

1 **Intraspecific variation promotes species coexistence and trait clustering through higher**
2 **order interactions**

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4 Gaurav Baruah¹, Robert John²

5 ¹ University of Zurich, Department of Evolutionary biology and Environmental studies

6 ² Indian Institute of Science Education and Research, Kolkata

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8 **Correspondence e-mail:**

9 gaurav.baruah@ieu.uzh.ch

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29 **Abstract**

30 Ecological and evolutionary effects of individual variation on species coexistence remains
31 unclear. Competition models for coexistence have emphasized species-level differences in
32 pairwise interactions, and invoked no role for intraspecific variation. These models show that
33 stronger competitive interactions result in smaller numbers of coexisting species. However,
34 the presence of higher-order interactions (HOIs) among species appears to have a stabilizing
35 influence on communities. How species coexistence is affected in a community where both
36 pairwise and higher-order interactions are pervasive is not known. Furthermore, the effect of
37 individual variation on species coexistence in complex communities with pairwise and HOIs
38 remains untested. Using a Lotka-Volterra model, we explore the effects of intraspecific
39 variation on the patterns of species coexistence in a competitive community dictated by
40 pairwise and HOIs. We found that HOIs greatly stabilize species coexistence across different
41 levels of strength in competition. Notably, high intraspecific variation promoted species
42 coexistence, particularly when competitive interactions were strong. However, species
43 coexistence promoted by higher levels of variation was less robust to environmental
44 perturbation. Additionally, species' traits tend to cluster together when individual variation in
45 the community increased. We argue that individual variation can promote species coexistence
46 by reducing trait divergence and attenuating the inhibitory effects of dominant species
47 through HOIs

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54 **Introduction**

55 Explanations for multi-species coexistence in ecological communities have largely been
56 sought at the species level by emphasizing average life history differences among species
57 driven by competitive interactions or trade-offs (Clark 2010a; Gravel et al. 2011; Violle et al.
58 2012; Kraft et al. 2015; Valladares et al. 2015; Letten et al. 2017; Wittmann and Fukami
59 2018). Such differences among species in multiple ecological dimensions could minimize
60 niche overlap and promote long-term species coexistence (Clark et al. 2010; Barabás and
61 D’Andrea 2016; Barabás et al. 2016). However, clear niche differences among species has
62 rarely been found, and in fact large numbers of species appear to compete for only a small
63 number of limiting resources, giving rise to a paradox (Hutchinson 1961; Laird and Schamp
64 2006; Shoresh et al. 2008; Li and Chesson 2016; Letten et al. 2018). Many species coexist
65 despite little measurable difference in demographic or resource-based niches (Condit et al.
66 2006). So, although there are strong theoretical arguments that average differences among
67 species can account for species coexistence, empirical support has remained scanty.

68 Classical competition models of coexistence consider interactions among species
69 pairs that require precise parameter trade-offs to stabilize communities or to limit the
70 strength of competition in accordance with the competitive exclusion principle (Barabás and
71 Meszéna 2009; Barabás et al. 2016). The implausibility of highly structured competitive
72 relationships in species-rich communities has prompted models of coexistence based on
73 ecological equivalence rather than life historical differences (Hubbell 2006; Rosindell et al.
74 2011; Segura et al. 2011). Theoretical studies with competition models further show that any
75 stability achieved through structured pairwise competitive interactions can be disrupted by
76 random interactions among species (Allesina and Levine 2011; Bairey et al. 2016; Barabás et

77 al. 2016). The number of coexisting species then declines inversely with the strength of
78 interactions among species pairs (Bairey et al. 2016). Interaction strength therefore places an
79 upper bound on the numbers of coexisting species, implying that strong pairwise competitive
80 interactions alone cannot promote species coexistence in a large community.

81 Interactions among species are not always constrained to species pairs but can involve
82 higher-order combinations (Wilson 1992; Laird and Schamp 2006; Bairey et al. 2016; Grilli
83 et al. 2017; Mayfield and Stouffer 2017; Terry et al. 2017) , where interactions between a
84 species pair is modulated by a third or more species (Fig. 1). In an ecological system where
85 communities are structured by pairwise interactions indirect or higher-order effects may alter
86 these interactions and restructure communities (Terhorst et al. n.d.; Levine et al. 2017). For
87 example, a species that is a superior competitor for a given resource can inhibit an inferior
88 competitor for the same resource, but a third species may modulate the strength of this
89 inhibition without affecting either of the two competitors directly (Bairey et al. 2016). Such
90 attenuation of the pairwise inhibitory effect can be density-mediated or trait-mediated, and
91 can lead to qualitatively different community dynamics compared to pure pairwise
92 interactions. The importance of such higher-order interactions has been recognised (Levine
93 et al. 2017), but the singular focus of coexistence studies on average species level differences
94 has meant that few investigations have been undertaken.

95 A further consequence of the emphasis on species-level differences is that within-
96 species or individual level variation has largely been ignored (Siefert 2012; Hart et al. 2016).
97 Observations that variation within species often exceeds the differences in species-level
98 averages have inspired much theoretical and empirical research (Barabas and D'Andrea
99 2016; Barabás et al. 2016; Hart et al. 2016; Hausch et al. 2018). Intraspecific variation can
100 have both ecological and evolutionary effects on competitive interactions, and therefore on
101 species coexistence. For example, intraspecific trait variation can hamper species coexistence

102 by increasing competitive ability, niche overlap and even-spacing among species (Barabas
103 and D'Andrea 2016), or by altering competitive outcomes through non-linear averaging of
104 performances (Hart et al. 2016). There is equally compelling evidence that intraspecific
105 variation promotes species coexistence, mainly through disruption of interspecific
106 competitive abilities and obscuring the effect of strongly competitive individuals in a
107 community (Bolnick et al. 2011). Experimental work has shown that while intraspecific
108 variation allows a community to be resilient to invaders, may create the opportunity for
109 competitive exclusion among strong competitors (Hausch et al. 2018). Empirical studies have
110 consistently found that most of the variation in plant life histories lies within individuals
111 rather than species. Tree growth rates vary remarkably within individuals (Rüger et al. 2011,
112 Clark 2010), and variation may be driven by several factors including light, soil resources,
113 herbivores, and pathogens, that affect growth. High intraspecific variation in leaf economics
114 such as specific leaf area, leaf N and P, may be driven by how individuals tap the variation
115 along these dimensions (Meziane and Shipley 1999; Vasseur et al. 2012). In multi-species
116 communities diversity appears to be positively correlated with intraspecific variability
117 (Fridley and Grime 2010). Conversely, the loss of individual trait variation in plant
118 communities could lead to increases in susceptibility to plant invasions (Crutsinger et al.
119 2007). Given that high levels of intraspecific trait variation within communities appears to be
120 more a rule than an exception, the combined influence of intraspecific variation, and pairwise
121 and higher-order species interactions on diversity and community structure merits detailed
122 investigation.

123 Theoretical research on species coexistence has largely focused on the importance of
124 higher-order species interactions and intraspecific variation separately. The effect of
125 intraspecific trait variation and eco-evolutionary dynamics on structuring large communities
126 where both pairwise and higher-order interactions dominate a community is unknown. Purely

127 pairwise interactions in a community may lead to even trait spacing when intraspecific
128 variation is high. Consequently, competitive exclusion of inferior species in a large
129 community becomes inevitable (Fig. 1). However, a community dominated by both pairwise
130 and higher-order interactions could lead to less-even spacing of species in a trait axis and
131 result in trait clustering. This could occur because with high intraspecific variation present in
132 the community, higher-order interactions could significantly alleviate and stabilize the
133 negative pairwise interactions that lead to distinct spacing in the first place. The link between
134 HOIs and intraspecific variation therefore appears critical to understand coexistence in
135 species-rich communities.

136 Here in this study, we examine the importance of higher order interactions and
137 intraspecific variation in structuring species coexistence and trait patterning. We do this using
138 a modified Lotka-Volterra modelling approach, where the dynamics of the whole community
139 is mediated both by pairwise competitive interactions as well as higher-order three-way
140 interactions. Specifically, we model a one-dimensional quantitative trait that contributes to
141 the competitive ability of species interacting in the community. We show that in the presence
142 of higher-order interactions, high intraspecific variation across different levels of strength in
143 competition leads to significantly greater numbers of species coexisting in a community than
144 when individual variation is low. We show analytically and with model simulations that
145 intraspecific variation not only contributes to species coexistence, but also stabilizes the
146 community to external perturbation. In addition, our analyses reveal that intraspecific
147 variation in a community where higher-order interactions dictates dynamics leads to stable
148 trait clustering. Our study links the recent ecological studies of higher-order interactions with
149 eco-evolutionary dynamics and intraspecific variation.

150

151 **2. Methods and Models**

152 *2.1 Community model with pairwise interactions*

153 In our community model, we consider species competing with each other in a one-
154 dimensional trait axis, where a species' competitive ability is determined by a one-
155 dimensional quantitative trait z . Individuals of a species vary along the competitive trait z of
156 interest such that the distribution of the primary trait z is normally distributed with mean u_i
157 for species i and variation given by σ_i^2 . Under such conditions, the dynamics of a species i is
158 given by Lotka-Volterra equations as (Barabas and D'Andrea 2016):

159

$$\frac{dN_i}{dt} = N_i(t) \left(b_i(t) - \sum_j^s \alpha_{ij}(t) N_j(t) \right). \quad (1)$$

160 And the dynamics of the mean competitive trait u_i is given by:

$$\frac{du_i}{dt} = h_i^2 \sigma_i^2(t) \left(\overline{b_i(t)} - \sum_j^s \beta_{ij}(t) N_j(t) \right), \quad (2)$$

161 where $\alpha_{ij}(t)$ describes the pairwise competition coefficient of species i with species j at any
162 time t . This competition coefficient derives directly from Gaussian competition kernel (See
163 appendix 2). If the two species are similar to each other in terms of their average trait value u ,
164 then competition between them is stronger than when they are farther apart in the trait axis;
165 h_i^2 is the heritability of species i , $b_i(t)$ describes the growth rate of the species i in the
166 absence of any competition which is determined by where they lie in the trait axis z ; $\overline{b_i(t)}$
167 describes the growth of the trait and $\beta_{ij}(t)$ quantifies the evolutionary pressure on the trait z
168 of species i due to competition with the species j in the community (this has been derived in
169 Barabas et al, 2016).

170

171 *2.2 Community model with higher-order interactions*

172 The above equations 1 and 2, captures the eco-evolutionary dynamics of a multispecies
 173 community where pairwise interactions dominate community dynamics. It is still plausible
 174 that such a community exhibits higher-order interactions than just between pairs of species.
 175 In extension to the above model, we include density-mediated three-way higher-order
 176 interactions where density of a third species influences pairwise competitive interactions.
 177 Under these circumstances, the equations become (see appendix 2):

178

$$179 \quad \frac{dN_i}{dt} = N_i(t) \left(b_i(t) - \sum_j^S \alpha_{ij}(t) N_j(t) - \sum_j^S \sum_k^S \epsilon_{ijk}(t) N_j(t) N_k(t) \right). \quad (3)$$

180

181 And the dynamics of the competitive trait u_i is given by:

$$182 \quad \frac{du_i}{dt} = h_i^2 \sigma_i^2 \frac{\partial}{\partial u_i} \left(\frac{1}{N_i} \frac{dN_i}{dt} \right),$$

$$183 \quad = h_i^2 \sigma_i^2 u_i(t) \left(\overline{b_i(t)} - \sum_j^S \beta_{ij}(t) N_j(t) - \sum_j^S \sum_k^S \gamma_{ijk}(t) N_j(t) N_k(t) \right), \quad (4)$$

184

185 where $\epsilon_{ijk}(t)$ gives the 3-way interactions that are density mediated HOIs (ϵ_{ijk} is termed
 186 inter-specific HOIs and ϵ_{iii} , ϵ_{ijj} termed as intraspecific HOIs) (Mayfield and Stouffer 2017;
 187 Letten and Stouffer 2019) ; γ_{ijk} denotes 3-way interactions (γ_{ijk} as interspecific
 188 evolutionary effects; γ_{iii} , γ_{ijj} as intraspecific evolutionary HOI effects) affecting evolutionary
 189 dynamics of mean trait u for species i . Similar to the pairwise Gaussian interaction kernel, the
 190 three way interaction remains Gaussian with a third species k influencing the interaction
 191 between the two species i and j given as (see appendix 2):

$$192 \quad \epsilon_{ijk}(t) = N_k(t) \frac{w}{\sqrt{2\sigma_i^2 + 2\sigma_j^2 + w^2}} e^{-\frac{(u_i(t) - u_j(t))^2}{2\sigma_i^2 + 2\sigma_j^2 + w^2}} = N_k(t) \alpha_{ij}(t),$$

193 And, $\gamma_{ijk}(t)$ can be written as (appendix 2):

$$194 \quad \gamma_{ijk}(t) = N_k(t) \frac{2w(u_i(t)-u_j(t))}{(2\sigma_i^2+2\sigma_j^2+w^2)^{\frac{3}{2}}} e^{-\frac{(u_i(t)-u_j(t))^2}{2\sigma_i^2+2\sigma_j^2+w^2}} = \beta_{ih}(t)N_k(t),$$

195 Where, $\epsilon_{ijk}(t)$ and $\gamma_{ijk}(t)$ are three-dimensional tensors of size (S x S x S), where S is the
196 total number of species in the community. Thus we can formally define intraspecific HOIs as
197 $\epsilon_{iik}(t)$ and $\epsilon_{iii}(t)$ and interspecific HOIs as $\epsilon_{ijk}(t)$. σ_i^2 and σ_j^2 are the intraspecific trait
198 variation for species i and species j respectively; w^2 is the width of the competition kernel
199 which is Gaussian (see appendix 2); $u_i(t)$ is the average trait value of species i and $u_j(t)$ is
200 the average trait value for species j . Thereby, eco-evolutionary dynamics in this purely
201 competitive community is dominated not only by pairwise trait-based competition but also by
202 three-way higher-order interactions. In such a case, eco-evolutionary dynamics might deviate
203 from dynamics dominated by purely pairwise competitive coefficients as in (Barabas and
204 D’Andrea 2016). For details of the formulation see appendix 1-2.

205 We must add that until now HOIs and evolutionary dynamics have not been
206 considered together. The role of HOIs and their links with evolutionary dynamics needs to be
207 evaluated rigorously to understand the implications for species coexistence and our models
208 could constitute a first step in that effort. We make our HOIs density dependent purely for
209 mathematical simplicity, and although density-mediated HOIs could be prevalent in nature,
210 we have no reason to presume that it is the norm. The importance of HOIs in mediating plant
211 species coexistence has for long been suspected. There is compelling evidence for the role of
212 soil microorganisms in stabilizing plant-plant interactions and promoting species coexistence
213 through pervasive plant soil feedbacks (Crawford et al. n.d.) .Here coexistence for pairs of
214 plant species could be mediated by interactions with mycorrhizal species, or native microbes
215 that play functional roles as pathogens or symbionts. For example, strong resource
216 competition between a species pair may result in exclusion of the weaker competitor, but a
217 third species may modulate the strength of the competitive interactions by modifying

218 resource availability (Hawkes et al. 2005; Hinsinger et al. 2009) and reduce the fitness
219 difference allowing for species coexistence.

220

221

222 *2.3 Species coexistence in higher-order competition models with and without intraspecific*
223 *variation*

224 Using the three-way interactions community model (see section 2.2 above), we assess the
225 influence of intraspecific trait variation on species coexistence. We examine analytically and
226 compare species richness in this multispecies community model with and without
227 intraspecific variation. For mathematical simplicity, in this section, we assume that
228 intraspecific variation is same for all the species in the community such that $\sigma_i^2 = \sigma_j^2 = \sigma^2$.

229 Based on strictly pairwise and three-way interactions in a diverse community, Bairey et al.
230 (2016) derived an upper bound for species richness. Accordingly, a diverse multispecies
231 community with pairwise as well as three-way interactions will follow (appendix 3):

232
$$S = \frac{1 - \epsilon_{ijk}}{\alpha_{ij}}.$$

233 Hence the ratio of species richness with and without intraspecific variation (see appendix 3)
234 will follow:

235
$$\frac{S_{var}}{S} = \frac{\left(\frac{1 - \epsilon_{ijk}}{\alpha_{ij}}\right)}{\frac{1 - \epsilon'_{ijk}}{\alpha'_{ij}}}, \quad (5)$$

236 Where $\epsilon'_{ijk}, \alpha'_{ij}$ are three way and pairwise interactions without intraspecific variation, *i.e.*,
237 $\sigma_i^2 = \sigma_j^2 = 0$ and S_{var} and S are species richness in the community with and without
238 intraspecific variation respectively. Bairey et al. 2016 derived the expression of species
239 richness S based on competition kernels with independent random variables. Their HOI
240 terms were randomly drawn from a uniform distribution. Our equation 5 is based on gaussian

241 competition kernels that are determined by average trait values of species. The trait values of
242 species that are picked in starting a community are however drawn randomly from a uniform
243 distribution (see section 2.4). The strength of competition between species is then dependent
244 on the starting trait values. Hence, our derivation of equation 5 still holds and is a subset of
245 the larger case presented in Bairey et. al 2016. We analyse the results from simulations of our
246 model with this derived analytical solution of species richness, with and without intraspecific
247 variation (see results).

248

249 *2.4 Simulations of the community model with higher-order interactions*

250 We assessed the effect of different levels of intraspecific trait variation on community
251 structure and species coexistence using data generated from simulations of our community
252 model. We simulated both trait dynamics and population dynamics resulting from equations
253 (3) and (4). Initial species number for the start of each simulation was 40. All the 40 species
254 were randomly assigned an initial trait value within -0.5 to 0.5 in the trait axis. Outside this
255 trait regime, fitness value of a species will be extreme and growth rate will be negative.
256 Effectively, this strict criterion qualitatively means that outside this trait boundary resource
257 acquisition by a species is too low to survive and have positive growth rate. We carried out
258 45 replicate simulations for each level of intraspecific variation. We also simultaneously
259 tested the influence of the width of the competition kernel, which signifies the strength of
260 pairwise interaction, using a full factorial design where all possible combinations of
261 intraspecific variation and interaction strength were examined for their influence on species
262 coexistence. In all our simulations, heritability h_i^2 of the trait for all species was fixed at 0.1.

263 We evolved our community for a maximum of 1×10^4 time points, but we concluded
264 each simulation when the community had reached a stable state. We assumed that the
265 community attained a stable state if the ratio of minimum value of the entropy of the

266 community given by, $-\sum N_i \log(N_i)$, at two different time points, 500 units apart ($\Delta t =$
267 500), remained bounded within 10^{-5} . This condition was checked when the community had
268 evolved for more than 5×10^3 time points. If this condition was not met, we kept the
269 simulation going for another 5×10^3 time points before checking for the same condition. This
270 condition was however met at almost every simulation indicating the tendency for
271 convergence toward stable species density values.

272

273 *2.4.1 Levels of width of the competition kernel and intraspecific variation*

274 The width of the competition kernel w , (see appendix 2) was varied from 0.2 through 0.45
275 with increments of 0.05. For each w , three different levels of intraspecific variation were
276 tested in a fully factorial manner (6 different w values \times 3 different σ^2 values \times 45
277 replicates). Specifically, for each w , intraspecific variation for each of the 40 species in the
278 community was randomly sampled from a uniform distribution with three different levels: a)
279 low variation: $\sigma^2 = [0.0006, 0.003]$; b) intermediate variation: $\sigma^2 = [0.003, 0.009]$; and c)
280 high variation: $\sigma^2 = [0.01, 0.05]$ (See Table 1, for parameters used).

281 *2.5 Trait clustering:*

282 Theoretical models have suggested that species coexisting together tend to spread more
283 evenly along a trait axis than expected (Barabas and D'Andrea 2016; D'Andrea and Ostling
284 2016a). However, empirical studies have shown that it is possible for species clusters to
285 emerge along a trait axis (Segura et al. 2011; Vergnon et al. 2012). Here, we use a
286 quantitative metric to evaluate the effect of intraspecific variation on the patterning of traits
287 in the trait-axis. We measured trait similarity among coexisting species by measuring the
288 coefficient of variation (CV) of adjacent trait means (D'Andrea and Ostling 2016a). High
289 values of CV would indicate clustering of trait means of species in the trait axis while lower

290 CV values would indicate even spacing of traits. In addition, we also compared results from
291 trait clustering in the presence and absence of HOIs (see appendix 4).

292

293 *2.6 Stability and robustness measures of species coexistence*

294 Stability of our community model with higher-order interactions was measured by calculating
295 the Jacobian at equilibrium. Specifically, the Jacobian of our dynamical system at a given
296 point is (see appendix 5):

297

$$J_{ij} = \delta_{ij} \left(b_i - \sum_j^s \alpha_{ij} N_j - \sum_j^s \sum_k^s \epsilon_{ijk} N_j N_k \right) + (-1) N_i \alpha_{ij} \\ + (-1) N_i \sum_k (\epsilon_{ijk} + \epsilon_{ikj}) N_k$$

298

299 where, δ_{ij} is the Kronecker delta. At the end of our simulations, it is possible that all the
300 species coexist, but for the community to be locally stable, the eigenvalues of the Jacobian at
301 that point must all be negative. Thereafter, we measured the average robustness of the
302 community by taking the geometric mean of the absolute values of the eigenvalues of the
303 Jacobian (May 1973) (see appendix 3). Alternatively, one could calculate average robustness
304 by the determinant of the Jacobian and that would also yield the same quantity as taking the
305 geometric mean of the absolute values of the eigenvalues of the Jacobian. Specifically, this
306 quantity measures the average return times in response to environmental perturbation for
307 each of the species in the community. For each replicate simulation of each level of
308 intraspecific variation, we calculated the average community robustness as the measure to
309 evaluate how intraspecific variation affected robustness of species coexistence. Here, low
310 values of average community robustness indicate lower stability.

