

## 1 Higher order interactions and coexistence theory

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12 of the manuscript.

## 13 Abstract

14 Higher order interactions (HOIs) have been suggested to stabilize diverse ecological communities.  
15 However, their role in maintaining species coexistence from the perspective of modern coexistence  
16 theory is unknown. Here, using a three-species Lotka-Volterra model, we derive a general rule for species  
17 coexistence modulated by HOIs. We show that negative HOIs that intensify pairwise competition,  
18 can promote coexistence across a wide range of fitness differences, provided that HOIs strengthen  
19 intraspecific competition more than interspecific competition. In contrast, positive HOIs that alleviate  
20 pairwise competition can also stabilize coexistence across a wide range of fitness differences, irrespective  
21 of differences in strength of inter- and intraspecific competition. Furthermore, we extend our three-  
22 species analytical result to multispecies competitive community and show, using simulations, that  
23 feasible multispecies coexistence is possible provided that strength of negative intraspecific HOIs is  
24 higher than interspecific HOIs. In addition, multispecies communities, however, become unstable with  
25 positive HOIs as such higher-order interactions could lead to disproportionately infeasible growth rates.  
26 This work provides crucial insights on the underlying mechanisms that could maintain species diversity  
27 and links HOIs with modern coexistence theory.

## 28 1. Introduction

29 In diverse ecological communities, species interact with other species in the community temporally (Li &  
30 Chesson, 2016) and/or spatially (Hart *et al.*, 2017). Understanding the mechanisms behind maintenance  
31 of species diversity has been one of the central goals of ecological research for decades (Levine *et al.*,  
32 2017). While our primary understanding of species coexistence empirically and theoretically has mostly  
33 come from a study of species pairs (Chesson, 2000; Hart *et al.*, 2016; Kraft *et al.*, 2015), understanding  
34 the dynamics and coexistence of multiple species from the viewpoint of species pairs becomes unfeasible  
35 and intractable as species richness increases (Barabas *et al.*, 2016; Bairey *et al.*, 2016).

36 In competition models, the underlying processes that facilitate species coexistence require parameter  
37 trade-offs in competitive interactions to stabilize multispecies coexistence (Barabas *et al.*, 2016). More-  
38 over, competitive interactions between species in a diverse community is difficult to structure based on  
39 the generalizations coming from simple coexistence rules, leading to formulation of models of coexistence  
40 based on ecological equivalence (Hubbell, 2006). In species-rich communities, underlying processes  
41 that cannot be captured by pairwise species interactions can emerge, and have been suggested to  
42 promote species coexistence (Abrams 1983). Such underlying processes, for example can be intransitive  
43 or “rock-paper-scissors” interactions (Laird & Schamp, 2006; Gallien *et al.*, 2017; Saavedra *et al.*,  
44 2017). Intransitive interactions are inherently pairwise in nature but they form interaction chains that  
45 favor species coexistence. For example, in a three species system, intransitive competitive interactions

46 can lead to coexistence of all the three species, although none of the species pair can coexist alone.  
 47 Advancing our understanding of species coexistence in diverse communities requires an understanding  
 48 of mechanisms that could inherently be high-dimensional.

49 When diverse species communities are modelled explicitly by considering only pairwise interactions,  
 50 multiple species coexistence is not always possible (Levine *et al.*, 2017; Bairey *et al.*, 2016; Wilson,  
 51 1992). Recent studies have suggested that in order for large number of species to coexist, interactions  
 52 between species should not be constrained to species pairs but should include higher order interactions  
 53 (HOIs) (Grilli *et al.*, 2017). Although, such HOIs have been suggested to stabilize large ecological  
 54 communities, their underlying role in maintaining species coexistence, from the purview of modern  
 55 coexistence theory (MCT) is unknown. This is primarily due to the difficulty of integrating MCT for  
 56 more than two species simultaneously (Saavedra *et al.*, 2017; Barabas *et al.*, 2016). MCT states that  
 57 coexistence is possible when fitness differences between species are smaller than their niche differences  
 58 (Chesson, 2000). In MCT, coexistence of species can be understood from a mutual invasibility criteria,  
 59 where the invasion growth rate of a species is analytically decomposed into stabilizing niche differences  
 60 and average fitness differences (Kremer & Klausmeier, 2013; Gallien *et al.*, 2017). Niche differences  
 61 increase the probability for species coexistence while fitness differences increase the probability of  
 62 competitive exclusion. Importantly, fitness and niche differences can be quantified from the terms of  
 63 the Lotka-Volterra pairwise competition model as (Saavedra *et al.*, 2017):

$$64 \quad \sqrt{\frac{\alpha_{11}\alpha_{22}}{\alpha_{12}\alpha_{21}}} > \frac{r_1}{r_2} \sqrt{\frac{\alpha_{22}\alpha_{21}}{\alpha_{11}\alpha_{12}}} > \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} \quad (1)$$

Niche Overlap<sup>-1</sup>      Fitness difference      Niche Overlap

65 If niche overlap is greater than the fitness difference between two species, then coexistence is not  
 66 possible. Under certain simplistic assumptions, one can integrate results from HOIs into the traditional  
 67 framework of pairwise species coexistence. Such an integration would make the relevance and the  
 68 understanding of HOIs more complete.

69 Here, using a three-species Lotka-Volterra model, we demonstrate the importance of HOIs in maintaining  
 70 and disrupting species coexistence. Specifically, using invasibility criterion, we modified pairwise  
 71 interspecific coefficients of the Lotka-Volterra model in a way that allowed us to create a range of fitness  
 72 differences ranging from low to high. We then show how negative three-way HOIs (HOIs that intensify  
 73 pairwise competitions), and positive three-way HOIs (HOIs that alleviate pairwise competition) can  
 74 stabilize species coexistence in fitness regions, where species coexistence is impossible if only pairwise  
 75 interactions are considered. We then extend our three-species HOIs case, to a multispecies competitive  
 76 community, and show that the conditions under which HOIs stabilize species coexistence in the  
 77 three-species case still holds in a multispecies community. We highlight the possible mechanisms by  
 78 which HOIs could promote coexistence in species-rich communities.

## 79 2. Methods

### 80 2.1 Higher order interactions

81 Lotka-Volterra model for three-way HOIs can be written as (Letten and Stouffer 2019b) (for four-way  
 82 HOIs see appendix A):

$$83 \quad \frac{dN_i}{dt} = N_i r_i (1 - \sum_j^n \alpha_{ij} N_j + \sum_j^n \sum_k^n \beta_{ijk} N_j N_k) \quad (2)$$

84 where  $\alpha_{ij}$  and  $\beta_{ijk}$  are pair-wise interactions and HOIs respectively. Here, higher-order terms could  
 85 broadly be defined as non-additive effects on per capita fitness of a species. HOIs could intensify or  
 86 alleviate the pairwise competition between two species depending on the sign of  $\beta_{ijk}$  as negative or  
 87 positive respectively. Here,  $n = 3$ , in this particular section, and we evaluate the effect of HOIs for  
 88 multispecies ( $n = 50$ ) communities later (see section 2.3). In this particular model, we make a few  
 89 assumptions while deriving the invasion growth rate for the three species case-

90 1) There is interspecific competitive interaction between species 1 and 2, but not with species 3. This  
 91 means that the matrix of competitive interactions will be:

$$\begin{pmatrix} \alpha_{11} & \alpha_{12} & \alpha_{13} \\ \alpha_{21} & \alpha_{22} & \alpha_{23} \\ \alpha_{31} & \alpha_{32} & \alpha_{33} \end{pmatrix} = \begin{pmatrix} \alpha_{11} & \alpha_{12} & 0 \\ \alpha_{21} & \alpha_{22} & 0 \\ 0 & 0 & \alpha_{33} \end{pmatrix} \quad (3)$$

2) Only interspecific HOIs are taken into account. This means that terms such as  $\beta_{iii} = 0$ , where  $i = 1, 2, 3$ .

3) Species 3 influences species 1, and species 2 only through HOIs. However, species 3 does not get influenced by species 1 or 2 through HOIs ( $\beta_{3jk} = 0$ ; where  $j, k = 1, 2$ ).

These assumptions were made to ensure that the number of terms in the HOI model are tractable for simple analysis (appendix A). Using these assumptions, we can expand the model in equation (2) as:

$$\frac{dN_i}{dt} = N_i r_i (1 - \alpha_{i1} N_1 - \alpha_{i2} N_2 + \beta_{i11} N_1^2 + \beta_{i12} N_1 N_2 + \beta_{i13} N_1 N_3 + \beta_{i21} N_2 N_1 + \beta_{i22} N_2^2 + \beta_{i23} N_2 N_3)$$

where  $i = 1, 2$  (for species 3 see appendix A). We can then write the HOI matrix for each of the species as:

$$\begin{pmatrix} \beta_{i11} & \beta_{i12} & \beta_{i13} \\ \beta_{i21} & \beta_{i22} & \beta_{i23} \\ \beta_{i31} & \beta_{i32} & \beta_{i33} \end{pmatrix} \quad (4)$$

Where  $i = 1, 2$ ;  $\beta_{i31} = \beta_{i32} = \beta_{i33} = 0$ ; and  $\beta_{iii} = 0$ .

We consider cases of both positive and negative HOIs, while calculating the invasion growth rates.

## 2.2 Invasion growth rate and coexistence theory

The invasion growth rate,  $r_i$ , is the per capita rate of increase in a species' abundance—when it is rare—in presence of the other species, which is at equilibrium in the community. This means  $\frac{1}{N_i} \frac{dN_i}{dt} > 0$  for species  $i$  in the community. Invasion growth rates of species 1 in the presence of HOIs in the community can be written as (see appendix A):

$$r_1^* = 1 - \left( \frac{\alpha_{12}(\alpha_{22} - \beta_{223} N_3^*) - \beta_{122} - \beta_{123}(\alpha_{22} - \beta_{223} N_3^*)}{(\alpha_{22} - \beta_{223} N_3^*)^2} \right) \quad (5)$$

where  $N_3^* = \frac{1}{\alpha_{33}}$  (appendix A).

We evaluated the effect of 3-way and 4-way HOIs in promoting coexistence by comparing invasion growth rates of species 1 in presence and absence of HOIs. Following Gallien et. al 2017, we created scenarios where pairwise competitive matrix (3) varied from purely symmetric pairwise interactions to asymmetric interactions with gradually increasing pairwise fitness differences. As pairwise fitness differences (calculated from equation 1) increase, niche difference (calculated from equation 1) should increase accordingly to stabilize species coexistence. This was done by modifying the pairwise interaction matrix to (Gallien *et al.*, 2017):

$$\begin{pmatrix} \alpha_{11} & \alpha_{12} & \alpha_{13} \\ \alpha_{21} & \alpha_{22} & \alpha_{23} \\ \alpha_{31} & \alpha_{32} & \alpha_{33} \end{pmatrix} = d \begin{pmatrix} 2\sqrt{\theta} & \theta & 0 \\ 1 & 2\sqrt{\theta} & 0 \\ 0 & 0 & \alpha_{33} \end{pmatrix} \quad (6)$$

Where  $d = 0.01$ . The above modified matrix ensures that niche overlap between species 1 and species 2 is at 0.5 even when fitness differences (calculated using equations 1), controlled by  $\theta$ , increases linearly. As  $\theta$  is varied from 0 to 7, fitness difference between species 2 and 1 increases linearly. Note that fitness difference of species 2 over species 1 is given from equation 1 as  $\sqrt{\frac{\alpha_{11}\alpha_{12}}{\alpha_{22}\alpha_{21}}}$ . For certain  $\theta = [5, 7]$  values, fitness difference of species 2 over species 1 exceeds niche difference. Consequently, following the pairwise coexistence rule, species 1 can never invade species 2. This means that pairwise coexistence is impossible for certain  $\theta = [5, 7]$  values.  $\theta = 5$  defines the boundary between stable pairwise coexistence and competitive exclusion, when there are no HOIs. Note that species 3 remains unaffected by this modification and only participates in HOIs.

Next, to evaluate whether the presence of three-way and four-way HOIs (appendix B) stabilizes pairwise coexistence in scenarios where fitness differences are extreme, we estimated invasion growth rates of species 1 ( $r_1^*$ ) when species 2 is present at equilibrium. When HOIs are absent, it is expected that given

132 niche overlap is at 0.5, pairwise coexistence becomes impossible as fitness differences increase. The  
133 importance of HOIs will be evident if species 1 could increase its invasion growth rates and invade  
134 when HOIs are present even when fitness differences are large, i.e. they could increase their numbers  
135 even when differences between the two species in terms of fitness are large. For sensitivity analysis of  
136 invasion growth rate to HOIs see appendix C.

### 137 2.3 Multispecies coexistence and higher order interactions

138 Multispecies generalization of two-species pairwise coexistence rule, however, is complicated. In  
139 multispecies communities, while all species pairs must satisfy the pairwise coexistence rule, this does  
140 not, however, guarantee stability (Barabas *et al.*, 2016). For multispecies competitive communities, the  
141 stability and feasibility of coexistence can be evaluated from Weyl's inequality (see below). A pairwise  
142 competitive community can be written as:

$$\frac{dN_i}{dt} = N_i r_i (1 - \sum_j \alpha_{ij} N_j)$$

143 Where,  $\alpha_{ij}$  represents pairwise competitive interactions.  $\alpha_{ij}$  is the element in the  $i$ -th row and  $j$ -th  
144 column of a matrix of pairwise competitive interactions. This pairwise matrix of competitive interactions  
145 can be denoted, by, say  $\mathbf{A}$ . Here, we consider  $\mathbf{A}$  as a symmetric matrix, such that,  $\alpha_{ij} = \alpha_{ji}$ .

146 Now,  $\mathbf{A}$  can be decomposed into inter- and intraspecific matrices, say  $\mathbf{B}$  and  $\mathbf{C}$  respectively, where  $\mathbf{B}$  is  
147 a matrix of only interspecific competitive interactions while  $\mathbf{C}$  is a matrix of intraspecific competitive  
148 interactions. Now, since  $\mathbf{C}$  contains only intraspecific coefficients,  $\mathbf{C}$  is a diagonal matrix, whereas  $\mathbf{B}$   
149 has zeros in the diagonal. The off-diagonal entries of  $\mathbf{B}$  capture the symmetric pairwise interspecific  
150 competitive interactions. Hence, we can write,  $\mathbf{A} = \mathbf{B} + \mathbf{C}$ . Since,  $\mathbf{A}$  is symmetric,  $\mathbf{B}$  and  $\mathbf{C}$   
151 are also symmetric, and hence all their eigenvalues are real. For a  $S$  species community,  $\mathbf{B}$ , and  
152  $\mathbf{C}$  will have  $S$  eigenvalues and these eigenvalues can be ordered as  $b_1 \geq b_2 \geq b_3 \geq \dots \geq b_s$  and  
153  $c_1 \geq c_2 \geq c_3 \geq \dots \geq c_s$ . The Weyl's inequality now states that the necessary and sufficient condition  
154 for multispecies coexistence to be stable is:

$$155 \quad b_1 + c_s < 0, \quad b_1 + c_1 < 0, \quad (7)$$

156 When all intraspecific coefficients (or the diagonal elements of  $\mathbf{C}$ ) are equal, all the eigenvalues have  
157 the same value i.e.,  $c_s = c_1 = c$ , and the necessary and sufficient condition for stable species coexistence  
158 then becomes (Barabas *et al.*, 2016):

$$159 \quad b_1 + c < 0. \quad (7a)$$

160 We thus structured our analysis in the following way – we took a 50 species competitive community  
161 where intraspecific competition coefficients, i.e., diagonal elements of  $\mathbf{C}$  were kept the same. The  
162 interspecific competitive interactions of  $\mathbf{B}$  were drawn from a random uniform distribution in a way  
163 that it either satisfied the Weyl's inequality or it did not. Typically, Weyl's inequality was fulfilled when  
164 intraspecific effects were much larger than all the interspecific effects (Barabas *et al.*, 2016); and the  
165 inequality of (7a) was not satisfied whenever random (but symmetric) interspecific interactions drawn  
166 from a uniform distribution had similar or higher values than intraspecific effects. When pairwise  
167 competitive interactions satisfied Weyl's inequality (7a), coexistence of all 50 species was stable (Fig.  
168 3C), and when it did not, coexistence was unstable (Fig. 3D).

169 Next, we wanted to evaluate the circumstances under which negative and positive HOIs could stabilize  
170 multispecies coexistence, when pairwise competitive interactions did not satisfy Weyl's inequality  
171  $b_1 + c_1 \not< 0$  (i.e. when pairwise species coexistence is destabilized). We assembled interspecific and  
172 intraspecific HOIs from random uniform distributions and investigated the effects on multispecies  
173 coexistence. In addition, we wanted to investigate whether HOIs can destabilize species coexistence  
174 when Weyl's inequality is fulfilled (i.e. species coexistence is stabilized by pairwise interactions).

## 175 3. Results

### 176 3.1 Negative higher-order interactions

177 In the simple pairwise interaction case, given a niche overlap of 0.5, coexistence between species 1  
178 and 2 was only possible when fitness differences between them ranged from 0 to 2. Beyond a fitness  
179 difference of 2, coexistence was not possible, as the invasion growth rate became negative.

180 Interestingly, we found that, when three-way HOIs were negative, invasion growth rate of species 1 was  
181 positive across the range of fitness differences, provided species 3 intensified intraspecific competition  
182 of species 2 ( $\beta_{223}$ ) more than it intensified interspecific competition ( $\beta_{123}$ ) (Fig. 1). However, if all  
183 negative three-way HOIs had the same magnitude, species coexistence was impossible even with low  
184 fitness differences (Fig. 1, symmetric case).

185 Negative four-way HOIs could also promote coexistence, even when fitness differences between two  
186 species were high, if their strength was an order of magnitude lower in comparison to inter and  
187 intraspecific pairwise competition and three-way higher order interactions (appendix B, Fig. B1-2,  
188 B5-6).

### 189 3.2 Positive higher-order interactions

190 Generally, positive three-way HOIs could lead to species coexistence despite substantial fitness difference  
191 between the two species and even in fitness regions where species coexistence is impossible if only  
192 pairwise interactions are considered (Fig. 2). For example, when species 3 alleviated intraspecific  
193 competition of species 2 ( $\beta_{223}$ ) more than it alleviated interspecific competition (of species 2 on 1),  
194 invasion growth rate of species 1 increased non-linearly, as fitness difference increased. This particular  
195 result could be understood by looking at the invasion growth rate of species 1 in the presence of  
196 non-zero  $\beta_{223}$  HOI (i.e. effect of species 3 on intraspecific interaction of species 2) while rest of the  
197 HOI terms are zero), which becomes:

$$198 r_1^* = 1 - \frac{\alpha_{12}}{(\alpha_{22} - \beta_{223} N_3^*)} \quad (8)$$

199 As fitness difference increased, due to  $\theta$  varying from 0 to 7 in (3), interspecific effect of species 2 on  
200 species 1 increased more rapidly than intraspecific competition of species 2. Because as  $\theta$  increases  
201 in (6), interspecific effects  $\alpha_{12}$  increases at the same rate as  $\theta$ , while intraspecific effects  $\alpha_{22}$  in (6)  
202 increases by  $2\sqrt{\theta}$ . With  $N_3^* = \frac{1}{\alpha_{33}} = 10$ ,  $\beta_{223}$  of 0.01 causes the invasion growth rate of species 1 (8)  
203 to increase rapidly as fitness difference increases. In all the cases, positive HOIs lead to high invasion  
204 growth rates.

205 Positive four-way HOIs led to species coexistence despite extreme fitness differences. As strength of  
206 positive four-way HOIs increased, invasion growth rate of species 1 when species 2 and species 3 are  
207 present, also increased (appendix Fig. B7-8).

### 208 3.3 Higher-order interactions and coexistence in a large competitive community

209 When Weyl's inequality was satisfied by pairwise competitive interactions, a 50 species community was  
210 feasible and stable in the absence of HOIs (Fig. 3 C). Failing to fulfil the inequality led to disruption  
211 of pairwise species coexistence (Fig. 3G).

212 Interestingly, in the presence of negative HOIs, even when Weyl's inequality was not fulfilled, coexistence  
213 of 50 species was possible provided intraspecific HOIs were stronger than interspecific HOIs (Fig. 3H,  
214 3J). When interspecific HOIs were stronger than intraspecific HOIs, coexistence of all 50 species was  
215 impossible, irrespective of whether Weyl's criteria was satisfied or not (Fig. 3D, 3A). Thus, failing to  
216 satisfy Weyl's criteria, stronger interspecific HOIs than intraspecific HOIs compounded the disruption  
217 of species coexistence.

218 Positive three-way HOIs led to unfeasible species densities when their magnitude was of similar strength  
219 to that of pairwise interactions. However, under certain parameter choices (low values of HOIs) of  
220 positive HOIs strength, coexistence of all 50 species was possible despite differences in strength of  
221 intraspecific or interspecific HOIs, provided Weyl's inequality was satisfied.

## 222 4. Discussion

223 While the assumption that interactions between species in a species rich community is inherently  
224 pairwise is pervasive in coexistence theory (Gallien *et al.*, 2017; Terhorst *et al.*; Levine *et al.*, 2017). The  
225 role of HOIs in stabilizing or destabilizing coexistence has been relatively understudied both empirically  
226 and theoretically (Letten & Stouffer, 2019; Grilli *et al.*, 2017; Baruah & John, 2019; Abrams, 1983).  
227 Lately, empirical understanding of species coexistence has been sought through modern coexistence  
228 theory where invading potential of a species in the presence of an established competitor species is  
229 explored (Grainger *et al.*, 2019). In this context, HOIs need to be elucidated clearly to fully understand  
230 multispecies coexistence, and the underlying mechanisms that leads to species coexistence (Levine  
231 *et al.*, 2017). Our study fills this gap by using concepts from modern coexistence theory (Chesson, 2000)  
232 to evaluate the effect of HOIs on species coexistence in a simple three species Lotka-Volterra model and  
233 in a more complex multispecies community. This study, in general, shows that HOIs promote species  
234 coexistence in parameter spaces where pairwise coexistence is unstable, provided certain conditions are  
235 fulfilled.

236 Using a three species Lotka-Volterra model, our results showed that positive HOI's stabilize coexistence  
237 across a wide range of fitness differences irrespective of differences in strength of inter- and intraspecific  
238 competition, while negative HOI's stabilize coexistence only if intraspecific competition was strengthened  
239 more than interspecific competition. If, however, in the case of negative HOIs, interspecific competition  
240 was strengthened more in relation to intraspecific competition (intraspecific HOIs < interspecific HOIs),  
241 species coexistence was impossible even when fitness differences were negligible. This particular result  
242 has been observed in another eco-evolutionary study, where negative density-mediated HOIs have been  
243 shown to promote multispecies coexistence (Baruah & John, 2019).

244 Positive HOIs lead to a decrease in the per-capita strength of competition between two species,  
245 while negative HOIs led to an increase in the per-capita strength of competition in our modelling  
246 scenario (Bailey *et al.*, 2016). Moreover, positive HOIs could lead to disproportionately high invasion  
247 growth rates, particularly when it alleviated intraspecific competition. Such high invasion growth rate  
248 could affect stability and lead to infeasible species densities (Terry *et al.*, 2018)(appendix Fig. C13).  
249 Importantly, when fitness differences between two species were extremely high, we believe positive  
250 HOIs could lead to species coexistence by decreasing interspecific competition more than intraspecific  
251 competition. For example, for extreme fitness difference between species 1 and species 2, say fitness  
252 difference of 3, positive HOIs ( $\beta_{123} = 0.01$ ), which decreased interspecific competition of species 2  
253 on species 1, will lead to species coexistence and proportionately low but positive invasion growth  
254 rate (Fig. 2). An earlier study had reported that HOIs could positively influence fitness of species by  
255 alleviating the dominating effect of neighboring species (Bailey *et al.*, 2016; Mayfield & Stouffer, 2017).

256 Our results suggested that invasion growth rates were generally sensitive to changes in the strength of  
257 HOIs, for both positive and negative HOIs (appendix Fig. C9), which suggests that parameter changes  
258 in HOIs has the potential to destabilize species coexistence. Hence under restricted parameter space,  
259 HOIs could stabilize species coexistence (AlAdwani & Saavedra, 2019). Four-way HOIs could lead  
260 to species coexistence across a range of fitness differences, if their direction was positive (appendix  
261 Fig. B3-4; B7-8). Negative four-way HOIs could also promote coexistence, provided their strength  
262 was an order of magnitude lower in comparison to pairwise interactions (appendix Fig. B1-2, B5-6).  
263 It is possible that four-way interactions could be prevalent in species communities, but empirically  
264 parameterizing such four-way interactions would be a difficult task (although see Mayfield & Stouffer  
265 (2017)). In addition, incorporating four-way HOIs in models parameterized from empirical data might  
266 not always provide additional explanatory power (AlAdwani & Saavedra, 2019).

267 In a multi-species community, pairwise coexistence rule does not hold (Barabas *et al.*, 2016; Saavedra  
268 *et al.*, 2017). However, multispecies coexistence could be understood by analyzing the Weyl's inequality  
269 (Fulton, 2000). When Weyl's inequality was not satisfied, pairwise species coexistence was impossible.  
270 In our models, positive HOIs decreased pairwise competition in a multispecies community, which  
271 consequently led to species coexistence provided self-regulation was strong (Mayfield & Stouffer, 2017)  
272 and Weyl's inequality was satisfied (appendix Fig. C13, column  $b_1 + c_1 < 0$ ). When Weyl's equality was

273 not satisfied, species coexistence was destabilized both with pairwise and with positive HOIs. Pairwise  
274 coexistence in such a scenario was disrupted particularly because strength of intraspecific competition  
275 was on average lower than interspecific competition between species. However, surprisingly, even in  
276 such a scenario, negative HOIs could still stabilize species coexistence. Particularly, if intraspecific  
277 HOIs was strictly greater than interspecific HOIs, species coexistence in a large competitive community  
278 was stabilized. This is analogous to the two-species coexistence rule, that species must limit themselves  
279 more than they limit competitors. In general, the simplest way to generalize multispecies coexistence  
280 in the presence of negative HOIs was that – when pairwise coexistence for multispecies community was  
281 impossible (Weyl’s inequality not satisfied), intraspecific competition should be strengthened more than  
282 interspecific competition by HOIs. If even a single species in the multispecies community violated this  
283 rule, coexistence in the multispecies community was disrupted, even in the presence of HOIs (appendix  
284 Fig. C11). On the contrary, when pairwise multispecies coexistence was possible (Weyl’s inequality  
285 was satisfied and pairwise intraspecific effects were substantially larger than interspecific effects),  
286 having intraspecific HOIs that had similar strength as interspecific HOIs could still stabilize species  
287 coexistence (appendix Fig. C12). This particular result was also reiterated by another study that dealt  
288 with eco-evolutionary processes that might emerge when species in a large competitive community  
289 had density-mediated HOIs (Baruah & John, 2019). The study showed that when negative HOIs were  
290 present, species not only coexisted but their traits also evolved to be very similar. Moreover, species  
291 structured themselves in a trait axis over evolutionary time in a way that negative HOIs strengthened  
292 pairwise intraspecific competition more than it intensified interspecific competition (Baruah & John,  
293 2019). Furthermore, from our simple three-species results, we observed that positive HOIs could lead  
294 to disproportionately high invasion growth rates and henceforth might negatively affect stability (Terry  
295 *et al.*, 2018, 2017).

296 Lotka-Volterra models of competition have been extensively used to understand mechanisms that could  
297 promote species coexistence through pairwise interactions (Barabas *et al.*, 2016; Hart *et al.*, 2016)  
298 and through HOIs (Wilson, 1992; Bairey *et al.*, 2016; Letten & Stouffer, 2019). Using Lotka-Volterra  
299 models, our results add to this emerging body of knowledge on HOIs and the prospect of extending  
300 simple tractable dynamics to understanding complex multispecies dynamics (Wilson, 1992; Bairey  
301 *et al.*, 2016; Letten & Stouffer, 2019; Baruah & John, 2019; Grilli *et al.*, 2017; Terry *et al.*, 2017). It is  
302 straightforward, although challenging, to estimate pairwise competition coefficients from experiments  
303 that involve manipulating competitor densities, or from long term observational field data. However,  
304 there are other obstacles in estimating higher-order coefficients and in understanding their effects on  
305 species coexistence (Mayfield & Stouffer, 2017). For instance, to implement a higher-order model  
306 empirically with just three competitors would require no less than 27 parameters at the very least.  
307 To collect such amount of empirical data whether observational or experimental is an enormous  
308 task. Nonetheless, invasion growth rates could be estimated from empirical data that are used to  
309 parameterize community models or mechanistic competition models by explicitly incorporating HOIs  
310 (Tilman, 1994; Letten & Stouffer, 2019).

311 Although we have much to understand about the effects of HOIs empirically, it is clear that effects of  
312 HOIs on species coexistence is dependent on their strength as well as on their direction. That being  
313 said, HOI terms in ecological models could increase the number of equilibrium points exponentially,  
314 though such equilibrium points can be ecologically feasible only under a restricted set of parameter  
315 space (AlAdwani & Saavedra, 2019).

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374 **Figures:**

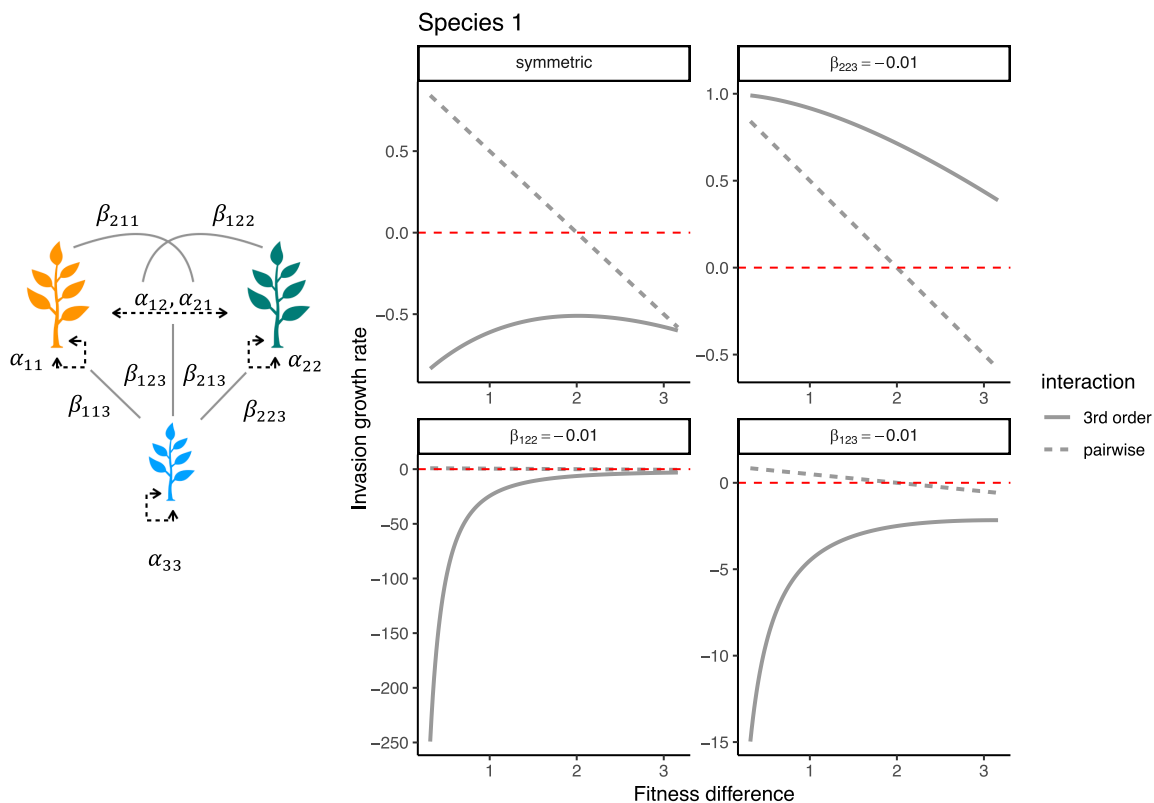


Figure 1: Invasion growth rate (Y-axis) of species 1 (top row) for pairwise species competition (dashed grey lines) and negative three-way HOIs (grey solid lines) for a range of fitness difference (X-axis). The red-dashed line marks the y-intercept at zero. Each panel of the plot compares invasion growth rate of species 1 under pairwise competition and under negative three-way HOIs, with the panel label referring to the values of the HOI terms. For instance, the panel “symmetric” would mean that all the HOI terms in the HOI matrix have the exact same magnitude of -0.01; and the panel  $\beta_{223} = -0.01$  (top row, species 1) would mean all the elements of HOI matrix are zero except  $\beta_{223}$  which is at -0.01 (i.e., more negative would mean more increase in strength of intraspecific competition of species 2,  $\alpha_{22}$ ). Panels  $\beta_{122} = -0.01$  and  $\beta_{123} = -0.01$ , would mean all terms of HOI matrix are zero except  $\beta_{122}$  and  $\beta_{123}$  respectively. Note that invasion growth rate of species 1 (top row) was negative across the range of fitness difference in negative three-way HOIs when interspecific competition was intensified more than intraspecific competition (panels:  $\beta_{122}$  and  $\beta_{123}$  for species 1).

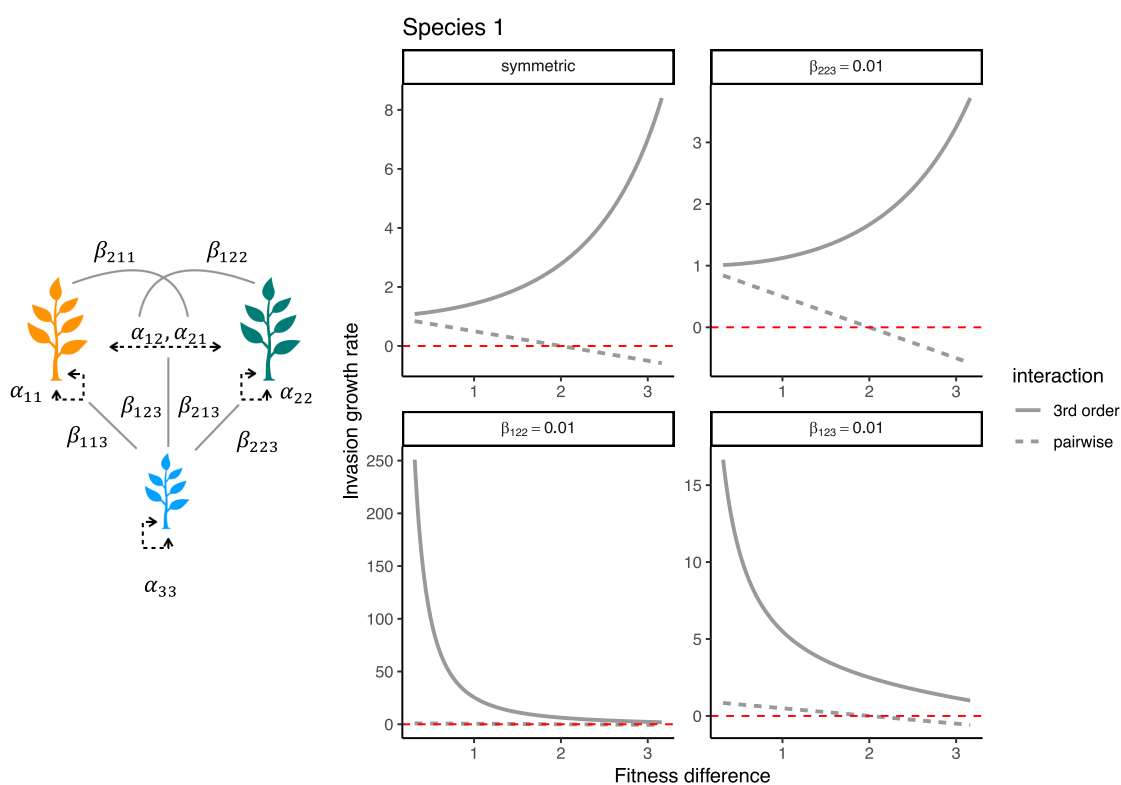


Figure 2: Figure. 2: Invasion growth rate (Y-axis) of species 1 (top row) for pairwise species competition (dashed grey lines) and positive three-way HOIs (grey solid lines in the figure) shown for a range of fitness difference (X-axis). The red-dashed line marks the y-axis at zero invasion growth rate. The panel label refers to the values of the terms in the HOI matrix. For instance, the panel “symmetric” would mean that all the HOI terms in the HOI matrix have the exact same magnitude of 0.01; and the panel  $\beta_{223} = 0.01$  (top row, species 1) would mean all the elements of HOI matrix are zero except  $\beta_{223}$  which is at 0.01 (i.e., more positive and hence more decrease in strength of intraspecific competition of species 2,  $\alpha_{22}$ ). Panel  $\beta_{122} = -0.01$  and panel  $\beta_{123} = 0.01$ , would mean all terms of HOI matrix are zero except  $\beta_{122}$  and  $\beta_{123}$  respectively. Note that invasion growth rate of species 1 (top row) was positive across the range of fitness difference in positive three-way HOIs (panels:  $\beta_{122}$  and  $\beta_{123}$  for species 1).

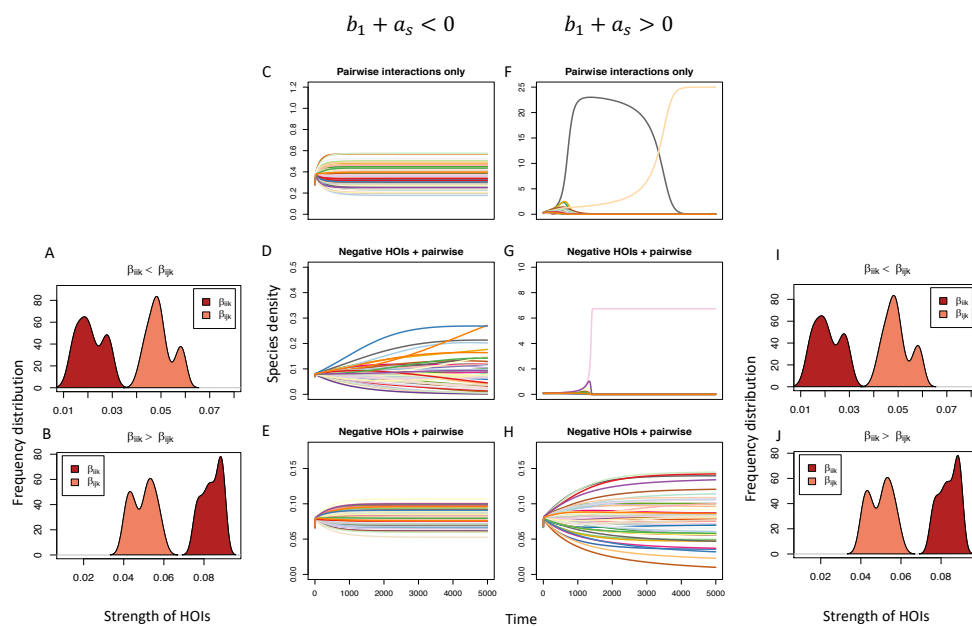


Figure 3: Figure 3: Multispecies coexistence in the presence and absence of negative HOIs that either satisfy Weyl's inequality ( $b_1 + a_s < 0$ ) or do not ( $b_1 + a_s > 0$ ). When 50 species in a competitive community compete in pairwise manner, and satisfies Weyl's inequality (C) species coexistence was always stabilized. However, in the presence of negative HOIs where interspecific HOIs were strictly stronger than intraspecific HOIs, i.e.,  $\beta_{ijk} > \beta_{iik}$  (A), species coexistence was destabilized (D), while when the opposite happens, i.e.,  $\beta_{iik} > \beta_{ijk}$  (B), which suggests intraspecific HOIs to be stronger than interspecific HOIs, species coexistence was again stabilized (E). When Weyl's inequality was not satisfied, ( $b_1 + a_s > 0$ ) (F), pairwise coexistence was impossible (F). However, in the presence of negative HOISs and if intraspecific HOIs were stronger than interspecific HOIs,  $\beta_{iik} > \beta_{ijk}$  (J), species coexistence was then stabilized (H), but disrupted again (G) if interspecific HOIs were stronger than intraspecific HOIs (I).