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

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Running Head: *Higher Order Interactions*

Key words: *resource competition, interaction modification, phenology, annual plants*

Submission Type: Article

Main Text Word Count: 6128 (including abstract)

Total Word Count: 8359 (including appendix and literature cited)

Total Pages: 44 (including appendix)

Parts: Main text, Supporting Information Figures and Tables, Appendix A, Computer Code (zip file)

1 **Abstract**

2   When species simultaneously compete with two or more species of competitor,

3 higher order interactions (HOIs) can lead to emergent properties not present when species

4 interact in isolated pairs. In order to extend ecological theory to multi-competitor

5 communities, ecologists must develop a practical and general definition for HOIs that can

6 be applied to a wide range of competition models. In this paper we propose a definition

7 for HOIs and outline a set of criteria for testing whether a model has or does not have

8 HOIs. These criteria are valuable for empirical ecologists in need of clarity when

9 discussing HOIs in empirical data. We also provide thorough discussion of how our

10 definition compares with previous definitions of HOIs and interaction modification in the

11 literature. In the second part of the paper we demonstrate the steps required for a rigorous

12 test of HOIs in empirical data. To do this we simulate resource competition between three

13 annual plant species which differ in phenology. We then fit phenomenological

14 competition models to the outcome of simulated competition and use these to test for the

15 presence of HOIs. In our simulations, we find the strength of HOIs varies with

16 phenology: species that grow later experience stronger HOIs than earlier growing species.

17 Our simulation shows how HOIs could emerge in ecosystems where resource availability

18 and individual size change rapidly throughout the course of the growing season and

19 where there are differences in the timing of resource acquisition between competitors.

20

21 **Introduction**

22   Almost all species interact with a diversity of predators, pathogens and

23   competitors. Despite this, most classical models in community ecology assume that the

24   per capita effects of each species on each other do not dependent on the densities of any

25   other species in the community. This simplifying assumption means that we can predict

26   the dynamics of multispecies communities from a model that only includes the

27   interaction between each pairs of species (Chesson 2000, Levine et al. 2017).

28   Higher order interactions (HOIs) between species invalidate the core assumption

29   of independent per capita interactions and thus HOIs could have profound consequences

30   for modeling community dynamics and species coexistence (Neill 1974, Mayfield and

31   Stouffer 2017, Levine et al. 2017, Grilli et al. 2017). If HOIs are strong, even a perfect

32   understanding of the interaction between each and every pair of species in isolation

33   would not be sufficient to describe what happens when all the species are simultaneously

34   interacting (Neill 1974, Billick and Case 1994, Levine et al. 2017). A specific example of

35   the potential for HOIs to impact our understanding of community dynamics is in the

36   application of the mutual invasibility criterion for determining the stability of coexistence

37   (Levine et al. 2017). In theory, HOIs can allow three competitor species to coexist even

38   where some pairs of competitors cannot coexist (Grilli et al. 2017).

39   Despite the theoretical importance of HOIs, measuring HOIs in nature has been

40   impeded by shifting definitions of what does and does not count as an HOIs (Pomerantz

41   1981, Adler and Morris 1994, Billick and Case 1994, Letten and Stouffer 2019).

42   Moreover, previous definitions of HOIs were developed with a small range of classical

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43   competition models in mind. Since that time, new statistical modeling software now

44   allows ecologists to fit a much wider range of interaction models (Mayfield and Stouffer

45   2017). This increase in model flexibility requires deriving a more general definition for

46   HOIs that can be applied to any density dependent model of population dynamics.

47   In addition, to the basic issue of producing a shared definition for HOIs,

48   ecologists lack a mechanistic understanding of how HOIs could emerge in nature (Levine

49   et al. 2017, Letten and Stouffer 2019). Such an understanding is necessary for predicting

50   the sets of competitors and ecosystems where strong HOIs are likely. One promising way

51   to address these outstanding issues is to simulate virtual competition experiments based

52   on mechanistic models in which the processes that cause competition are fully known,

53   and then evaluate for which species, and under which conditions HOIs emerge (Letten

54   and Stouffer 2018).

55   We provide a general definition for HOIs based on interaction modification that

56   distinguishes HOIs from related phenomena such as non-linear density dependence and

57   indirect effects. In the second part of the paper, we use a simulation experiment to

58   illustrate how our definition can be applied to properly identify interaction modification

59   even against a backdrop of nonlinear density dependence. We then use the results of the

60   simulation to shed light on possible mechanisms that could generate HOIs in nature.

61   *Higher order interactions result from interaction modification*

62   For the purpose of defining HOIs we focus on modeling a focal species'

63   performance (usually per capita population growth rate) as a function of the population

64   density of multiple species of competitor. This can be expressed generally as,

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$$\frac{1}{n_i}\frac{dn_i}{dt} = F_i(n_1, \dots n_m), \tag{1}$$

65 where F_i gives the per capita population growth rate of the focal species i, and n_j are the

66 population densities of competitor species one through m in the community, including the

67 population density of the focal species, n_i. An analogous equation holds for population

68 growth rate over discrete time intervals: $\frac{n_i(t+1)}{n_i(t)} = F_i(n_1, \dots n_m)$. In most widely used

69 models of species interactions, each competitor has one effect on itself and one effect on

70 each of the other species in the community. The simplest example of such a pairwise

71 competition model is the Lotka-Volterra (LV) model,

$$\frac{1}{n_i}\frac{dn_i}{dt} = r_i\left(1 - \sum_{j=1}^{m}\alpha_{ij}n_j\right), \tag{2}$$

72 where, r_i is the intrinsic rate of growth of the focal species i and α_{ij} is the per capita

73 effect of competitor j on the growth rate of the focal species. This model is pairwise

74 because each interaction is specified by the pair of species involved, the focal species i

75 and the competitor j. The defining property of any pairwise model, such as the LV model,

76 is that the per capita effect of each species of competitor is independent of the densities of

77 any *other* species of competitor (Figure 1A).

78   By contrast, interaction modification disrupts pairwise competition and leads to

79 HOIs. Interaction modification occurs when the effect of one competitor species is

80 modified by the density of another competitor species (Adler and Morris 1994). We can

81 introduce an interaction modification into the LV model by replacing any of the constant

82 terms α_{ij} with a function of the density of another competitor (Billick and Case 1994).

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83   For instance, in the following LV model, the focal species performance is dependent on

84   two competitor species,

$$\frac{1}{n_i}\frac{dn_i}{dt} = F_i(n_1, n_2) = r_i(1 - \alpha_{i1}n_1 - \alpha_{i2}n_2). \tag{3}$$

85   Replacing the term α_{i1} with the expression $\alpha_{i1} + \beta_{i(12)}n_2$, makes the per capita effect of

86   species one dependent on the density of another competitor, n_2. More specifically the

87   parameter $\beta_{i(12)}$ measures the strength of this interaction modification (Figure 1B).

88   Substituting this function into the model introduces the product of competitors one and

89   two as a new term,

$$\frac{1}{n_i}\frac{dn_i}{dt} = F_i^{HOI}(n_1, n_2) = r_i(1 - \alpha_{i1}n_1 - \alpha_{i2}n_2 - \beta_{i(12)}n_1 n_2). \tag{4}$$

90   Interaction modifications such as these imply that competition is functionally different

91   when more than one competitor species is present and that there are emergent properties

92   in the community that cannot be predicted by single species effects. These may suggest

93   specific biological hypotheses: something about the behavior or traits of the competitors

94   are functionally disctinct when they are together as compared to when they are separate.

95   Importantly, an interaction modification cannot be attributed to any one competitor—

96   rather it is an emergent property of the multi-species system, what we call an HOI (Figure

97   1B).

98   *An improved general definition of HOIs*

99   While the section above captures the essential connection between interaction

100   modifications and HOIs, ecologists do not have a shared definition for HOIs that captures

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101   this idea and which can be applied to any density dependent model of competition

102   (Hairston et al. 1968, Pomerantz 1981, Billick and Case 1994, Grilli et al. 2017, Letten

103   and Stouffer 2019). Here we provide a formal mathematical definition for HOIs rooted in

104   their important implications for ecological theory and which can be applied to any

105   interaction model of any functional form. We first present this more formal definition but

106   follow up with a simple empirical heuristic which can be used to evaluate a model for

107   HOIs.

108   Let $F_i(n_1, \dots n_m)$ be a generic model describing the density dependent effects of

109   m competitor species on the per capita growth of species i, where $m > 1$. Let Θ be the set

110   of all parameters in the model, $\Theta = \{\theta \mid F_i(n_1 \dots n_m | \theta)\}$. Here, the term parameter refers

111   to constants in a model that are not themselves dependent variables (Bard 1974). Let

112    $f_{ij}(n_j)$ be a model describing the response of the focal species to competition from a

113   single competitor species, j, where j is one of the competitor species included in

114    $F_i(n_1, \dots n_m)$. For any model F_i, we find $f_{ij}(n_j)$ by setting the densities of all

115   competitors except j to zero and simplifying the model. Next, let Ψ_j be the set of

116   parameters in $f_{ij}(n_j)$, $\Psi_j = \{\psi \mid f_{ij}(n_j | \psi)\}$. For most realistic competition models the

117   parameters in Ψ_j will be a subset of those in Θ, i.e. $\Psi_j \subseteq \Theta$. Next, let Φ be the set of all

118   parameters found across all m sets Ψ_j: $\Phi = \Psi_1 \cup \Psi_2 \cup \dots \Psi_m = \bigcup_{j=1}^{m} \Psi_j$. A model is

119   pairwise if all parameters in Θ are found in the set Φ, i.e. $\Theta = \Phi$. **Models with HOIs are**

120   **defined by having parameters in F_i that are not found in the m single-competitor**

121   **functions, or more precisely, when Θ is a proper superset of Φ, $\Theta \supset \Phi$.** Finally, let B

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122 be the set of parameters in Θ but not in Φ, $B = \Theta - \Phi$. The parameters in B are those that

123 define the HOI in the model.

124   As a concrete illustration of our definition, consider the two competitor LV model

125 defined in equation (3): for the full model $\Theta = \{\alpha_{i1}, \alpha_{i2}, r_i\}$ and $\Phi = \bigcup_{j=1}^{2} \Psi_j =$

126 $\{\alpha_{i1}, \alpha_{i2}, r_i\}$, thus $\Theta = \Phi$ and the model is pairwise. By contrast, for the HOI model F_i^{HOI}

127 defined in equation (4), $\Theta = \{\alpha_{i1}, \alpha_{i2}, \beta_{i(12)}, r_i\}$ and $\Phi = \bigcup_{j=1}^{2} \Psi_j = \{\alpha_{i1}, \alpha_{i2}, r_i\}$, thus

128 $\Theta \supset \Phi$ and the model contains HOIs. Moreover, $B = \Theta - \Phi = \{\beta_{i(12)}\}$, thus the

129 parameter $\beta_{i(12)}$ is specifically the one that captures the HOI.

130   This abstract representation belies a simple empirical heuristic for determining

131 whether a model has HOIs: in order to parameterize a model with HOIs, the response of

132 the focal species must be measured against density gradients of each competitor

133 separately, as well as against varying combinations of competitors grown together

134 (Figure 2). This is a natural consequence of the above definition. *In essence, a model with*

135 *HOIs includes additional parameters that an empiricist cannot measure when the*

136 *response of a focal individual is measured against a single competitor species*

137 *(Pomerantz 1981).* Note, however, there is no way to determine whether there are HOIs

138 among *m* competitors by examining all *m* pairwise models f_{ij}, rather the form for the

139 multi-competitor model F_i must be chosen first in order to apply any HOI definition

140 (Adler and Morris 1994).

141   We refer to the type of HOIs captured by our definition above as *hard HOIs* and

142 contrast them with the wider phenomenon of non-linear density dependence which

143 produces what we term *soft HOIs*. A general test for soft HOIs is to take the partial

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144 derivative of the competition function, F_i in equation (1), with respect to the density of a

145 single competitor species, $\frac{\partial F_i}{\partial n_j}$. This partial derivative defines the focal species' sensitivity

146 to a single competitor. If this partial derivative is a function of more than one

147 competitors' density, then there are soft HOIs. In general, all models with hard HOIs will

148 be non-linear and have soft HOIs, but not all non-linear models will have hard HOIs.

149 This is similar to definitions used in earlier discussions of HOIs based on LV forms of

150 competition (Case and Bender 1981), and closely follows the verbal argument that HOIs

151 emerge when the effect of one competitor on another depends on any other competitors.

152 The problem is that **any model in which growth is a nonlinear function of**

153 **interspecific density will involve soft HOIs**, and thus this definition does not distinguish

154 interaction modification or HOIs from non-linear density dependence (Pomerantz 1981,

155 Adler and Morris 1994). As an example consider the multi-competitor Hassel model

156 (Hassell and Comins 1976),

$$\frac{n_i(t+1)}{n_i(t)} = F(n_1, \dots n_m) = \lambda_i \left(1 + \sum_i \alpha_{ij} n_j \right)^{-\tau_i}, \qquad (5)$$

157 where $\lambda_i, > 0$ is the maximum per capita seed production, α_{ij} is the per capita effect of

158 species j on species i and $\tau_i > 0$ allows each focal species to respond differently to the

159 sum of competitor effects. This function has the partial derivative $\frac{\partial F_i}{\partial n_j} = -\alpha_{ij} \lambda_i \big(1 +$

160 $\sum_i \alpha_{ij} n_j \big)^{-\tau_i - 1}$. Thus, the effect of competitor j on the focal species i is a function of the

161 density of all other competitor species. However, as in the LV model, there are no hard

162 HOIs in this model by our definition because all of the parameters in the multi-competitor

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163 model are also found in the *m* separate single competitor functions, i.e. $\Theta = \Phi =$

164 $\{\alpha_{i1}, \dots \alpha_{im}, \lambda_i, \tau_i\}$.

165 *Why distinguish hard HOIs and non-linear density dependence (soft HOIs)?*

166 Hard HOIs and soft HOIs have different interpretations and these differences are

167 important to recognize if we are to advance our understanding of competition in

168 multispecies communities. The question of whether population growth rate declines with

169 competitor density, and whether this decline is linear or non-linear is a longstanding issue

170 in ecology (Hassell and Comins 1976). It would be confusing at best to define HOIs as

171 any non-linear decrease in performance with density—essentially renaming the issue of

172 non-linear density dependence.

173 More importantly, hard HOIs and non-linear density dependence are ecologically

174 distinct as well. Hard HOIs indicate a qualitative change in the way competitors affect a

175 focal species when other competitor species are present. Non-linear density dependence,

176 soft HOIs, does not have the same interpretation. For instance, the net outcome of

177 competition over discrete time intervals may be non-linear when the interaction between

178 competitors is linear in continuous time—the discrete time Hassel model, which is non-

179 linear, is derived from a LV competition model, which is linear in continuous time

180 (Hassell and Comins 1976, O'Dwyer 2018). In the case of the discrete time model, the

181 lifetime competitive effect of each individual declines with competitor density because

182 each individual competitor is smaller and thus has less of an effect on the focal species.

183 Thus, the non-linearity in the model arguably reflects a quantitative not a qualitative

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184   change in the nature of competition when more than one species is present. In models

185   with hard HOIs, the qualitative, or functional change in the nature of competition is

186   defined mathematically by the introduction of additional parameters in Θ that are not

187   present in Φ as defined above.

188   Adler and Morris (1994) provide another specific example where it is ecologically

189   meaningful to differentiate between HOIs and non-linear density dependence. They

190   describe a hypothetical scenario in which different species of plants compete for light and

191   each species simply blocks a proportion of the light that passes through its canopy—thus

192   taller species reduce the amount of light received by shorter species. In this way, the

193   *qualitative* nature of the interaction between a tall species and a shorter one is

194   independent of all other species. Nevertheless, this mechanism of interaction means that

195   the effect of a taller species on a shorter species below it depends non-additively on the

196   density of other competitors with a canopy between the two. Per capita competition is

197   non-additive, but arguably there is no ecologically distinct interaction modification

198   between the different competitors—they simply reduce the fraction of light received

199   regardless of the presence of other species. By contrast, hard HOIs as we define them

200   introduce new parameters, or new functional dependencies, between competitors that

201   only kick in when more than one competitor is present.

202   Our definition also helps resolve the question of whether single species effects

203   can involve HOIs. For instance, recent papers by Letten and Stouffer (2019) and

204   Mayfield and Letten (2017) define HOIs as any higher order terms of competitor density,

205   including single species quadratic terms, $\beta_{i(jj)}N_j^2$. Our definition, does not count these as

206   HOIs, and this agrees with the emphasis in the literature that HOIs are a phenomenon that

207   arises between two or more *different species* of competitor (Hairston et al. 1968,

208   Vandermeer 1969, Neill 1974, Morin et al. 1988). As per our definition, the coefficients

209   for these terms, $\beta_{i(jj)}$, are parameters in a pairwise model, $f_{ij}(n_j)$, and thus are not hard

210   HOIs. Nor can single species higher order *terms* (not to be confused with higher order

211   *interactions*) generally be interpreted as examples of *intraspecific* interaction

212   modification, i.e. the effect of each additional individual being modified by other

213   individuals of the same species (Mayfield and Stouffer 2017). This interpretation only

214   makes sense in the context of a model where density dependence is strictly linear. In non-

215   linear models, such as those fit in Mayfield and Stouffer (2017), higher order terms added

216   to the model cannot be interpreted as individual-level interaction modifications; rather

217   these additional terms simply allow an already non-linear function to more closely

218   approximate the observed relationship between density and performance.

219   Another definition for HOIs that is largely equivalent to ours is provided by Adler

220   and Morris (1994). Like our definition, Adler and Morris distinguished between HOIs

221   and non-linear density dependence, and their definition agrees with ours in most cases.

222   However, there are some cases with three or more competitor species where the Adler

223   and Morris approach would indicate an HOI and our definition would not. We believe

224   our definition is more general, it does not depend on the number of competitor species

225   present and it can be more directly related to the traditional verbal definitions that

226   ecologists have used when discussing HOIs.

227   In the remainder of this paper we outline the experimental set-up and statistical

228   analyses required to test for HOIs in empirical data. Because real world data that would

229   allow for rigorous tests of HOIs are limited, we use a mechanistic growth model to

230   simulate a virtual competition experiment among three annual plant species (Figure 3).

231   We then fit species' responses to interspecific competition using phenomenological

232   competition models with and without HOIs and evaluate which species' responses are

233   best fit by competition model with HOIs. By considering when HOIs emerge in this

234   simple simulation we show the steps required to detect HOIs in empirical data and shed

235   light on the processes that could generate HOIs in nature.

236   **Simulating a Higher Order Competition Experiment**

237   A rigorous demonstration of HOIs requires measuring how focal species'

238   performance changes in response to increasing densities of each competitor species in

239   isolation, as well as to varying densities of combinations of different competitor species.

240   This requires an orthogonal response surface design where each competitor's density is

241   varied independently of each other species.

242   Instead of analyzing real data, we used a mechanistic growth model to simulate a

243   virtual experiment in which individuals of each annual plant species are grown in

244   separate plots with a range of competitor densities (Figure 2). The simulation lasts one

245   growing season (200 days). After the simulation ends, we find the per capita seed output

246   of each focal individual and record this as a measure of performance. We quantified

247   performance in plots with densities of 0, 1, 2, 3, 4, 9, 16, 25 or 36 individuals of each

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248   other competitor species, including intraspecific competition. We also measured

249   performance when the focal species was grown against all possible combinations of two

250   competitor species at the same densities. This design allows us to fit non-linear functions

251   to the interaction between each pair of species and test for any HOIs when more than two

252   competitors are present together.

253   We developed a mechanistic growth and resource competition model intended to

254   simulate the growth of annual plants in a Mediterranean climate (Figure S 1). The

255   simulated individuals germinate in the winter and then grow, flower, and produce seeds

256   by the early summer (Godoy and Levine 2014). In our model, we track a single pool of

257   soil resources, most easily thought of as water or water-soluble nutrients. This pool is not

258   resupplied during the season and is depleted over time. As the resource concentration

259   declines, plant growth slows and eventually stops (Figure 3). We make the assumption

260   that when individual net growth is zero, the plant will convert a fraction of its biomass

261   into seeds that remain dormant until the start of the next growing season (Cohen 1976).

262   Assuming all seeds germinate at the same time, and no seed mortality, we can use the per

263   capita seed production as a direct measure of population growth rate in each competition

264   treatment.

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

$$\frac{dR}{du} = I - \sum_{i=1}^{m} n_i g_i(b_i) h(R(u)), \tag{6}$$

266   where $R(u)$ is the resource availability at time u (u being day within the growing

267   season), I is the resource supply rate, and the final term is the sum of resource uptake

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268   rates of all m species in the community. Biomass per individual of each species i at time

269   u is given by b_i and the number of individuals in the population is given by n_i. The

270   function $g_i(b_i)$ converts per capita biomass into surface area of fine roots. Total resource

271   uptake rate is the product of root surface area and the rate of resource conductance per

272   unit root surface area. The rate of resource conductance into the roots is a function, $h(R)$,

273   of soil resource concentration, which we specify below. We simulate a Mediterranean

274   climate by setting initial resource availability high, $R(u = 0) \gg 0$, and setting the

275   resource supply rate, I, to zero.

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

$$\frac{dB_i}{du} = \begin{cases} n_i g_i(b_i)h(R)q - \delta_i B_i, & n_i g_i(b_i)h(R)q > \delta_i B_i \\ 0, & n_i g_i(b_i)h(R)q \leq \delta_i B_i \end{cases} \qquad (7)$$

277   where, q is the rate of resource conversion into biomass and δ_i is the rate of biomass loss

278   and respiration. The conditions indicate that when net growth of each species is less than

279   or equal to zero, growth and resource consumption stops (i.e. is set to zero). Biomass per

280   individual plant, b_i, is converted into root surface area for each individual via the function

281   $g_i(b_i) = \left(\frac{p b_i}{d_i}\right)^\nu$, where p is the proportion of growth allocated to roots, d_i is root tissue

282   density in g cm^{-3} and ν is an exponent that scales root volume to root surface area (see

283   Kooijmans (1986) for a conceptually similar approach to protists). The rate of resource

284   uptake per unit root surface area is dependent on resource concentration following

285   Michaelis-Menton kinetics:

$$h(R) = \frac{V_{max}R}{K + R}. \qquad (8)$$

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286   The equations above describe growth in total population biomass, B_i, over the

287   course of days within a single growing season. In contrast, a population-level

288   phenomenological competition model would track the total population density, n_i, over

289   annual time steps, t. In order to convert population density into biomass, we assume that

290   individuals start the growing season as seeds with a fixed size. Thus, the initial biomass

291   is $B_i(0) = \mu n_i(t)$, where μ is mass per seed and $n_i(t)$ is the number of seeds in the

292   population in year t. The population density in the following year $n_i(t + 1)$ is the total

293   number of seeds produced by the mature plants at the end of the growing season,

$$n_i(t + 1) = \frac{c}{\mu}(\max B_i), \tag{9}$$

294   where $\max B_i$ is the final accumulated biomass of species i and c gives the proportion of

295   total biomass converted to seeds.

296   We simulate the dynamics of three virtual annual plant species that differ in their

297   allocation to roots and in their rates of resource uptake (Table S 1). This difference leads

298   to phenology differences, i.e. some species stop growing earlier than others (Figure 3).

299   Phenology differences emerge because of the assumed trade-off between species rank in

300   terms of root density d_i and rank in terms of tissue respiration and loss rate, δ_i, (Tjoelker

301   et al. 2005, Birouste et al. 2014) (Table S1). Species with lower root density convert each

302   gram of biomass into more root surface area and this allows them to grow faster early in

303   the season when resource concentrations are high. In contrast, species with denser roots

304   but lower rates of tissue loss and respiration grow more slowly but continue growing later

305   into the season as resource availability declines. Thus, we refer to the three species in our

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306   simulations as 'early', 'mid' and 'late', depending on when they stop growing during the

307   simulation (Figure 3).

308   We chose parameters that produced growth and phenology patterns qualitatively

309   similar to biomass accumulation curves observed in annual plant communities (Godoy

310   and Levine 2014). A table of parameter values for the simulations are provided in the

311   supporting information (Table S 1). We simulated growth and resource dynamics by

312   solving equations (6) and (7) with the package `desolve` in the statistical program R (R

313   Core Team 2015). Code to reproduce analyses is available in a zip file and on github:

314   https://github.com/akleinhesselink/Competitive_HOI/releases/tag/1.0

315   *Phenomenological annual plant model*

316   In order to investigate whether this simulation produces HOIs between the

317   competitors, we fit non-linear phenomenological competition models to the per capita

318   seed production of each species. After evaluating a number of non-linear models, we

319   found that the Hassel model (Eq. [5]) fit the outcome of simulated pairwise competition

320   well. We specified an HOI version of the Hassel model as follows,

$$\frac{n_i(t+1)}{n_i(t)} = \frac{\lambda_i}{\left(1 + \sum_{j=1}^{3} \alpha_{ij} n_j + \sum_{j=1}^{3} \sum_{k=j+1}^{3} \beta_{i(jk)} n_j n_k\right)^{\tau_i}}, \qquad (10)$$

321   where all HOI effects of two competitor species on the focal species i are fitted with the

322   coefficients $\beta_{i(jk)}$ (following the notation in Mayfield and Stouffer (2017)). By our

323   definition, $\beta_{i(jk)}$ is a hard HOI when $j \neq k$.

324   Finally, we also considered a pairwise multiplicative version of the Hassel form,

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$$\frac{n_i(t+1)}{n_i(t)} = \frac{\lambda_i}{\left(\prod_{j=1}^{3}\left(1+\alpha_{ij}n_j\right)\right)^{\tau_i}}. \tag{11}$$

325 This model does not have HOIs per our definition—all α_{ij} and τ_i parameters can be

326 estimated from the pairwise cases where the focal species i competes with each other

327 species j in isolation. However, when there are two or more competitors the denominator

328 becomes a polynomial with multiplicative terms of competitor density. In the case of only

329 one competitor species, it collapses to the same pairwise Hassel model. Thus, contrasting

330 this model with the HOI model allows us to test whether hard HOIs are required as

331 opposed to a simpler non-linear function without HOIs.

332   We first fit the Hassel model to the pairwise cases and checked the model fit

333 graphically. We then fit the Hassel models (Eq. [5]), the HOI model (Eq. [10]) and the

334 multiplicative pairwise model (Eq. [11]) to the full set of two competitor densities. For

335 each focal species and model, we calculated root mean squared error (RMSE) as a

336 measure of goodness of fit and evaluated the strength and direction of HOIs by

337 examining the HOI coefficients, $\beta_{i(jk)}$. We fit all models with the non-linear least squares

338 modelling function, `nls,` in R. Code to run the simulations, fit the models and produce

339 the figures is given in the online supporting information.

340 **Results**

341   For all three species we found the Hassel model fit the simulated pairwise data

342 accurately (Figure 4). Next, we compared the three models fit to the full range of

343 competitor densities (Figure 5). For the early season species, the Hassel model with and

344 without the HOI showed more or less equivalent fits to the data with only a slight

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345   decrease in RMSE for the HOI model (Figure 5A&G). For the mid-season and late-

346   season species, we found that the HOI model fit the data better than the pairwise Hassel

347   model (Figure 5 B-I). The inability of the pairwise Hassel model to fit the per capita seed

348   output of the mid and late-season species can be seen by plotting the observed and per

349   capita seed production against two competitor densities at once (Figure S 2). In all cases,

350   the fitted HOI coefficients, $\beta_{i(jk)}$, were of smaller magnitude than the fitted pairwise

351   effects, α_{ij} (Figure 6). The fitted HOIs were stronger for the mid and late season species

352   than for the early season species (Figure 6). The multiplicative model (Eq. [11]) fit the

353   multi-competitor dynamics poorly when compared to the pairwise model and the HOI

354   model (Figure 5).

355   **Discussion**

356   *Evidence for higher order interactions*

357   Our simulation shows clear evidence for HOIs affecting two of the three virtual

358   species in our simulations (Figure 6). For the mid and late season species, the functional

359   form of per capita competition changed depending on the presence of other interspecific

360   competitors. Specifically, the presence of early or mid-season competitors increased the

361   per capita effects of competition on the late-season species (Figure 6F). Likewise, the

362   presence of the early season species increased the per capita effects of competition on the

363   mid-season species (Figure 6E). For the early season species, no clear HOIs were

364   detected: the pairwise interaction Hassel model fit the data nearly as well as the HOI

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365   model (Figure 5A&G) and the magnitudes of the HOI coefficients were small (Figure

366   6D).

367   We observe competition in our simulations because of a feedback between

368   individual density and resource concentration. As individuals grow, they draw down

369   resource concentrations (Figure S 1), this decreases the rate of resource acquisition into

370   the roots by equation (8) and slows the growth of other individuals in the community.

371   The magnitudes of pairwise interactions between species is easily understood from this

372   perspective. For instance, the late season species has a weak per capita effect on the early

373   season species because while the early species is active, roughly day 0 to day 30, the late-

374   season species remains small and has a slow absolute rate of resource uptake (Figure

375   3A—blue line). In contrast, the mid-season species has a stronger effect on the early

376   season species because it grows faster during the same period (Figure 3—red line). On

377   the other hand, the early season species has a weak effect on the late season species

378   because the former stops growing before the latter does the majority of its growth (Figure

379   3—black line).

380   The simplicity of the simulation makes it possible to understand how HOIs

381   emerge as well. The HOIs that affect the mid and late season species are in part due to an

382   indirect effect of resource uptake on competitor size and in part due to changes in

383   competitor phenology. For instance, in a scenario with one individual of each species the

384   early season species slows the growth of both the mid and the late-season species, this

385   keeps them smaller later into the season and makes them both more sensitive to

386   competition as the season progresses (Figure 3). This is reflected in the HOI coefficients

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387   that magnify competition for the mid and late-season species (Figure 6E&F). In contrast,

388   the early season species grows fast and exerts the dominant effect on the resource while it

389   is active, this makes it relatively insensitive to changes in the size of its interspecific

390   competitors (Figure 6D).

391   While the HOIs in this system are similar to competition mediated indirect effects

392   (Levine et al. 2017) there are two important differences between the HOIs we observed

393   and traditional indirect effects. First, indirect effects are not emergent properties of a

394   multi-competitor system, rather they are a predictable result of pairwise per capita

395   competition coefficients (Kleinhesselink and Adler 2015). Second, indirect effects can

396   generally be understood as emerging because of changes in the density of competitors

397   over time, not because of changes in per capita competition. For example, one species

398   may have an indirect effect on its competitor by changing the density of a second

399   competitor over the course of several year. In contrast, the HOIs in our simulation emerge

400   over the course of a single growing season with fixed population densities. Thus, these

401   HOIs indicate ecologically meaningful changes in the per capita effect of one species on

402   another.

403   Our example can be contrasted with a recent simulation of forest dynamics that

404   demonstrated how HOIs could affect species coexistence (Grilli et al. 2017). In that

405   simulation, unlike ours, per capita interactions between species were fixed. What the

406   authors called HOIs in that model, were not due to changes in the per capita effect of

407   competition, but were caused by changes in competitor density over time that were not

408   explicitly tracked by the model.

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409   *The phenomenological nature of HOIs*

410   HOIs can only be defined and quantified within the context of phenomenological

411   models of competition. Phenomenological models simplify community dynamics by

412   tracking population densities and not the resources for which species compete (Chesson

413   2000). HOIs emerge in phenomenological models precisely because they leave out

414   mechanistic detail and do not explicitly model resource dynamics (Abrams 1983,

415   O'Dwyer 2018, Letten and Stouffer 2019). Given this, one may be tempted to conclude

416   that HOIs are an artifact of the inadequacy of such models. However, any concept of

417   species *interactions* (at least competitive interactions) is essentially phenomenological in

418   nature—biomass and nutrients do not flow directly between competing individuals, rather

419   competitors influence each other's growth or survival indirectly through changes in the

420   abundance of shared resources. Thus one could sidestep the problem of HOIs by instead

421   modeling communities mechanistically as biomass and resources (e.g. Dybzinski and

422   Tilman (2007)). However, doing may require re-thinking ecological theory formulated on

423   the concept of species *interactions*.

424   Phenomenological competition coefficients can sometimes be derived analytically

425   from mechanistic competition models by making the assumption that resource

426   concentrations are near a fixed equilibrium (Tilman 1977, Meszéna et al. 2006,

427   Kleinhesselink and Adler 2015, Letten et al. 2017). However, in many natural systems,

428   such as such as those involving annual plants, resource concentrations and individual size

429   fluctuate rapidly over the course of a single growing season or generation. This makes

430   deriving competition coefficients directly from the resource dynamics more difficult,

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431 perhaps impossible (O'Dwyer 2018). Thus, even in cases in which we actually know

432 which resources species compete for, fitting a phenomenological model to population

433 dynamics may be the only way to quantitively describe species interactions. Our work

434 clarifies the what it means to fit models with and without HOIs to multi-competitor

435 settings.

436 *Are HOIs widespread?*

437 In our virtual experiment, HOIs arise because individual size and phenology, the

438 traits that determine each species' impact on and sensitivity to resource availability, are

439 themselves governed by resource availability. More generally, changes in individual size

440 and corresponding changes in resource uptake rate may be a common cause of HOIs in

441 nature. We predict that HOIs will likely be common in systems in which 1) consumers

442 cause large resource fluctuations, 2) the per capita rate of resource uptake changes in

443 response to resource availability, and 3) the strength of this response varies across

444 species. Instead of changes in individual size, another mechanism that could generate

445 HOIs would be density-dependent changes in resource acquisition traits. For example,

446 traits such as height, specific leaf area, and phenology, have been shown to change in

447 response to competition or resource availability (e.g. Aronson et al. 1992, Bennett et al.

448 2016, Conti et al. 2018). If per capita competition coefficients are a function of these

449 traits, then it would not be surprising if changes in these traits led to HOIs. If changes in

450 individual size within a season, or trait plasticity are common, and are also likely to cause

451 HOIs, this begs the question of why there have been so few documented examples of

452 HOIs in natural communities (but see Mayfield and Stouffer 2017).

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453   One hypothesis is that HOIs are common but usually too weak to detect. A key

454   factor in producing HOIs in our simulation is that each species has a uniquely shaped

455   growth curve and phenology. In additional simulations, we found that as species became

456   more similar in their traits HOIs became weaker (Appendix A). In nature, such large

457   functional differences in the way species take-up resources over time may be rare. At the

458   same time, these simulations suggest that quantifying how functional traits change in

459   response to competitors provides a likely path to further understanding of HOIs.

460   A second factor generating the HOIs in our simulation are the rapid changes in

461   resource availability and average plant size, and consequently, species interactions, over

462   the course of a season (Figure 3). Without these dynamics, species might have relatively

463   constant per capita effects on one another and no HOIs would emerge. For instance,

464   compare our system to an idealized version of resource competition for perennial plants

465   (Dybzinski and Tilman 2007). Due to their large size perennial plants can be assumed to

466   quickly draw resources down to a dynamic equilibrium. By contrast, seasonally forced

467   systems such as annual plant communities in Mediterranean climates may be a good

468   place to look for strong HOIs (Mayfield and Stouffer 2017).

469   **Conclusion**

470   HOIs have profound implications for how we understand and model multispecies

471   communities. However, before ecologists can embark on measuring HOIs in nature, they

472   must have a shared definition for what HOIs are. We have provided a more general

473   definition of HOIs caused by interaction modifications that will be useful as ecologists

474   seek empirical evidence for HOIs in nature. By simulating growth and resource

475   competition in a virtual experiment, we outline the steps required to fit pairwise and HOI

476   models to field data. This simulation also sheds light on the environmental conditions and

477   life-history traits that may be more likely to generate HOIs. While we believe that HOIs

478   should be common in nature this does not mean that they will be strong enough to detect

479   statistically. Our work suggests that environments in which resource availability and

480   competitor size change rapidly during a single growing season may be a likely place for

481   detectable HOIs to emerge.

482   **Acknowledgments**

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563 **Figures**
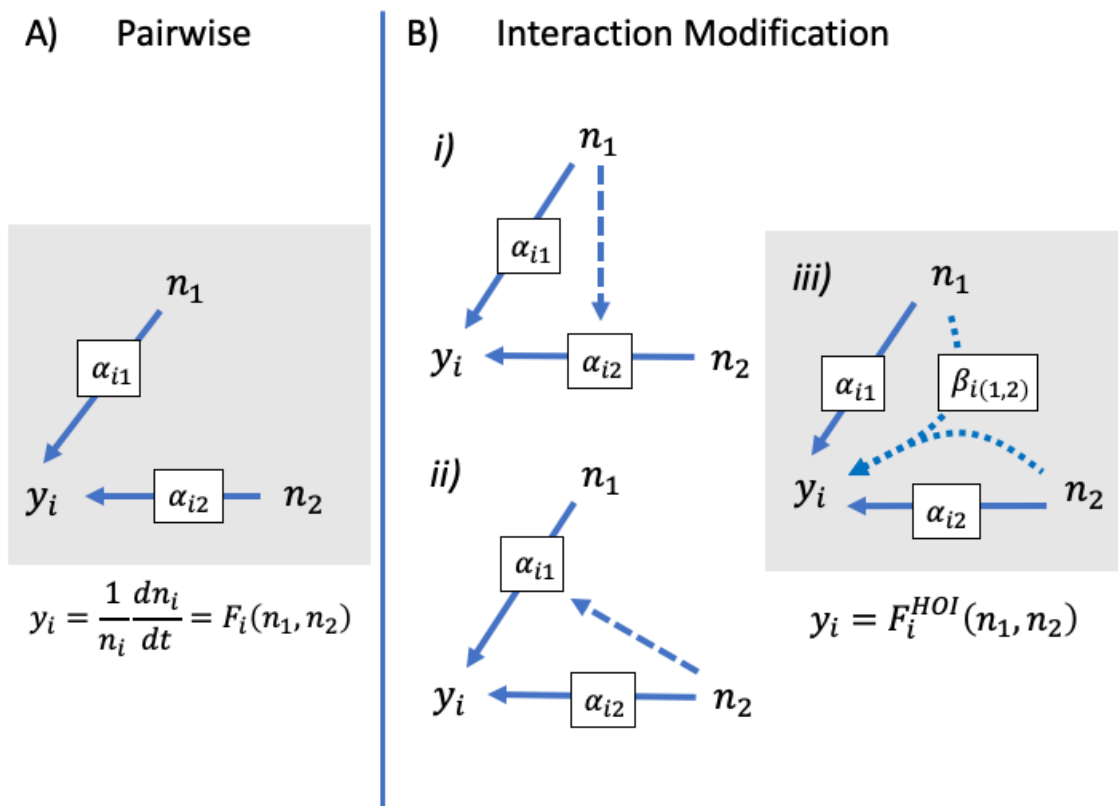
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565 **Figure 1. How interaction modifications lead to higher order interactions. In A, a**

566 **pairwise model is shown without interaction modification. The competitive effect of**

567 **species one and two on the per capita growth of the focal species *i*, are shown as**

568 **separate blue arrows. These effects may be simple per competition coefficients, α_{12}**

569 **and α_{13}, or could be more complicated non-linear functions of density. In B, a**

570 **model with interaction modification is shown: in *i)* the dashed arrow shows that the**

571 **effect of two is modified by the density of one; in *ii)* the effect of one is modified by**

572 **the density of two. In reality, one cannot assign either species as the modifier, rather**

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573   they modify each other's effects in a way that emerges a single HOI. The HOI in

574   this case is quantified by introducing the new parameter $\beta_{i(1,2)}$, and shown with the

575   curved arrows in *iii*.

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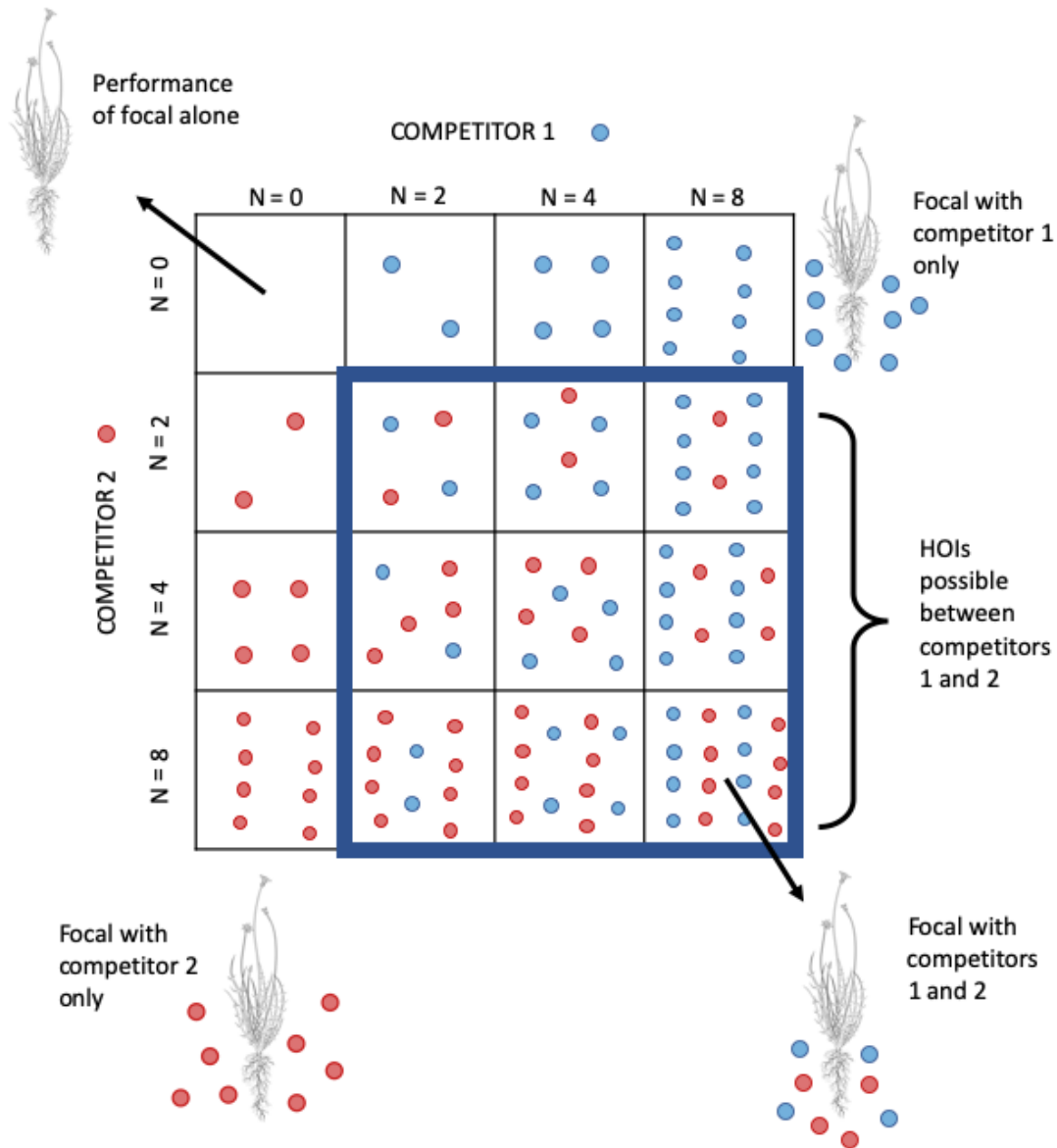
Figure 2 Schematic of orthogonal competition experiment required to detect higher order interactions. Each square represents a separate study plot. Competitor 1, (blue circles) and Competitor 2 (red circles) are grown in a gradient of increasing density alone and together. A single individual of the focal species (line drawing) is grown in

581 **each plot allowing the response to competition from each competitor species to be**

582 **fitted.**

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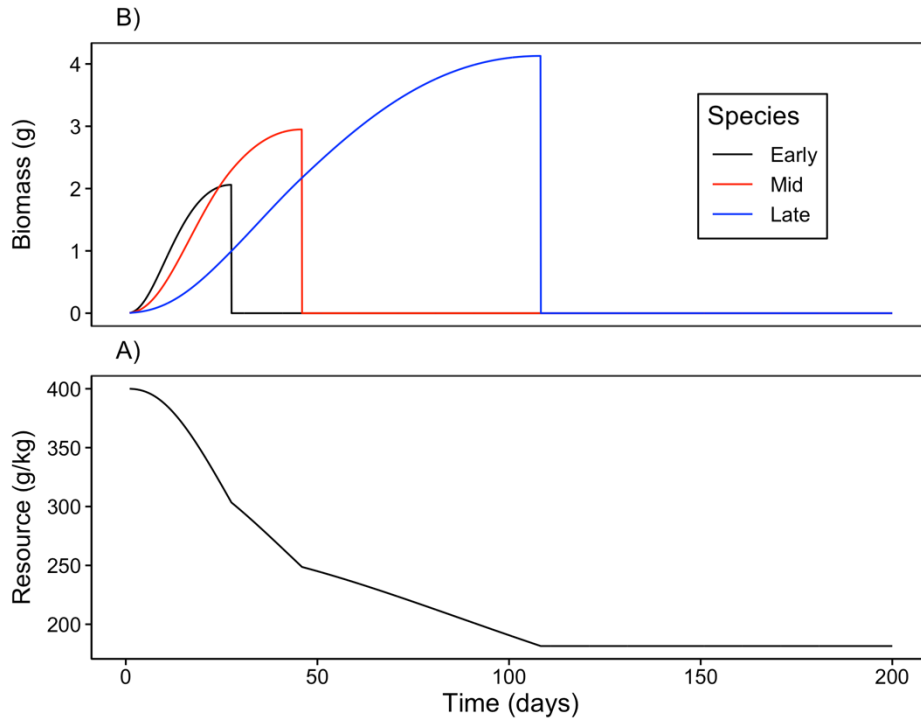
Figure 3. Example time course of A) annual plant growth and B) resource concentration during a single simulated growing season. In this example, each species' population consists of a single individual. The early season species (black) grows rapidly when resource availability is high and senesces early. 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.

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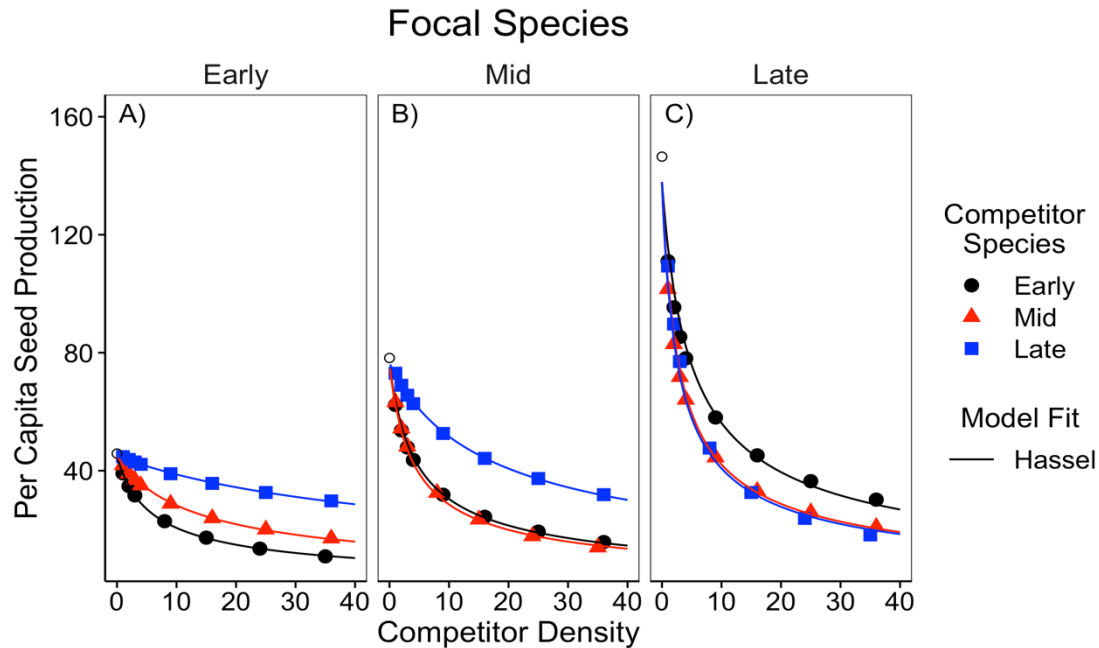
Figure 4. Simulated per capita seed production of the A) early, B) middle and C) late season species in response to a single competitor species at a time. Competitor density is shown on the x-axis. Colors and shapes indicate the identity of the competitor species. Open circles show the per capita seed production of each focal species in the absence of any competitors. The solid line shows the fit of the Hassel model.

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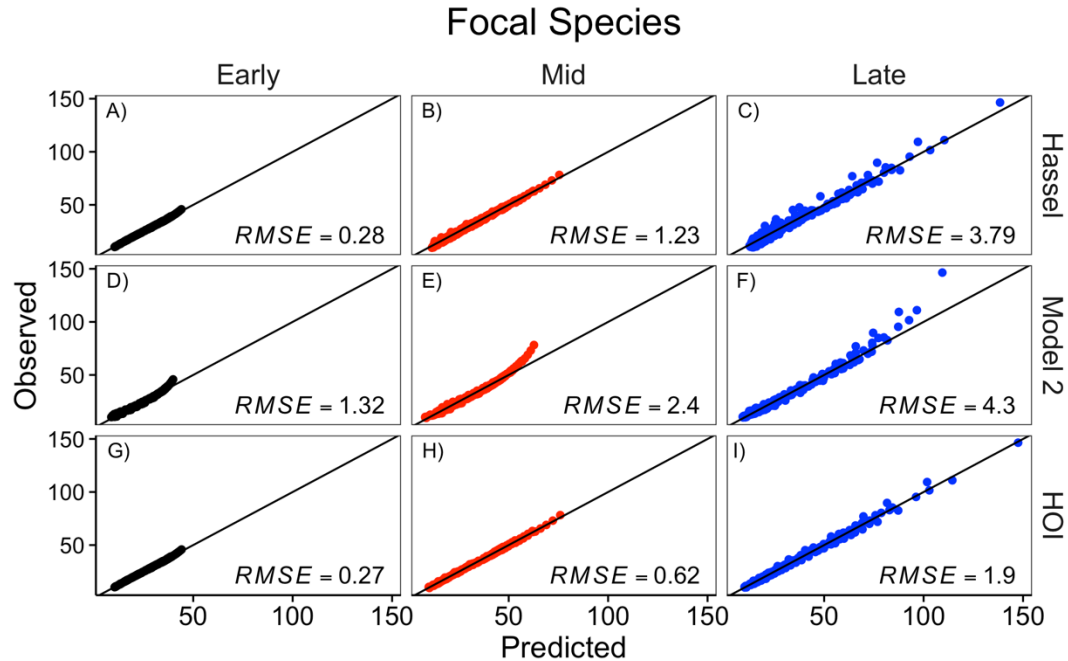
Figure 5. Comparison of the Hassel, multiplicative ('model 2'), and HOI models fit to each focal species. The y-axis shows the simulated per capita seed production of the focal species. The x-axis shows the per capita seed production predicted by the phenomenological model. The top row, A-C, shows the prediction for the pairwise Hassel model (eq. [5]); the middle row, D-F, shows the prediction from the multiplicative model (eq. [11]); and the bottom row, G-I, shows the prediction from the HOI model (eq. [10]). The one-to-one line and root-mean-squared error (RMSE) for predictions from each model are shown.

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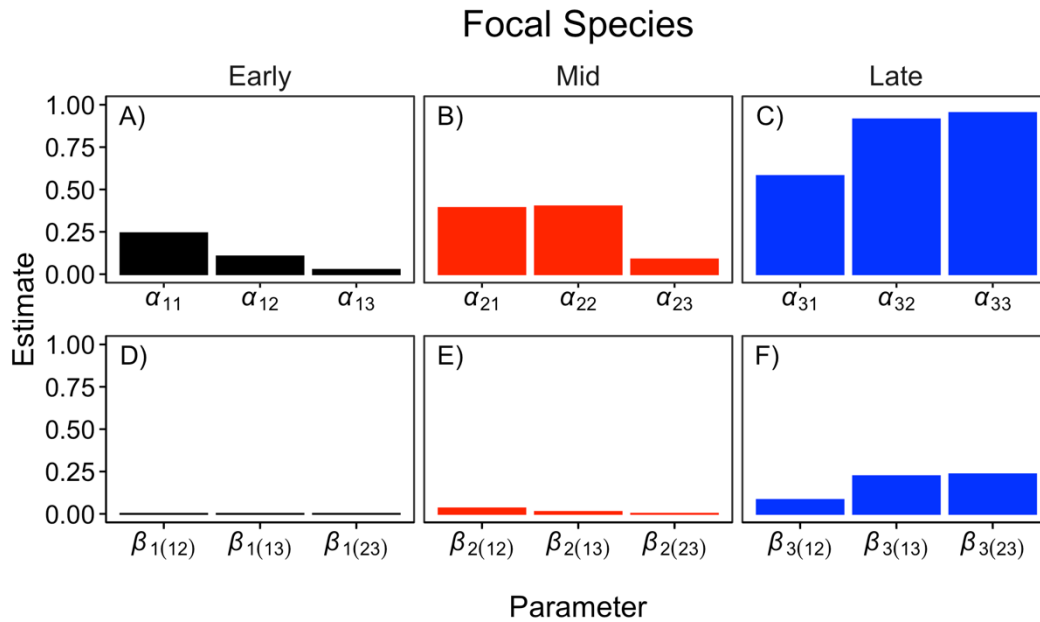
Figure 6. Interaction coefficients for each of focal species from the HOI model. The top row, A-C, shows the pairwise competition coefficients for the focal species and each competitor. The bottom row, D-F, shows the two-species HOI coefficients. Coefficient subscripts indicate which focal species and competitor species are involved, 1 = Early, 2 = Mid, 3 = Late.

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613 **Supporting Information – Additional Tables**

614 **Table S 1 Table of parameter values used in the growth simulation experiment in**

615 **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})
d_1	0.06	Early competitor root density (g cm^{-3})
d_2	0.12	Mid competitor root density (g cm^{-3})
d_3	0.36	Late competitor root density (g cm^{-3})
δ_1	0.3	Early competitor loss and respiration rate (g g^{-1}d^{-1})
δ_2	0.15	Mid competitor loss and respiration rate (g g^{-1}d^{-1})
δ_3	0.053	Late competitor loss and respiration rate (g g^{-1}d^{-1})
K	350	Resource half-saturation constant (g kg^{-1})
V_{max}	1	Maximum resource conductance (g d^{-1}cm^{-2})
p	0.5	Ratio of root biomass to total biomass
ν	0.66	Scaling exponent (unitless)
q	0.2	Biomass assimilation rate (g g^{-1}d^{-1})
μ	0.005	Seed mass (g per seed)
c	0.1	Conversion of final biomass to seed mass (g g^{-1})

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618   **Supporting Information – Additional figures**
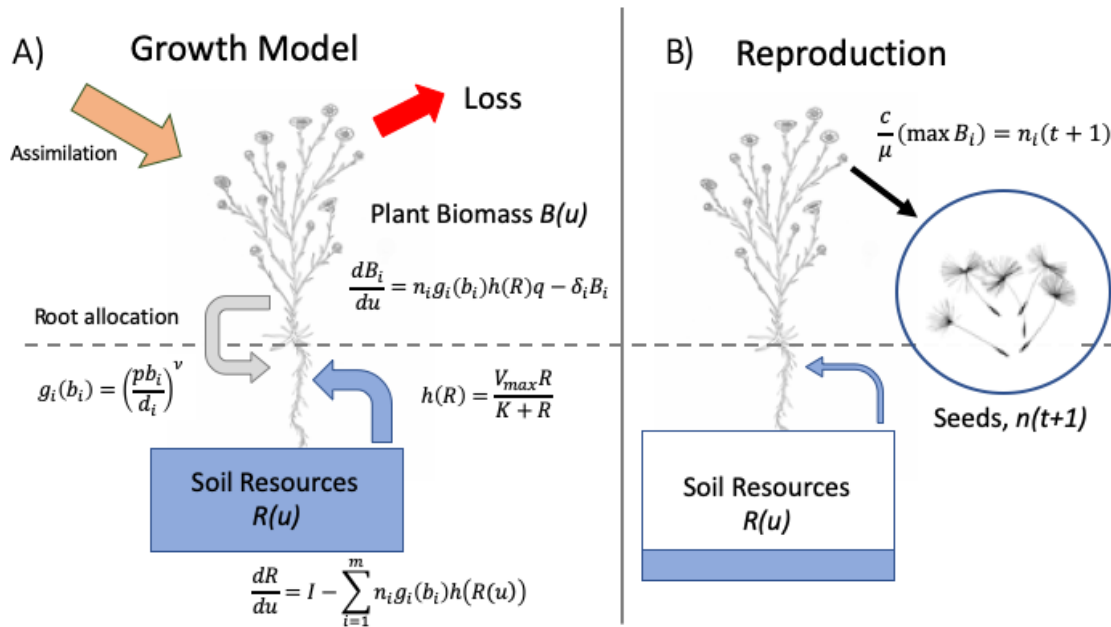
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620   **Figure S 1 Diagram schematic of annual plant growth model used in simulation. A)**

621   **in the model each individual plant start as a seed, grows over the course of a single**

622   **growing season. Growth is a function of plant biomass, root surface area and soil**

623   **resource availability. B) Over time the soil resources are depleted and plant growth**

624   **slows down. Plants reach a maximum size when losses due to respiration and tissue**

625   **senescence are greater than growth. At this point the plants convert stored**

626   **resources to seeds. The number of seeds in the next growing season is determined as**

627   **the total mass of seeds produced per species divided by the weight of a single seed.**

628   **Supporting Information – Additional figures**

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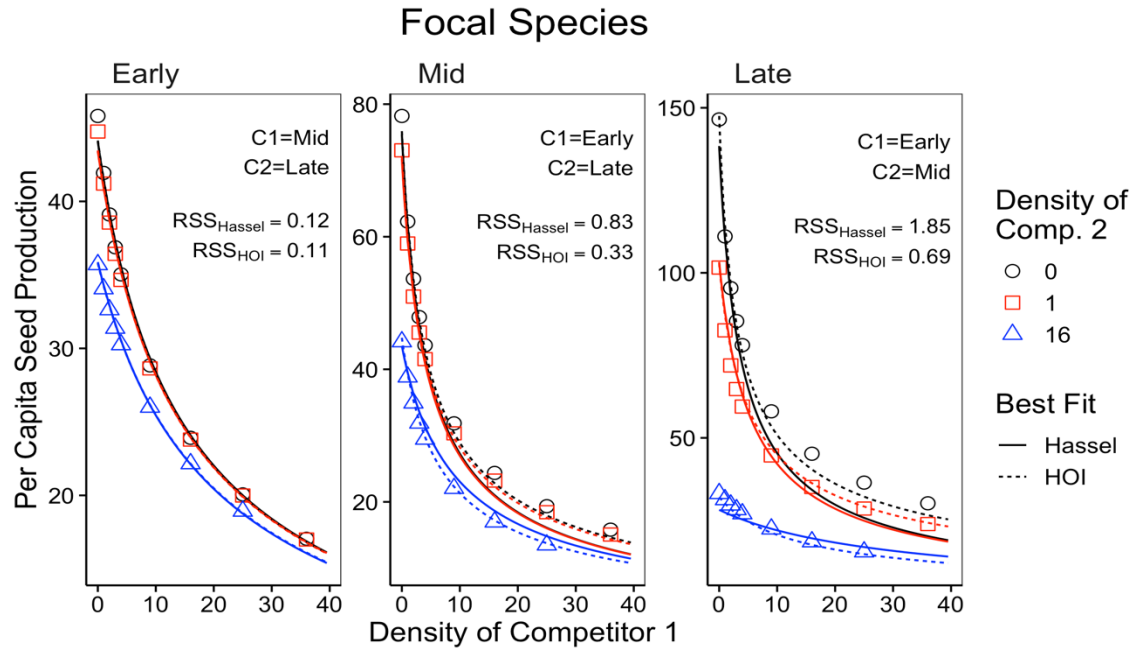
630   **Figure S 2 Simulated per capita seed production of the A) early, B) mid and C) late**

631   **season species in response to density of two interspecific competitors. Densities of**

632   **two competitors are shown in each panel—the x-axis shows the density of the first**

633   **competitor, while different colored lines and shapes show the density of a second**

634   **competitor. Text in each panel lists the identities of competitor one and two (early,**

635   **mid or late). Lines show best fit from phenomenological models. Residual sum of**

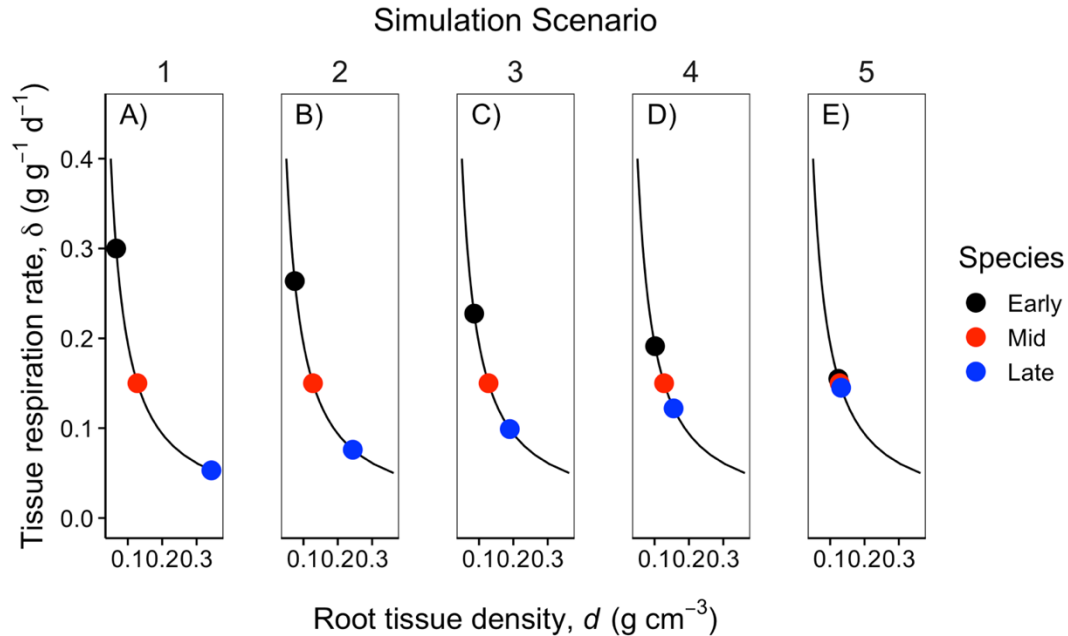636   **squared error is shown for each model and focal species.**

637 **Appendix A – The effect of trait differences on higher order interactions**

638   We used an additional simulation experiment to test whether the strength of

639   higher order interactions (HOIs) was associated with the magnitude of functional

640   differences between competitor species. We started with the same parameter values as in

641   the simulation in the main text in which there was a large difference between the species

642   in root density (d_i) and tissue respiration rate (δ_i). In four additional simulation scenarios,

643   we gradually decreased the average difference between species in these traits (Table A1).

644   Specifically, we held the traits of the mid-season species constant and decreased the

645   difference in the root density trait, d_i, between the early and late-season species. We

646   assumed a trade-off between root density and tissue respiration rate such that changing

647   root density was accompanied by a change in tissue respiration rate, δ_i (Figure A1). We

648   quantified the average functional difference between species as the standard deviation of

649   root density among all species. In each scenario, we simulated competition and fitted the

650   phenomenological HOI model as in the main text. For each species in each scenario, we

651   quantified the strength of HOIs as the average magnitude of the β coefficients divided by

652   the average magnitude of the α coefficients. For the mid and late season species, the

653   strength of the HOIs increased with the functional difference between species (Figure A1

654   B&C). For the early season species, HOIs were weak in all five scenarios (Figure A1 A).

655   These simulations show that the functional differences between competitors drive the

656   HOIs we observed in this system.

657 **Table A 1. Parameter values for five simulations with gradually decreasing the trait**

658 **difference between the early season and late season species. All other simulation**

659 **parameters are the same as in Table S1.**

Functional Difference	Scenario	Species	Root density d (g cm^{-3})	Respiration rate δ_i (g g^{-1}d^{-1})	Standard deviation of d
Large	1	Early	0.066	0.300	
		Mid	0.128	0.150	0.1460
		Late	0.343	0.053	
	2	Early	0.075	0.261	
		Mid	0.128	0.150	0.0821
		Late	0.236	0.078	
	3	Early	0.088	0.222	
		Mid	0.128	0.150	0.0467
		Late	0.181	0.104	
	4	Early	0.105	0.184	
		Mid	0.128	0.150	0.0208
		Late	0.147	0.130	
Small	5	Early	0.132	0.145	
		Mid	0.128	0.150	0.0405
		Late	0.124	0.155	

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Figure A 1. Colored points show the value of functional traits, root density and tissue loss rate, for each of the three species in each of the five simulation scenarios (A-E). Across the five scenarios, the differences between the early season and late season species' root density and respiration rates were gradually decreased. The mid-season species' traits were held constant. The black line indicates the trade-off between the root density and tissue respiration rate traits.

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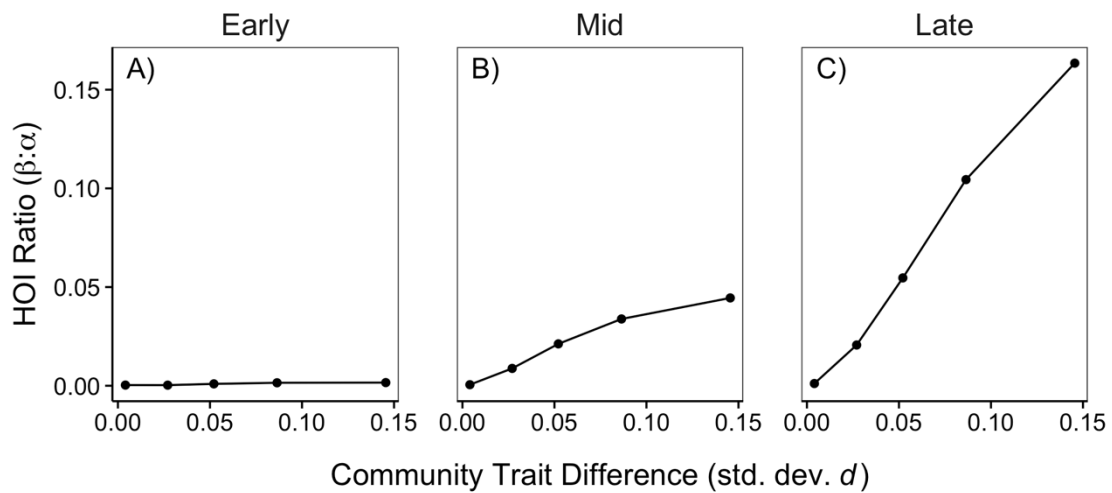
Figure A 2. The strength of HOIs depends on the difference in species functional traits. The y-axis quantifies the strength of HOIs affecting the early (A), mid (B) and late (C) species as the ratio of the of the average magnitude of the $\beta_{i(jk)}$ coefficients to the average magnitude of the α coefficients in the phenomenological HOI model. A larger ratio $\beta{:}\alpha$ ratio indicates stronger HOIs compared to pairwise interactions. The x-axis quantifies the community-level trait difference as the standard deviation of the root density trait, _d_.

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