311

312 **3. Results**

313 *3.1 Analytical solution for the three-way competition model with and without intraspecific* 314 *variation*

315 We found that communities with higher intraspecific variation resulted in greater numbers of
316 coexisting species than communities that had no intraspecific variation (Fig. 3). At low levels
317 of intraspecific variation, the ratio of species richness with and without intraspecific variation
318 was around 1. But as intraspecific variation increased, the ratio $\frac{S_{var}}{S}$ also increased
319 significantly (Fig. 3).

320

321 *3.2 Effect of intraspecific variation and strength in competition on species coexistence*

322 We found that (see above) with increases in intraspecific variation, the numbers of coexisting
323 species increased. When we tested the interaction between competition and intraspecific
324 variation, we found that at low levels of competition w , the effect of intraspecific variation on
325 species coexistence was minimal, particularly for $w = 0.2$ and $w = 0.25$. But as the intensity
326 of competition increased, we observed intraspecific variation had a stabilizing effect on
327 species coexistence. At high levels of competition w , high intraspecific variation allowed a
328 greater number of species to coexist on the trait axis (Fig. 2, Fig. 3).

329

330 *3.3 Trait clustering*

331 The coefficient of variation (CV) of trait values increased as intraspecific variation increased
332 in the presence of HOIs, only for certain values of strength of competition (Fig. 4).
333 Particularly, in comparison to low intraspecific variation, high intraspecific variation across
334 different competition levels resulted in high CVs of trait values (Fig. 4). In the absence of
335 HOIs, however, trait clustering decreases as intraspecific variation increased.

336

337 *3.4 Robustness of species coexistence*

338 With increases in intraspecific variation, average robustness of the community decreased.

339 The community became less robust to external perturbation with increasing intraspecific trait

340 variation when compared with a community where intraspecific variation was low (Fig. 5).

341

342 **4. Discussion**

343 The importance and consequences of high intraspecific variation for species diversity and

344 community structure is intensely debated (Clark 2010*b*; Clark et al. 2010; Violle et al. 2012),

345 with contrasting findings being reported. Some studies have shown that the ecological and

346 evolutionary consequences of individual variation are to weaken species coexistence

347 (Barabas and D'Andrea 2016; Hart et al. 2016). Others have argued that high levels of

348 intraspecific variation indicate that species differ primarily in the way individuals within

349 species respond to environmental variation along multiple hidden niche dimensions. Such

350 variable individual responses ensure that intraspecific effects are stronger than interspecific

351 effects, a condition needed for stable species coexistence (Chesson 2000; Barabás et al.

352 2016). However, the nature of competitive interactions appears to be critical in determining

353 the consequences of intraspecific variation. We investigated the ecological and evolutionary

354 effects of intraspecific variation on coexistence in communities with both pairwise and HOIs

355 and found strong evidence for the stabilizing effect of intraspecific variation on species

356 coexistence.

357 The assumption that pairwise interactions between species are sufficient to describe

358 competition in a community is ubiquitous in coexistence theory (Levine et al. 2017). Here,

359 strong competition (e.g., for shared limiting resources) between pairs of species would drive

360 species apart in niche space, structure communities, and maintain diversity. However, there is

361 little evidence that the observed species-level differences in mean demographic rates (Condit
362 et al. 2006) or resource use are sufficient to explain species coexistence (John et al. 2007).
363 Here, we found strong stabilizing effect of individual variation in structuring patterns of
364 species coexistence, provided that species interactions are mediated through HOIs.

365 In mechanistic models of competition where the underlying biology is modelled
366 explicitly, HOIs can emerge subsequently in the process (Abrams 1983; Letten and Stouffer
367 2019). Where HOIs have been explicitly modelled in phenomenological ecological models,
368 they act as a stabilizing factor in maintaining species diversity (Bairey et al. 2016; Grilli et al.
369 2017). We modelled the evolution of a trait that dictates competitive ability between species
370 and introduced higher order competitive interactions where pairwise interactions were
371 modulated by the density of a third species. Consistent with earlier studies on the role of
372 HOIs (Wilson 1992; Bairey et al. 2016; Grilli et al. 2017) we found that such interactions
373 greatly stabilize the dynamics of species in the community. Expectedly, purely pairwise
374 interactions led to lower numbers of coexisting species as the strength of pairwise
375 competitive interactions increased (Bairey et al. 2016) (Fig A3). In addition, as intraspecific
376 variation increased, analogous to the results in Barabas and D'Andrea (2016), species
377 richness in pairwise community decreased significantly (Fig A3).

378 A strong competitor in the trait axis can negatively affect the growth of inferior
379 competitors. This results in a disproportionately higher abundance for the dominant
380 competitor compared to inferior one. However, our results suggest that with the introduction
381 of three-way interactions, this dominance of the competitively superior species is
382 significantly reduced due to the presence of the third species, leading to proportionately
383 similar densities for all the three species (Fig.1, Fig. A1). Our eco-evolutionary model that
384 includes HOIs leads to stable coexistence of almost all distinct phenotypes, particularly when
385 competitive interactions are weak. With increases in the strength of pairwise competition,

386 higher heritable individual variation in the phenotypes stabilized ecological dynamics and led
387 to higher numbers of coexisting species. HOIs that could emerge in species-rich competitive
388 systems have not been well explored in the context of species coexistence (Saavedra et al.
389 2017). Although, empirical studies on quantifying HOIs in natural ecosystems is exceedingly
390 difficult (Mayfield and Stouffer 2017), ignoring such interactions would limit fundamental
391 understanding of the mechanisms behind species coexistence in complex communities.

392 Our results show that greater levels of intraspecific variation can lead to higher
393 species richness, but this effect was more prominent when pairwise competition was strong
394 ($w > 0.25$) (Fig. 2-3). Earlier studies have shown that the numbers of species that coexists
395 stably in eco-evolutionary models incorporating purely pairwise interactions are always less
396 than the number of species that coexists in the absence of evolutionary dynamics (Edwards et
397 al. 2018). With sufficient intraspecific variation, a species can evolve into a uninvincible
398 phenotype that can lead to significant increases in its density. Consequently, the species with
399 uninvincible phenotypes could easily displace other species in the community (Barabas and
400 D'Andrea 2016; Edwards et al. 2018). However, with the inclusion of three-way HOIs and
401 sufficient intraspecific variation the increase in density of superior species is significantly
402 limited, resulting in a higher number of coexisting species. With purely pairwise interactions,
403 eco-evolutionary models with higher intraspecific trait variation would lead to greater overlap
404 in the trait axis and species would limit other species more than they limit themselves.
405 Consequently, the number of species coexisting with high intraspecific variation decreases
406 substantially (Fig A3). Under pure pairwise competition, species coexistence will be
407 disrupted as the strength of competition increases, given a particular level of intraspecific
408 variation. Similarly, as individual variation increases, given a particular level of competition,
409 species coexistence will again be disrupted. Selection should therefore promote trait
410 divergence over evolutionary time scales. Since, in our simulations we begin with saturated

411 communities, as heritable individual variation increases species will tend to evolve away
412 faster from one another. But in doing so, they will encounter other species at other points in
413 the trait axis more often than when individual variation is low. Consequently, coexistence
414 between species will decrease in the case of high individual variation. Indeed, we do observe
415 such a result, when interactions are purely dominated by pairwise interactions. As individual
416 heritable variation increased in the pairwise interaction case (HOIs are zero), trait clustering
417 decreased leading to a smaller number of species that eventually coexisted (Fig A3-4).

418 Trait patterning varies widely, often conforming to even spacing or sometimes
419 displaying extensive overlap (Götzenberger et al. 2012; Siefert 2012; Vergnon et al. 2012;
420 D’Andrea and Ostling 2016*b*). In our eco-evolutionary model, where competition between
421 species includes both pairwise and HOIs, increases in trait variation led to trait clustering
422 (Fig. 4). Lotka-Volterra models dominated by only pairwise interactions generally support
423 the idea that species tend to distribute more evenly along a trait axis than expected by neutral
424 evolution for the given trait (Barabás et al. 2012; Barabas and D’Andrea 2016). This is
425 mostly due of the underlying competition kernel and the fitness function that is generally
426 used. Because, of the Gaussian competition kernel and the rectangular fitness function, in
427 comparison to the species at the centre of the trait axis, species at the extreme ends of the axis
428 will have a slight fitness advantage. This is due to the fact that species at the ends of the trait
429 axis compete only in one direction in contrast to the species at the centre of the axis where
430 competition is bi-directional. Expectedly, in such a scenario, due to fitness maxima at the
431 ends of the axis, species would be displaced with respect to each other in order to minimize
432 competitive overlap. When coupled with high heritable variation, evolution would be faster
433 compared to when there is low heritable variation, and we should observe greater trait
434 divergence in the former case. Indeed, in purely pairwise competitive community, we found
435 that as intraspecific variation increased, trait convergence decreased substantially (Fig A4).

436 A biologically realistic case that can evaluate the sensitivity of our results and simultaneously
437 tackle the scenario of fitness peaks at the ends of the trait axis would be by modelling a
438 fitness function that is quadratic, such that fitness decreases unimodally towards the extremes
439 of the trait axis. Using such an approach, however, did not alter our results (Fig A6-7). In
440 fact, regardless of the fitness function, in the presence of HOIs, trait clustering still occurs
441 (Fig A7). When HOIs come into play, trait divergence due to strong pairwise competition is
442 no longer necessary as fitness loss is stabilized by a third species, and species could still
443 persist and evolve while retaining considerable overlap in the trait axis. In other words, with
444 the addition of HOIs, the even spacing is decreased because the third species attenuates the
445 inhibitory or the displacing effect of the dominant species in the pairwise interaction
446 community, thereby maintaining stable coexistence even under high trait overlap (and thus
447 overhauling the ‘limiting similarity principle’) (Bailey et al. 2016). When high-intraspecific
448 variation is strictly heritable, this pattern of trait clustering becomes more evident as species
449 tend to converge on the trait axis (Tobias et al. 2014). Indeed, as intraspecific variation
450 increased, across strength of competition, trait convergence increased, although this pattern
451 was more or less consistent with varying strength of competition (Fig A4).

452 Understanding community stability when eco-evolutionary dynamics are at play is
453 generally difficult. However, recent theory suggests that an ecological equilibrium might not
454 be stable when different aspects of evolutionary timescales are taken into account (Patel et al.
455 2018). Here, our model results on community robustness are based on a time point that might
456 not be at ecological or evolutionary equilibrium. Nevertheless, our results suggest that higher
457 intraspecific variation leads to slightly less-robust species coexistence in the presence of
458 HOIs (Fig. 5). This means, that with higher intraspecific trait variation, communities become
459 less robust to external environmental perturbation (Barabas and D’Andrea 2016). High
460 intraspecific variation led to faster evolutionary dynamics and more species coexisting

461 together in a uni-dimensional trait axis only in the presence of HOIs. Consequently, traits of
462 persisting species had fewer locations in the trait axis that were advantageous for average
463 community stability. Contrastingly, studies that focused on pairwise interactions alone, have
464 reported the stabilizing effect of higher intraspecific variation on community robustness
465 (Barabas and D'Andrea 2016).

466 Although our results demonstrate the power of HOIs in structuring patterns of species
467 coexistence, they do not yet link with insights gained from modern coexistence theory (MCT)
468 (Chesson 2000). MCT hinges on the mechanisms that stabilize or equalize fitness differences
469 among coexisting species (Adler et al. 2007). A recent study on linking HOIs with MCT
470 shows that species coexistence is possible when HOIs alleviate interspecific competition
471 between species to a greater extent than the decrease in intraspecific competition (Singh and
472 Baruah 2019). Regardless of large fitness differences where pairwise species coexistence was
473 impossible, it was suggested that HOIs can stabilize species coexistence provided, $\epsilon_{ijk} <$
474 ϵ_{iik} , where $i \neq j$. This means, if a third species k intensifies intraspecific competition more
475 than interspecific competition, species coexistence is possible even when there are large
476 fitness differences (Singh and Baruah 2019). With the rectangular fitness function in our
477 model, we ensure that at any time point fitness differences between any two species is 1.
478 Hence, when niche overlap increases due to increases in intraspecific variation, and when
479 interactions between species are predominantly pairwise, the probability of species
480 coexistence of a species pair decreases. The only way possible for density-mediated HOIs to
481 promote coexistence even when there is high overlap is when intraspecific competition is
482 further strengthened by a third species. Indeed, this is what we also observe from our results
483 (Fig A5). However, investigations on linking these dynamics to the concepts of MCT would
484 be necessary to further confirm our exploratory results.

485 We are getting closer to understanding how species richness is maintained despite
486 differences in competitive abilities. Density mediated HOIs as modelled here, intensifies
487 competition rather than alleviating pairwise competition, and could stabilize fitness
488 differences by increasing pairwise intraspecific effects relative to interspecific effects (Fig
489 A5). Even when competition was further intensified species coexistence was still possible
490 implying the stabilizing effects of HOIs, with strength of intraspecific HOI being higher than
491 interspecific HOIs (Fig. A5). This suggests that, in terms of MCT, HOIs as modelled here
492 strengthened intraspecific effects more than it strengthened interspecific effects (Fig. A5)
493 (also see Singh and Baruah 2019). HOI terms could also be positive, indicating the
494 facilitative effects of HOIs on species pairwise interactions. It has been shown recently,
495 however, that positive HOIs can lead to infeasible invasion growth rates (Baruah and Singh,
496 2019). However, further developments on this aspect is needed to understand the effect of
497 positive HOIs on species coexistence.

498 Another mechanism of HOI, which has not been tested either empirically or
499 theoretically, that could emerge when there are more than two competitors is trait-mediated
500 HOIs (Levine et al. 2017). For instance, trait-mediated HOI could emerge when a third
501 competitor induces a plastic change in the trait of a species in direct competition with another
502 species. Such a trait-mediated change could intensify or alleviate pairwise competitive
503 interactions, and in turn could either destabilize or stabilize species coexistence respectively.
504 However, the results from such an approach might differ from the results of density-mediated
505 HOI, particularly because of how plasticity of the trait is modelled in relation to other
506 competitors. If plasticity is modelled as adaptive to changes in competitor's trait, then such
507 trait change could stabilize coexistence. However, in a saturated community this could
508 become complicated because of multiple competitors that could potentially lead to a change
509 in the trait in a direction that might not be favourable for species coexistence.

510 Our work demonstrates the importance of within species variation in maintaining
511 species coexistence. The significance of our results demonstrates that HOIs in competition
512 and coexistence studies should not be ignored. Thus an important next step would be to
513 characterize higher order interactions as well as individual variation in relation to capturing
514 variation in fitness in a diverse species community.

515

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517 We thank David Vassuer and another anonymous reviewer whose comments substantially
518 improved the manuscript.

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520 **Author contributions**

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523 **References**

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526 Table 1: List of parameters, variables and functions of the model and their respective
527 description and values.

528

<i>Parameters/ variables/ functions</i>	<i>Description</i>	<i>Value</i>
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N_i	Density of species i
θ		0.5

b_i	Growth rate of species i	$\frac{1}{\sqrt{2\pi}\sigma_i} \left[\operatorname{erf}\left(\frac{\theta - u_i}{\sqrt{2}\sigma_i}\right) + \operatorname{erf}\left(\frac{\theta + u_i}{\sqrt{2}\sigma_i}\right) \right]$
		Where erf is the error function
α_{ij}	Competition coefficient between species i and j	$\frac{w}{\sqrt{2\sigma_i^2 + 2\sigma_j^2 + w^2}} \exp\left(-\frac{(u_i - u_j)^2}{2\sigma_i^2 + 2\sigma_j^2 + w^2}\right)$
ϵ_{ijk}	Three-way interaction : competition between species i and j is influenced by species k (a tensor of size SxSxS)	As given in equation
u_i	Mean trait value of species i	Can take values in the range from -0.5 to 0.5. Initial mean trait values are randomly assigned uniformly to species in the range [-0.5, 0.5]
\bar{b}_i		$\frac{1}{\sqrt{2\pi}\sigma_i} \left[\exp\left(\frac{-(\theta + u_i)^2}{2\sigma_i^2}\right) - \exp\left(\frac{-(\theta - u_i)^2}{2\sigma_i^2}\right) \right]$
β_{ij}	Evolutionary pressure by species j on species i 's mean trait value u_i	$\frac{2w(u_j - u_i)}{\sqrt{(2\sigma_i^2 + 2\sigma_j^2 + w^2)^3}} \exp\left(-\frac{(u_i - u_j)^2}{2\sigma_i^2 + 2\sigma_j^2 + w^2}\right)$
γ_{ijk}	Evolutionary pressure on trait value of species i due to three-way interactions, such that pairwise competition between two species i and j is modulated by the third species k , (a tensor of size SxSxS)	As given in equation

σ_i^2, σ_j^2	Trait variance of species i, j ;	Three levels- a) High variation [0.01,0.05] ; b) medium variation [0.003,0.009]; c) low variation [0.0006,0.003] Species trait variance are uniformly sampled for each replicate from the ranges given above
S	Total number of starting species in the community	40
w	Width of the competition kernel signifying the strength in competition	Various= 0.2,0.25,0.3,0.35,0.4,0.45

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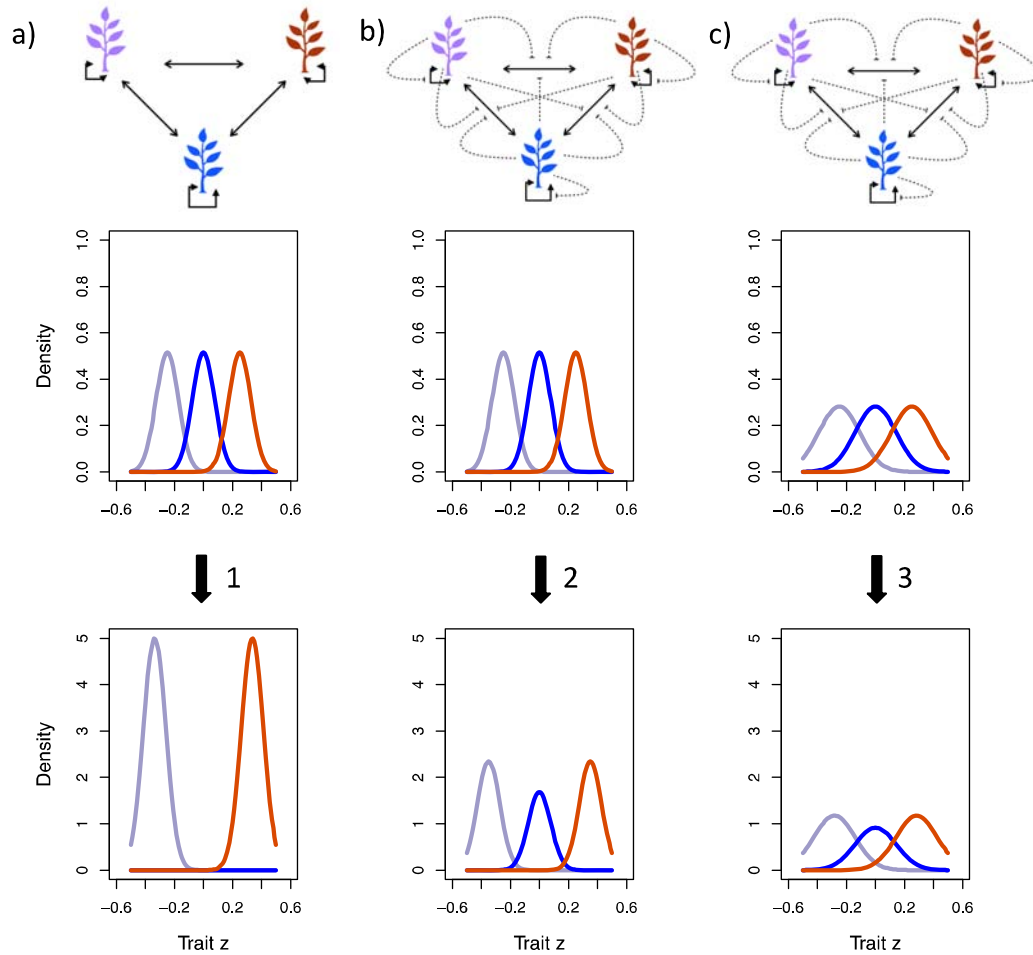
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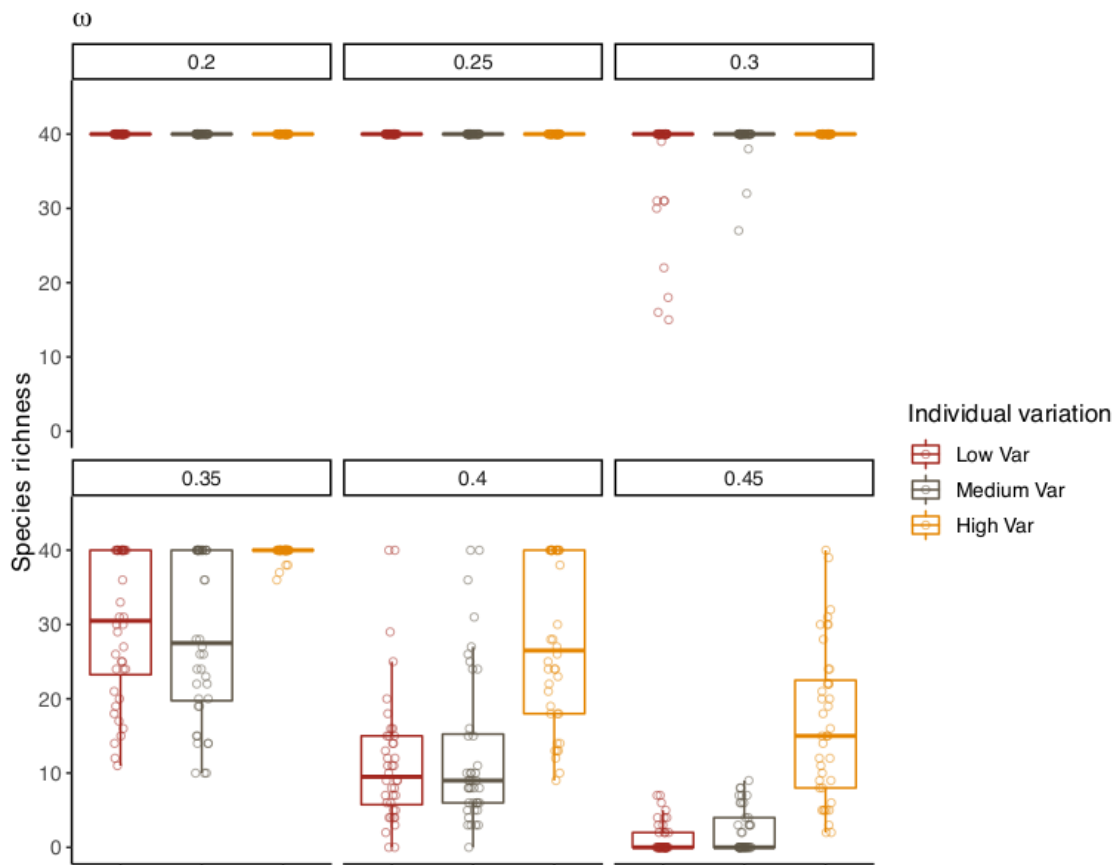
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536 List of figures:



538 Figure 1. An example image of how intraspecific trait variation in communities with (a) pairwise
 539 competitive interactions (black arrows) and (b), (c) higher-order interactions (dashed-arrows) can
 540 affect trait patterning and coexistence. (a) Three different species (Red, blue and orange) are spaced
 541 along a trait axis with high variation. Interactions between the three species are inherently pairwise.
 542 Starting with purely pairwise competitive communities' initial high intraspecific variation will
 543 ultimately eventually lead (1) to competitive exclusion of the red species. In addition, the other two
 544 remaining species (blue and orange) will space themselves far apart minimizing trait overlap and
 545 leading to the emergence of what is called the 'limiting similarity' principle. However, with the
 546 introduction of higher-order interactions, low levels of intraspecific variation (b) will also lead to (2)
 547 species minimizing trait overlap but leading to all species coexisting. However, (c) high intraspecific
 548 variation and with higher-order interactions will lead to (3) more trait overlap as well as coexistence
 549 of all the three species.

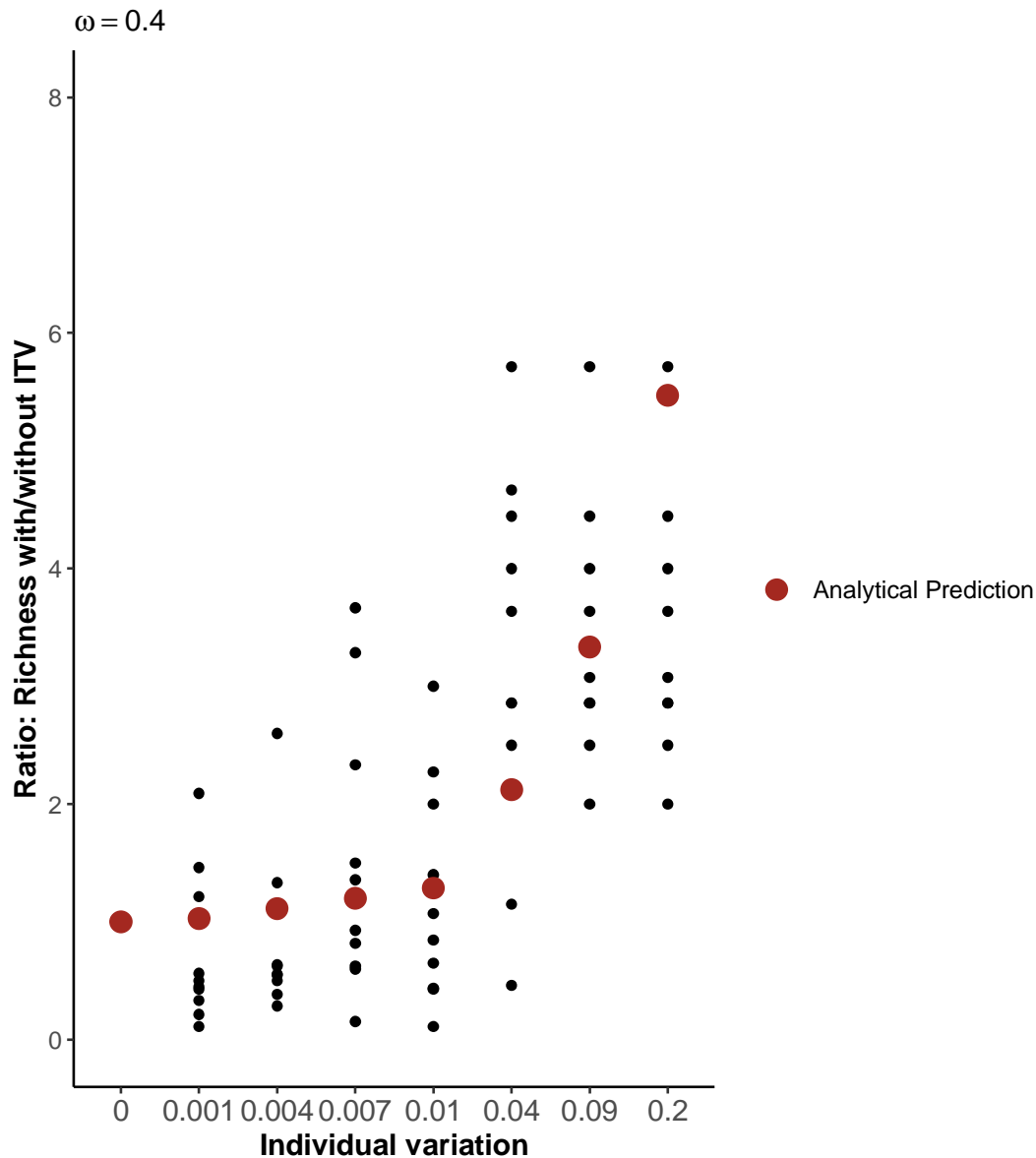
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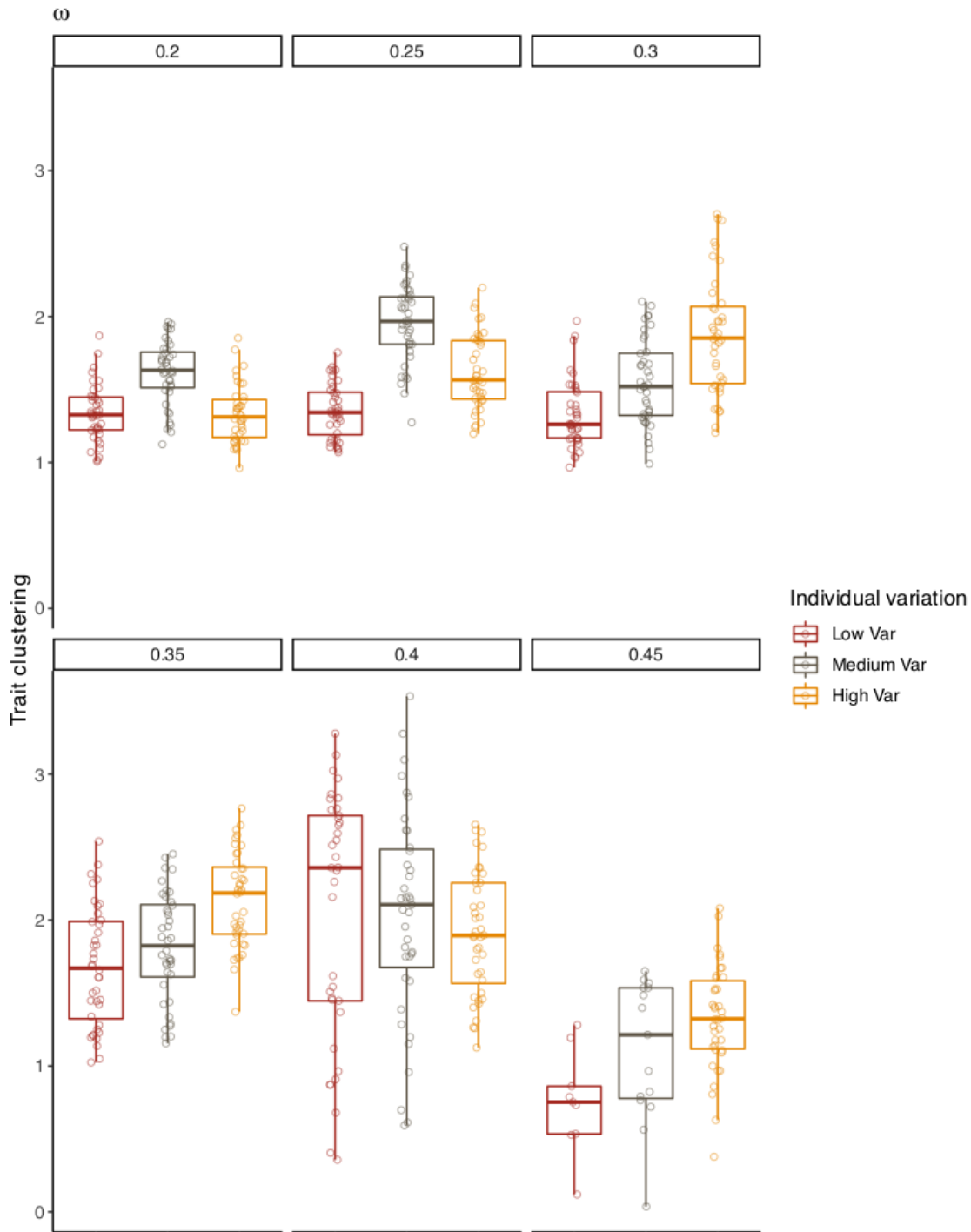
553 Figure 2. Effect of intraspecific trait variation on species richness. Boxplots denote the total number
554 of species that coexisted at the end of the simulations for different levels of competition denoted by w
555 levels. Grey colour indicates low individual variation; red colours represent medium intraspecific
556 variation; brown colour denotes high level of intraspecific variation.



557

558 Figure 3. Effect of intraspecific trait variation on ratio of species richness with and without
559 intraspecific variation. Red color dots denotes the analytical prediction of the model as given by
560 equation (5). Black dots represent replicate model simulations for each level of intraspecific variance.
561 Note that there is a shift in the ratio of species richness with to without intraspecific variation (ITV)
562 once intraspecific trait variation increases above 0.01. This denotes that number of species coexisting
563 increases significantly after intraspecific variation increases above the threshold of 0.01. This
564 simulation and analytical prediction were shown for $w = 0.4$.

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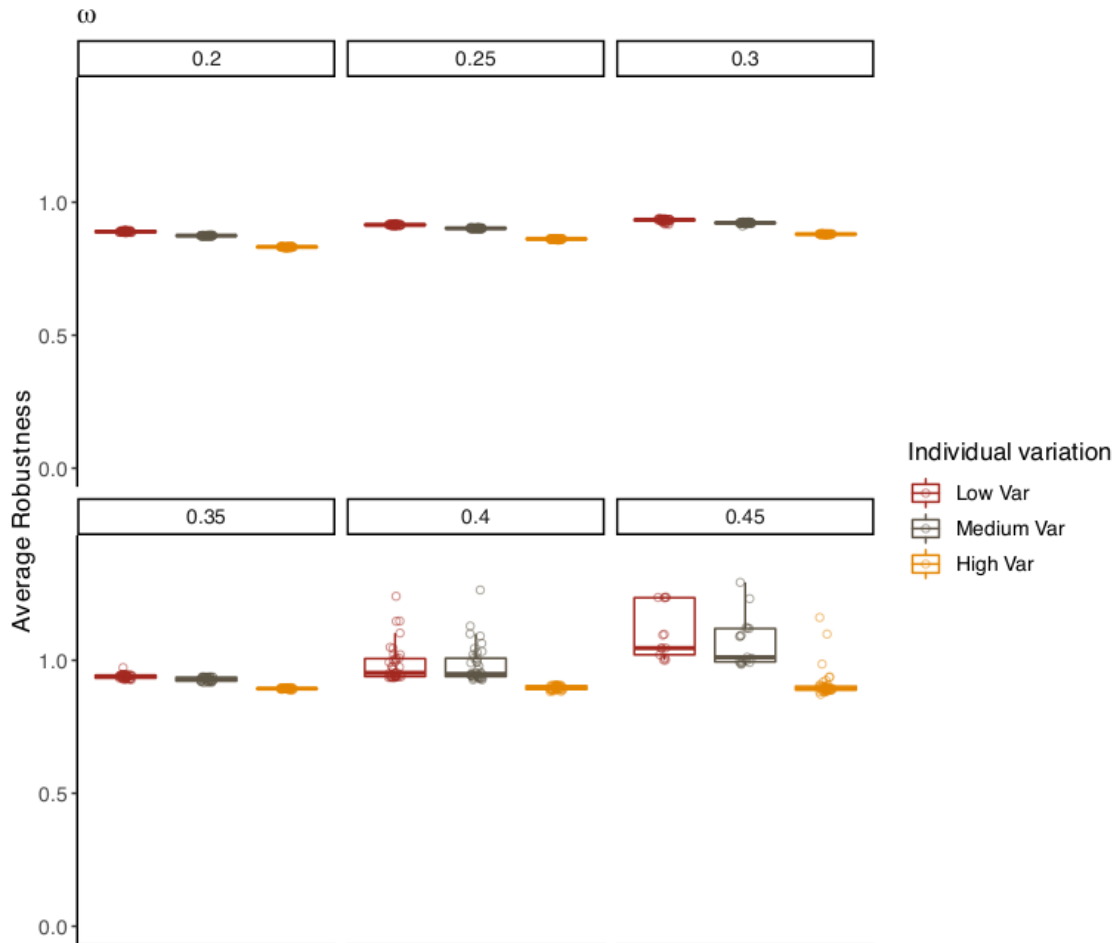
568 Figure 4. Effect of intraspecific variation on trait convergence for different levels of strength in

569 competition, w . Note that trait convergence increases substantially with increasing levels of

570 intraspecific variation across different w . Grey colour indicates low individual variation; red colours
571 represent medium intraspecific variation, brown colour denotes high level of intraspecific variation.

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576 Figure 5. Effect of intraspecific variation on average community robustness for different levels of
577 competition strength, w . Note that lower value of average robustness signifies greater community
578 stability. With increases in intraspecific variation, average community robustness decreased across
579 different levels of strength in competition, w .

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