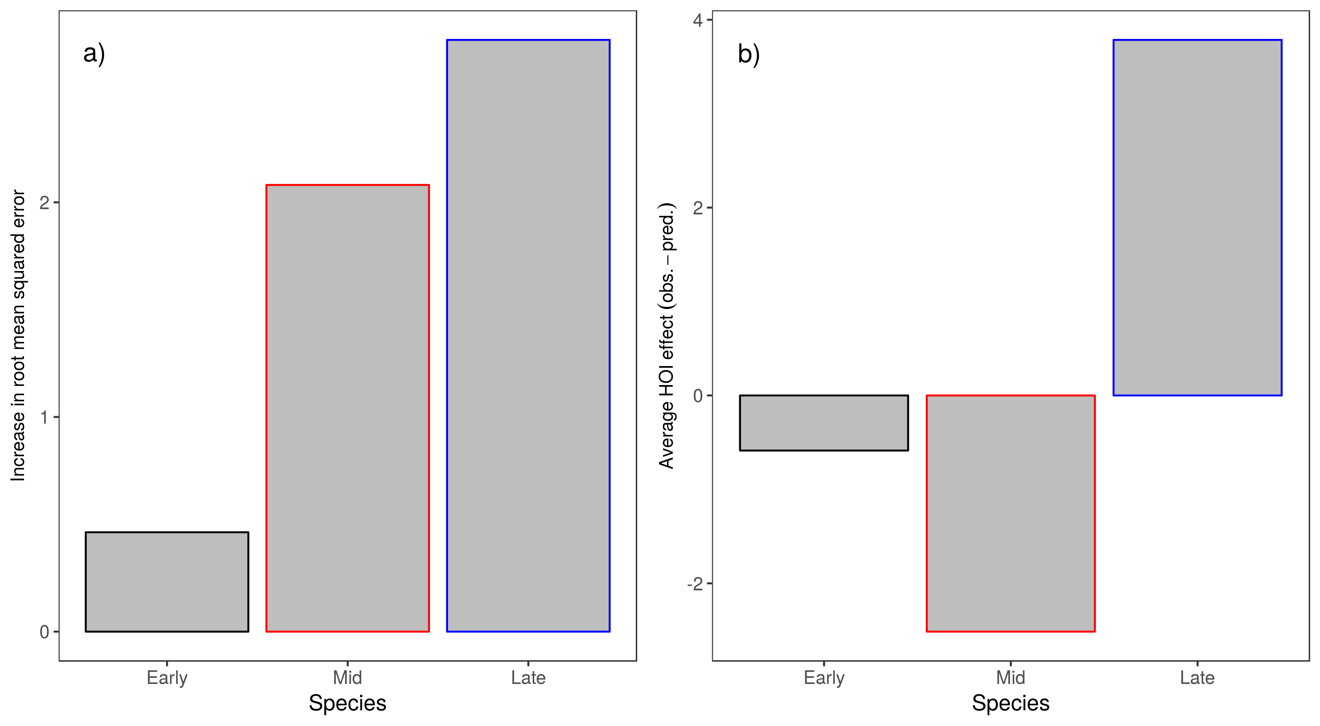


Figure 5. Non-additivity of two-species interspecific competition for each of the focal species. Non-additivity is shown as the differences between the observed effects of two species competition and effects predicted by the second model (eq. 8) assuming the effects of each species are additive. In panel a) this is shown as the increase in root mean squared error over the single species fits, and in b) the average error is shown (observed – predicted). Panel b) shows the direction of the error, positive values show that competition was less than predicted, positive effect of the HOI, negative values show where competition was greater than predicted, negative effect of the HOI.

# Appendix A – Interaction modification leads to non-additive competition:

Assume that competition affecting species one is given by . If we relax the assumption that pairwise competition coefficients are fixed and instead allow for interaction modifications, then competition coefficients may depend on other competitor densities. We can show this by replacing with a linear function of : . Now the competitive effect of on depends on . If we re-write taking into account this interaction modification we arrive at a model that looks equivalent to the one in the main text: .

# Supporting Information – Figures: