**Higher Order Interactions in Simple Competition Models**

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Running Title: Higher Order Interactions

Word Count:

# Abstract

Most communities on earth contain many more than two species, and almost every species interacts with many more than one other competitor. When species interact with two or more competitors at a time, higher order interactions (HOIs) could invalidate the application of classical theories of species competition based on pairwise competition. HOIs occur when competition between two species is not fixed and instead depends on the density of other species in the community. The question of if and how HOIs arise in nature is thus critical to extending ecological theory to multi-species communities. In this paper we use simple competition models to illustrate some possible causes of HOIs and their ecological interpretation. We discuss possible pitfalls in detecting HOIs in empirical data. We conclude that HOIs may be likely to arise when we aggregate competitive effects across periods of time where 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 the stability of multi-species communities.

*Key words: competition, coexistence theory*

# Introduction

Almost every species on earth interacts with a vast number 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. Nonetheless, most classical models in community ecology summarize species interactions with fixed pairwise interaction coefficients. In particular, pairwise competition coefficients have been critical to the development of modern coexistence theory (Chesson 2000). A powerful implication arising from the assumption of fixed pairwise competition coefficients is that the feasibility and stability of multi-species species competition can be predicted by measuring the outcome of competition between all pairs of species in that community (Grilli et al. 2017a). Moreover, this idea is foundational to recent efforts to map pairwise differences in species’ traits to species pairwise competition coefficients (Adler et al. 2013, Kraft et al. 2015).

The possibility of higher order interactions (HOIs) between species challenges the core assumption of many classical models in ecology (Billick and Case 1994, Grilli et al. 2017b). By definition, HOIs mean that pairwise competition coefficients are not fixed but instead change as the densities of other species in the community change (Abrams 1983, Billick and Case 1994). Among other issues that arise in a world with HOIs are classical definitions of coexistence and the niche which rely upon comparing pairwise intraspecific competition coefficients to interspecific competition coefficients (Adler et al. 2007, Grilli et al. 2017b). If HOIs are common, then predicting community assembly in natural multi-species communities might not be achieved by measuring all possible pairwise competitive interactions (Kraft et al. 2015). Moreover, there may be cases where HOIs allow for coexistence in multi-species communities but not in simpler communities of only a few species (Grilli et al. 2017b). Thus, a thorough empirical and theoretical investigation of HOI in natural communities is critical to expanding ecological beyond two species models and increasing its relevance in the natural world.

## Defining higher order interactions

Despite the potential importance of HOIs in a multi-species world, competitive HOIs have received relatively little theoretical or empirical attention. This extends even to the matter of defining what they are. To even begin discussing HOIs, we need to first define competition. We approach the definition from a mechanistic perspective first and then a phenomenological perspective. From a mechanistic perspective, competition occurs when individuals consume the same limiting resources. Increases in consumer densities change the availability of resources which then changes the growth rate of consumers. Thus, resource competition can be thought of as an indirect effect between individuals mediated by resource concentrations. Equivalent models apply to any limiting environmental factors, such as shared mutualists and shared predators and pathogens (Chesson and Kuang 2008).

In contrast, the phenomenological definition of competition dispenses with external environmental factors such as resource concentration and instead focuses on the indirect effects themselves. Phenomenological competition is measured as the reduction in a per-capita population growth rate due to an increase in density of individuals of the same trophic level (Chesson 2000). This perspective on competition is powerful because it includes all shared resources and other environmental feedbacks into one effect that can be measured empirically. A phenomenological definition of competition also encompasses direct interactions between individuals of the same trophic level, such as hemiparisitism, intra-guild predation, interference competition and allelopathy (Amarasekare 2002).

We contrast mechanistic and phenomenological approaches to competition because HOIs are largely a problem for phenomenological models. In a mechanistic model, it is quite hard to define HOIs. If one knows the resource consumption rates of each species, and the value of those resources to each species’ population growth rate, then you can calculate the indirect effects of each species on each other and the stability and trajectory of multi-species communities. HOIs are a non-issue because they are implicit in the model (I think this is true… any reason to qualify this?).

In phenomenological models, by contrast, HOIs have a definition, unfortunately sometimes more than one. Billick and Case (1994) laid out three definitions of HOI used in the literature: 1) interaction modifications, 2) non-additive interactions between species, and 3) statistical HOIs. These three types of HOI are distinct conceptually but could yield similar dynamics for the community. In this paper we take as the primary definition of HOIs non-additive effects of species densities on the per capita growth rate of a focal species. Additive per capita competition can be visualized as the solid arrows pointing between species, and back to themselves, in figure 1. The per capita effect of species two on the population growth rate of species one is given by , and the per capita effect of species three is The converging arrows from two and three to one show a that the effects of species two and three together are non-additive. Such a non-additivity can also be explained as an interaction modification where species two modifies the effect of species three on species one, or vice versa. By our definition HOIs can occur between only two species, when the effect of interspecific and intraspecific competition are non-additive (Billick and Case 1994).

As further illustration of how non-additive HOIs and interaction modification HOIs are similar we start with a general model for species phenomenological competition,

where is the density of species at time , is a function that gives the per capita population growth rate as a function of total competition experienced . Competition between species , and is pairwise and does not involve HOIs if each species contributes additively to competition such that , where is a function of competitor density . In contrast, HOIs occur whenever overall competition cannot be broken down into additive pairwise components.

Consider defining the competition experienced by species 1 as: . 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. Replace with a linear function of , . Now the competitive effect of on depends on . The equation for competition can be re-written as, .

In this example, captures a second order HOI effect of species two and three together. As long as we can no longer isolate the pairwise effect of species two and three on one—i.e. competition is now non-additive. Similarly, the effects of species one on itself and the effects of species two on one could be non-additive, an HOI involving only two species (Billick and Case 1994). In general, more diverse communities allow for HOIs of greater order, with a community of species having HOIs of the order possible. From a statistical perspective, the presence of HOIs means that if we measure the per capita population growth rate of each focal species when it is rare (), and we vary the density of each of the competitors (including itself), this will not be enough to predict the dynamics in a three, or even a two species community.

Now that we have defined HOIs, we explore phenomenological and mechanistic models in order to try to understand when and how HOIs emerge. Finally, we evaluate whether any of the examples are likely to generate HOIs in nature.

# HOIs arising from cycles of pairwise competition

The arguments in Billick and Case (1994) are structured around differential equations where competition operates as a function of continuously changing species densities. However, ecologists have rarely quantified competition using models that are explicitly continuous in time. Empirically, we often measure competition by observing the reduction in species performance with increasing competitor density over some discrete period of time (Kraft et al. 2015). Usually competitor density is measured at the start of the time interval and focal species performance is measured at the end of the time interval. When this is done, intermediate stages of focal species’ density are skipped over and only the final outcome of competition is measured. When measuring competition over discrete intervals of time like this it may lead to HOIs.

In a recent theoretical analysis, Grilli et al. (Grilli et al. 2017b) provided a concise demonstration of this effect. In their model, seedling trees compete to fill a forest gap. If competition for the gap occurs as a sequence of competitive rounds between pairs of individuals then HOIs naturally emerge. This counter intuitive result occurs because the probability that a species wins the gap depends not only on its direct pairwise interactions, but also on the pairwise interactions between its competitors. In effect, which competitor the species interacts with in round two of the tournament depends on those competitor’s interactions in round one. Because there are unobserved states of competitor density within the time interval from seedling to filling the gap, the dynamics can only be summarized with HOI.

In the Grilli model, competition involved a tournament of discrete winner-take-all competitive events. The idea of having plant competition occur one at a time may perhaps seem unrealistic. However, their model captures a general process that could apply to many types of models. As another example we consider an annual plant population that follows a two-stage model. Seeds germinate and survive into adults with probability : , where is adult density at an intermediate time within the growing season, and is the initial seed density at the time . After that, adults produce the next generation of seeds via a fecundity rate : . Because the plants are annuals there is no adult survival.

We can introduce competition by making per capita fecundity of adults of species a function of the sum of adult density of all species in the community: . Seedling germination and survival to the adult stage could also be function of competition, so we could make a function of initial seed density such that .

Now we consider a three species community and calculate the per capita seed production of species one over the time step to ,

In the model above, adult density at time is an intermediate state variable that both determines competition during the second half of the growing season but also is set up by competition during the first part of the growing season. Re-writing to eliminate the intermediate phase,

This equation shows that the effect of the initial densities of any competitor species j on focal species i will no longer be additive. For instance, the net effect of two on one, will depend also on how the survival of two to the adult stage is affected by initial densities of species three. We see this in the equation above within the function : each species initial density is multiplied by the survival function of each of the other species.

One way of interpreting the above model is to consider it a case where there is a distinct survival niche and a distinct fecundity niche. The survival niche is encoded by the set of pairwise interaction functions within the survival function, whereas the fecundity niche is encoded by a set of pairwise interaction functions within the fecundity function. This leads to non-additive, HOI interactions in aggregate. Modeling of many plant populations is improved by introducing some kind of stage structure and it seems likely that competitive effects between individuals probably vary depending on the stage structure (Chu and Adler 2015).

# HOIs in a mechanistic resource competition model

Unlike the phenomenological model above, we can also imagine HOIs emerging from mechanistic models. Because experimental data evaluating HOIs at the demographic level is lacking, we developed a mechanistic simulation of annual plant competition for a single shared resource. We then try and describe competition in the system using a simple phenomenological competition model.

Our mechanistic model is inspired by California annual plant communities growing in a Mediterranean climate. In this environment, rainfall starts in the winter and gradually declines through the spring while temperature and evaporative demand increase. Plants germinate in the winter and 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, perhaps water or mobile inorganic nutrients. The resource supply rate spikes in early spring and then goes to zero as the spring progresses. Thus, the pool of resources is exemplified by non-equilibrium pulse dynamics and never reaches an equilibrium.

In our model, rates of plant growth depend on resource availability. As spring progresses, plants grow larger but resource supply diminishes. Eventually plants reach a point where their resource uptake rates cannot keep up with respiration and maintenance costs. At this point, we assume that plants stop producing vegetative biomass and start producing seeds. We simplify this by assuming that all biomass is converted to seed biomass at a fixed rate instantaneously. At this point the adult plants die and stop taking up resources.

The model is expressed as a set of differential equations,

where gives the resource availability at time , and gives the resource supply rate at time . The final term expresses the loss of resources due to uptake by plants. We sum over each of the species in the community to get total uptake. Annual plant biomass of species at time is given by and the uptake rate is a function of total resource availability. We simulate a Mediterranean climate by setting initial resource availability high, , and setting the resource supply rate to zero.

Growth of each species depends on resource availability,

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.

In this model, the growth of each species stops when meaning that biomass gained is equal to biomass lost to respiration and maintenance. Because the summer drought will only further reduce resource concentrations, the optimal behavior of the plant at this point is to stop growing and convert stored resources to seed mass. We impose this behavior on the model by setting biomass at time to zero when matches resource uptake and conversion: .

Different species are likely to have different rates of resource uptake, respiration and tissue loss rates. In our simulations we assume a trade-off between rates of resource uptake at high resource availability and rates of resource uptake at low resource availability. This means that species which dominate early in the season when resource availability is high will stop growing earlier in the season as resource availability declines. In contrast, species that grow slower early in the growing season are able to persist later into the season when resource availability is low (Godoy and Levine 2013).

We enforce this trade-off between species by giving each species a unique resource uptake function (following, Miller and Klausmeier 2017),

where, is the maximum rate of resource capture and is the half-saturation constant of resource capture. Example resource uptake curves for a fast-growing early season species, a mid-season species, and a slower growing late season species are shown in figure 2. The unique resource uptake curves result in unique growth and phenology for species one, two and three. Species one grows fastest early in the season but flowers and senesces earlier, species two flowers a little later, and species three flowers last (Figure 3).

So far, we have described a model run in continuous time within a single generation. For this model we denote rates of change of biomass and resources within the season in terms of very small time intervals . By contrast, we keep track of total population size of each generation at a discrete annual time scale . To calculate the total population size of each species at time step we take each species’ maximum vegetative biomass during the growing season, multiply that by a conversion factor to get a seed mass, and then multiply that by a constant seed per gram ratio, . Thus,

where is the number of seeds produced at the end of the growing season. To simplify the interpretation of the model, 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.

## Response surface experiment

Using the model described above we simulated a response surface experiment where individuals of each of the three species are grown against increasing densities of inter- or intraspecific competitors. We then calculate the per capita reproductive output of the focal species and fit phenomenological competition models to our simulated data. We only include simulations in which the focal species faces fewer than three competitor species at once.

## 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 use a standard functional form for phenomenological competition that has been used a number empirical studies of annual plant competition (Kraft et al. 2015),

where and denotes maximum per capita reproductive output, is the per capita competitive effect of species on and and is a species-specific parameter controlling how steep fecundity declines with competition in general. We refer to this functional form as the basic model.

In order to assess the importance of HOIs, we can include various higher order terms in the basic functional form. In the case of three species, this includes three pairwise effects, three quadratic effects and three second order HOI terms,

where is coefficient for the quadratic effects of species , and is the HOI effect of species and acting together on species . We refer to this competition model as the HOI model. We fit separate competition models for each of three species using the nls package in R. We calculate 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.

## Model fits

The basic Beverton-Holt functional form is a good fit for the effects of both inter and intraspecific competition on species one and adding HOI terms does not qualitatively improve model fit (Figure 4). For species two we see more of a discrepancy between the basic and HOI model fits (Figure 5). This is especially apparent in the third panel of the figure which shows the interaction between the densities of species one and species three. The basic model tends to under predict the impact of species one and two together on species two. Finally, for species three, we see an even greater discrepancy between the basic and HOI model fits (Figure 6). The HOI fit appears to be quite good in the first two panels but is not very accurate at high densities of species one and low densities of species two (rightmost panel, Figure 6).

For each of the three species, including HOI and quadratic terms improves model fit in terms of residual squared error (Table 1). For species one, the quadratic and HOI terms are small relative to the pairwise effects. For species two and three, the HOI terms are of similar magnitude to the pairwise effects, in some cases stronger.

It is clear from the above example that a relatively simple resource consumption model may require HOI terms in order to be fit by a phenomenological model. The obvious question is how to interpret the additional quadratic and second order HOI terms. On the one hand it should not be surprising that adding additional terms improves model fit. Many functions can be approximated to an arbitrary level of precision by a power series. We essentially are approximating a power series by summing over polynomial terms of ever increasing order.

However, in this case we believe the HOI effects play a more meaningful role than simply helping us approximate a completely unknown function. In support of this argument, we note that the basic Beverton-Holt model does an adequate job fitting the response of species one to the competitive effects of one and two. It is only for species two and three that we begin see evidence of important HOI effects.

We believe this has to do with the temporal nature of competition in this system. While species one is active, species two and three are also always active. Thus, the effects of initial competitor density on species one is relatively simple. Increasing densities of competitors will suppress the resource capture by species one and thus change its overall performance in a constant manner regardless of the mix of species.

However, for species two and three the competitive environment is more complex. For example, take species two competing only against species one. The growing season can be split up into two phases: the first part of the growing season over which species two interacts with species one and itself; and the second part of the growing season where species two only interacts with itself. Working backwards from the time when species two flowers, we might be able to predict its ultimate size and fecundity from its biomass at the time that species one stops growing. That part of the growing season only involves intraspecific competition so it should be relatively simple. But the intraspecific competition experienced by species two over this second part of the growing season depends on how large it is at the start of this second phase of growth. So we have to predict its size at the start of phase two. This in turn, depends on the inter- and intraspecific competition experienced over the first phase of the growing season.

Keeping this in mind we can rationalize the HOI terms for species two as describing the inter- and intraspecific effects of competitor density on species two during the first phase of the growing season, multiplied by only the intraspecific over the second phase of the growing season. For species two this leads to a strong effect of intraspecific densities squared, and an effect of interspecific density multiplied by intraspecific density (table above). Noticeably absent is a quadratic effect on the density of species one, which makes sense given this interpretation (table).

Likewise, there is an HOI term for the effects of species one and three acting together on species two. Once again, we need to consider the two phases of competition experienced by species two. First the density of species one and three will determine the biomass of species three when species one flowers. This will then determine the interspecific effects of species three on two during the second phase of the growing season for species two. Thus, we see a strong effect of species three’s density squared and a strong HOI between the initial density of species three and species one.

The competitive dynamics for species three are even more complex. This late season species goes through three distinct phases of competition, first competing with all three species, then only with two and then finally with only itself. Working backwards from its final biomass and reproductive output, species three’s performance will depend on its size when species two flowers, which will depend on the size of two and three when species one flowers, which will depend on the initial densities of all three species. Because there are effectively three cycles of competitor density and response to consider for species three it is reasonable to expect that third order HOI terms resolve some of the lack of fit observed for this species (Figure 6).

This system is characterized by a seasonal pulse of resource availability and the lack of an equilibrium between species biomass and resource concentrations in the environment. In contrast, if resources were supplied continually, at some level , then eventually species biomass would increase until resource uptake matched this level of resource supply. This is a classic result from mechanistic resource modeling (Tilman 1977). At this equilibrium, the sensitivity of each species to the densities of each other species can be approximated with a linear phenomenological model (Chesson 2000, Meszéna et al. 2006, Kleinhesselink and Adler 2015). This focus on the equilibrium dynamics, and an avoidance of the messiness inherent in periodically forced non-equilibrium systems may be one reason HOI’s have received little attention among competing species.

# Discussion

# Conclusions/Summary (?? )

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 two hypothetical models of species competition. In the first model, simple pairwise interactions iterated over multiple life stages could lead to HOI’s. In the second, we show that a community characterized by pulses of resource supply and sequential cycles of species competition and senescence could also lead to HOI’s. A general theme in both models is that HOI’s arise when the competitive environment and species abundances change at a time step shorter than the interval over which the effects of competition are observed.

# Acknowledgments

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# Figures

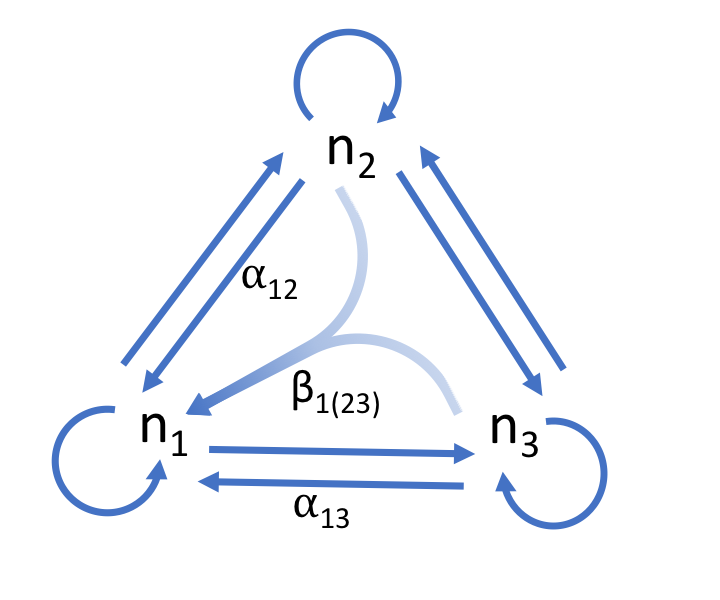


Figure 1. Three species competitive network. Inter- and intraspecific competition between species is depicted with the blue arrows. The effect of species two on one can be described by the per capita effect α12. An HOI, β1(23), is depicted as converging arrows showing that the effects of two and three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

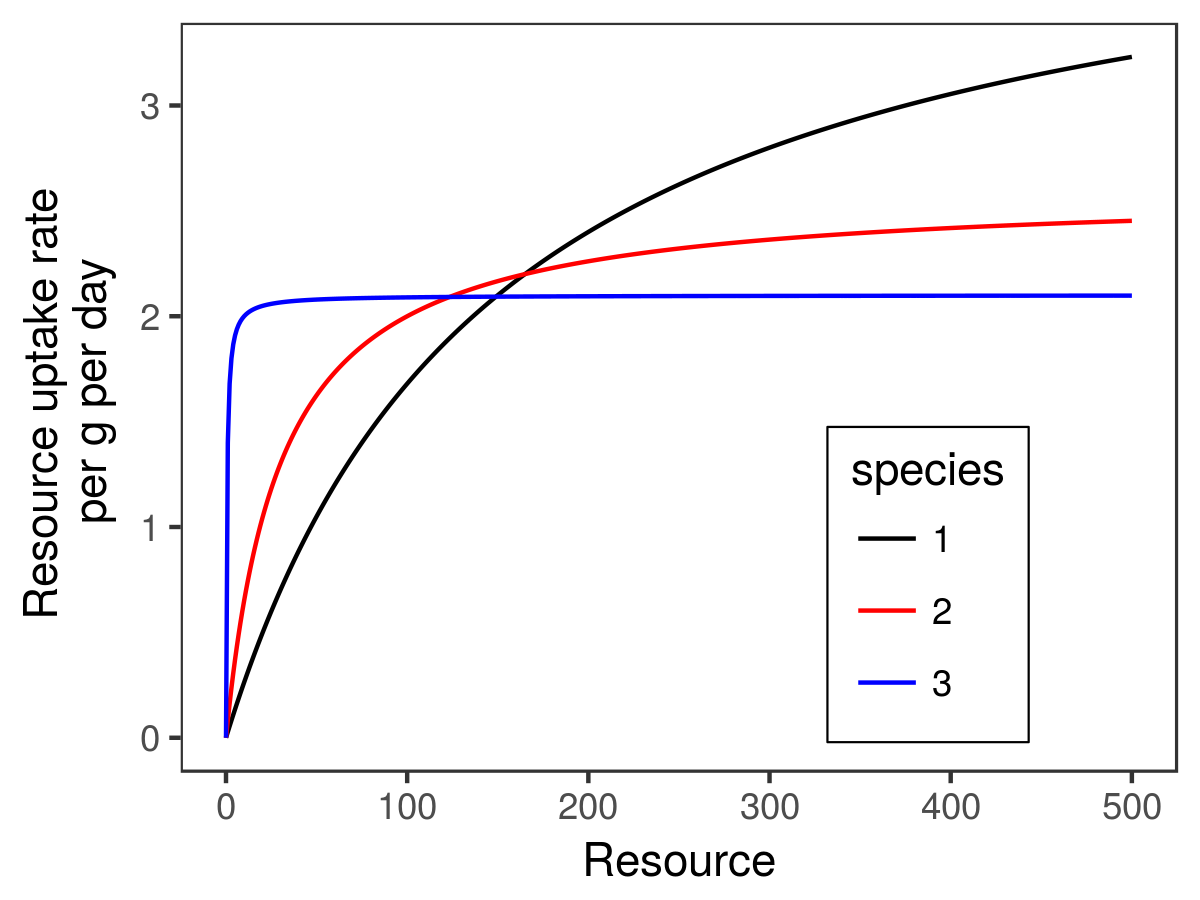


Figure 2. Resource curves for three simulated species. Species one has a resource uptake advantage when resource availability is high whereas species three has a resource uptake advantage when resource availability is low.

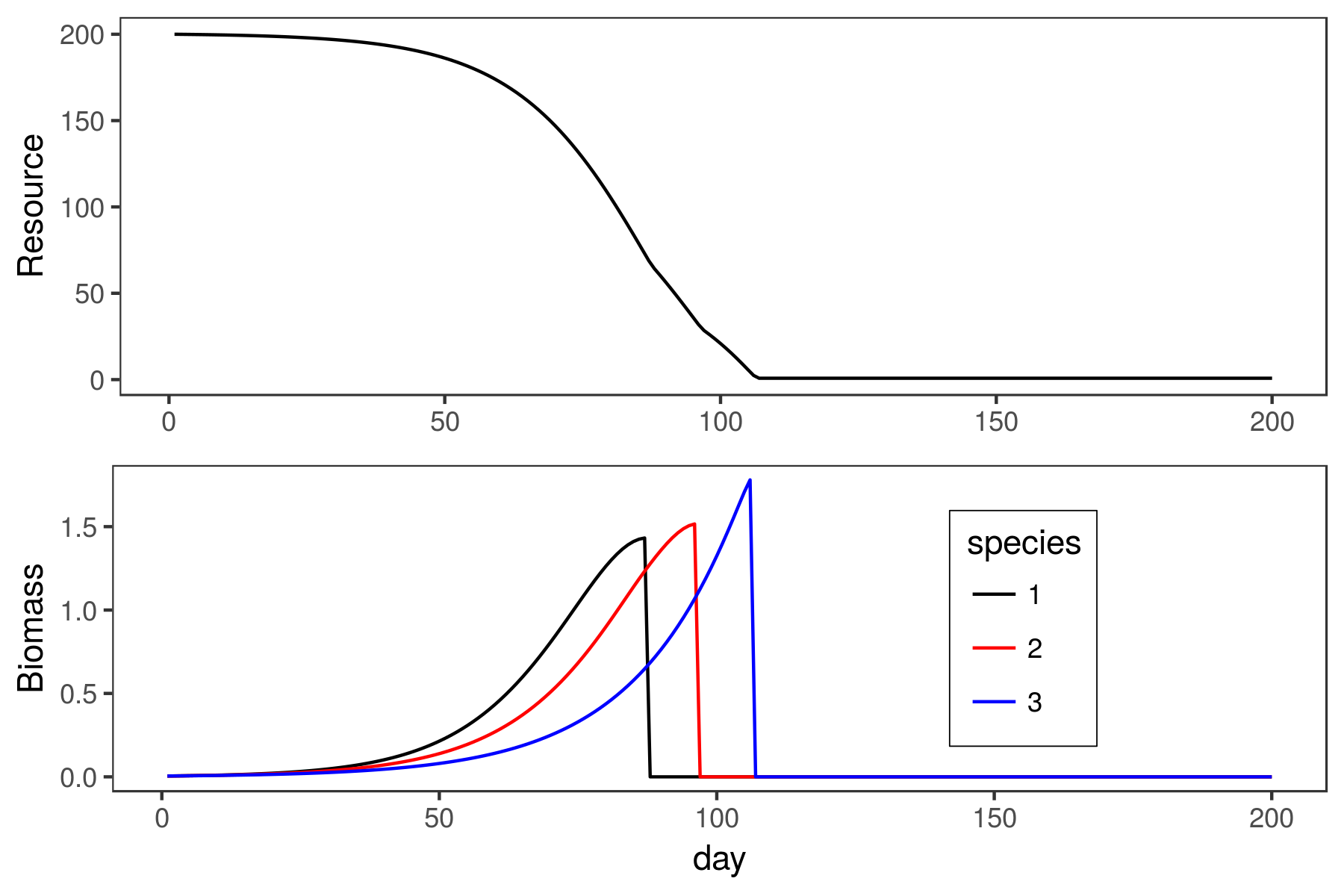


Figure 3. Example time series showing draw down of the resource during the course of the simulation, upper panel, and growth of each of the species, lower panel. Species one grows rapidly early in the season but senesces early as well. Species three grows slowly early in the season but grows for a longer period of time. Species is somewhere between these extremes. Each species reaches its peak biomass at a different time, at which point we assume all vegetative biomass is converted to seed mass, and resource uptake by that species stops.

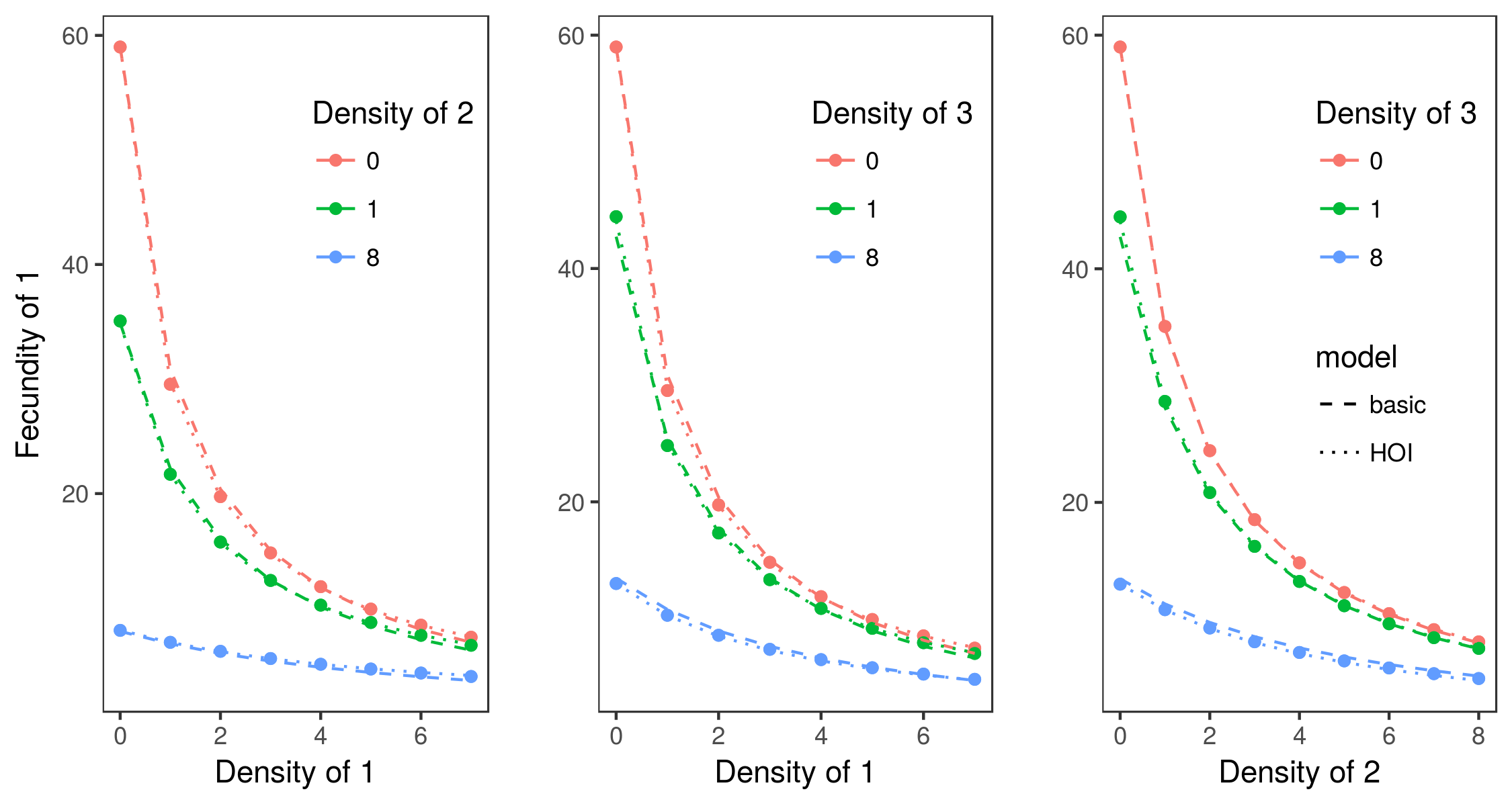


Figure 4. Simulated per capita seed production of species one in response to increasing competitor density on the x-axis. Colored lines show three different levels of density of a second competitor. The dashed line shows the best fit line from the basic model and the dotted line shows the best fit from the HOI model

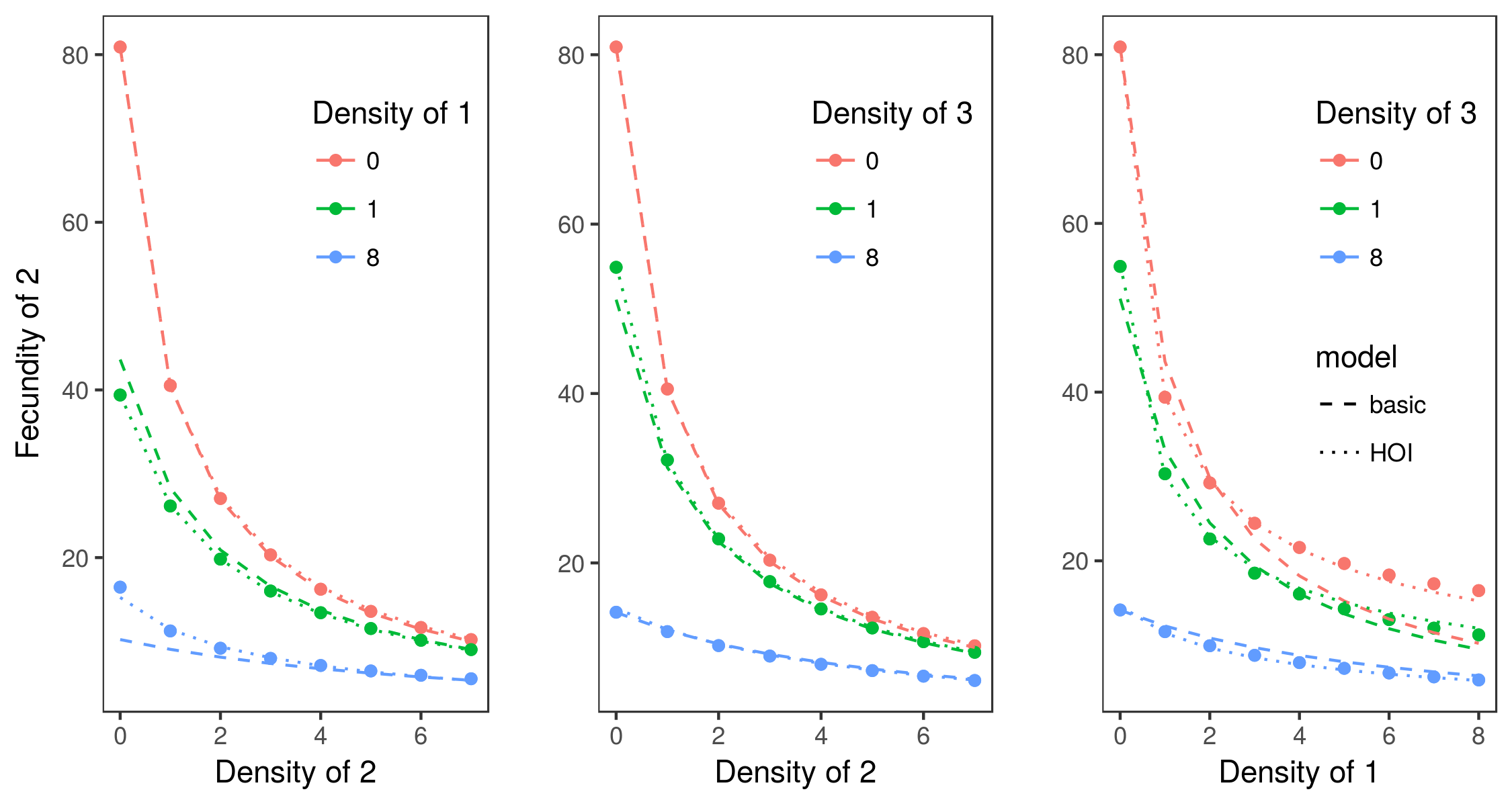


Figure 5. Simulated per capita seed production of species two in response to increasing competitor density on the x-axis. Colored lines show three different levels of density of a second competitor. The dashed line shows the best fit line from the basic model and the dotted line shows the best fit from the HOI model

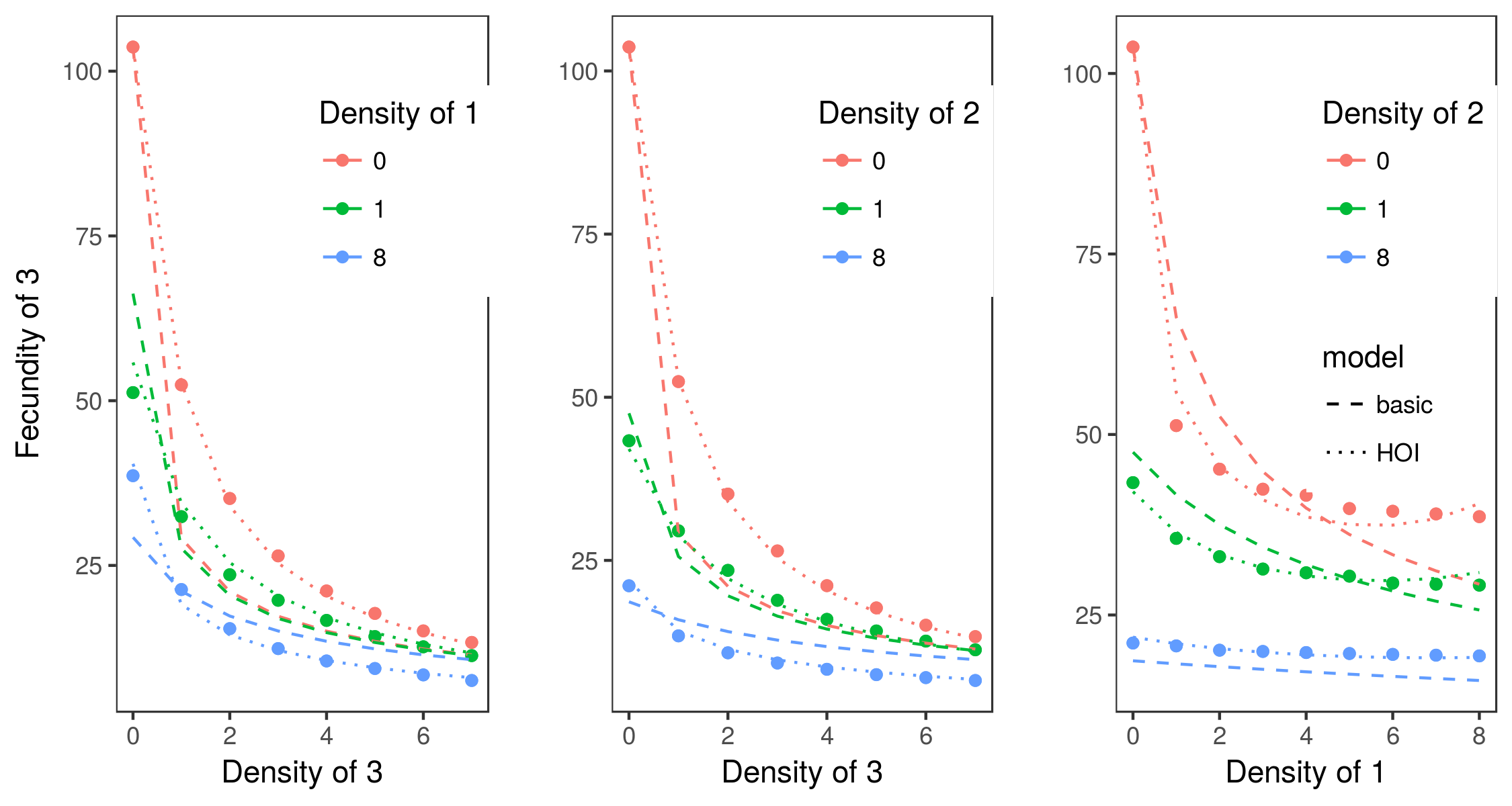


Figure 6. Simulated per capita seed production of species three in response to increasing competitor density on the x-axis. Colored lines show three different levels of density of a second competitor. The dashed line shows the best fit line from the basic model and the dotted line shows the best fit from the HOI model

**Table 1. Fitted HOI parameters and residiual squared error for the basic model and the model containing higher order interaction terms**

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| species | model |  |  |  |  |  |  |  |  |  | error |
| 1 | basic | 0.74 | 0.57 | 0.32 | - | - | - | - | - | - | 0.33 |
| 1 | HOI | 0.83 | 0.58 | 0.28 | -0.02 | 0.00 | 0.01 | -0.01 | 0.00 | 0.01 | 0.08 |
| 2 | basic | 0.84 | 0.98 | 0.58 | - | - | - | - | - | - | 1.19 |
| 2 | HOI | 2.97 | 2.03 | 0.78 | 0.00 | 0.74 | 0.30 | 1.91 | 1.64 | 1.09 | 0.28 |
| 3 | basic | 1.46 | 3.78 | 11.78 | - | - | - | - | - | - | 3.41 |
| 3 | HOI | 3.69 | 7.89 | 1.43 | -0.33 | -0.38 | 2.57 | 0.11 | 5.33 | 8.60 | 0.76 |