Intraspecific variation promotes trait clustering and species coexistence through higher-order interactions.

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Abstract

Within species variation is widespread in nature. Ecological and evolutionary effects of such variation have been suggested to be detrimental for species coexistence. Community level studies of species coexistence have largely focused on competitive interactions that are characteristically pairwise, although, species interactions could involve combinations of higher-order. Mechanistic ecological models that included higher-order interactions have indicated the stabilizing effect of such interactions. It is however unknown how evolutionary dynamics could affect species coexistence in a community dictated by both pairwise and

higher-order interactions. Also unknown are the effects of individual variation on species coexistence in a community where higher order interactions are pervasive. In this study, we explore the effects of intraspecific variation on patterns of species coexistence in a competitive community dictated by both pairwise and higher-order interactions. We found that higher-order interactions greatly stabilize species coexistence across different levels of strength in competition. Surprisingly, high intraspecific variation promoted species coexistence, which was prominent at high levels of strength in competition. Further, species coexistence promoted by higher levels of individual variation were also robust to external environmental perturbation. In addition to that, species' traits tend to cluster together as individual variation in the community increased. Our results indicated that individual variation can significantly promote species coexistence by reducing trait divergence and consequently attenuating the inhibitory effect of dominant species through higher-order interactions.

Introduction

Explanations for multi-species coexistence in ecological communities have largely been sought at the species level by emphasizing average differences among species driven by competitive interactions or life history trade-offs (Clark 2010a; Violle et al. 2012; Kraft, Godoy, and Levine 2015; Letten, Ke, and Fukami 2017; Valladares et al. 2015; Gravel, Guichard, and Hochberg 2011; Wittmann and Fukami 2018). These differences among species along multiple ecological dimensions could minimise niche overlap and allow for long-term species coexistence (Clark et al. 2010; Barabás, J Michalska-Smith, and Allesina 2016; Barabas and D'Andrea 2016). However, species appear to compete for only a small number of limiting resources giving rise to the paradox of large numbers of coexisting species on apparently a small number of limiting resources (Hutchinson 1961; Letten et al.

2018; Shoresh, Hegreness, and Kishony 2008). It has also become apparent that many species coexist despite little difference in demographic or resource-based niches, at least along the few dimensions that have been measured (Condit et al. 2006). So, although there are strong theoretical arguments that average differences among species can account for species coexistence, adequate empirical support has rarely been found.

Classical competition models of coexistence consider interactions among species pairs and such models require parameter trade-offs to stabilize communities or to limit the strength of competition among coexisting species in accordance with the competitive exclusion principle (Barabás and Meszéna 2009; Barabás, J Michalska-Smith, and Allesina 2016). The implausibility of highly structured competitive relationships in species-rich communities has prompted models of coexistence based on ecological equivalence rather than life historical differences (Hubbell 2006; Rosindell, Hubbell, and Etienne 2011; Segura et al. 2011). Theoretical studies with competition models further show that any stability achieved through pairwise competitive interactions can be disrupted by random interactions among species (Bairey, Kelsic, and Kishony 2016; Barabás, J Michalska-Smith, and Allesina 2016; Allesina and Levine 2011). The number of coexisting species then declines inversely with the strength of interactions among species pairs (Bairey, Kelsic, and Kishony 2016). Interaction strength therefore places an upper bound on the numbers of coexisting species, implying that strong pairwise competitive interactions alone cannot promote species coexistence in a large community.

Interactions among species are not always constrained to species pairs and can involve higher-order combinations (Wilson 1992; Mayfield and Stouffer 2017; Bairey, Kelsic, and Kishony 2016; Grilli et al. 2017; Terry, Morris, and Bonsall 2017) , where interactions between a species pair is modulated by one or more other species (Fig. 1). In an ecological system where pairwise interactions structure communities, indirect or higher-order effects

may alter these interactions and restructure communities (Terhorst et al. 2018; Levine et al. 2017). For example, a species that is a superior competitor for a given resource can inhibit an inferior competitor for the same resource, but a third species may modulate the strength of this inhibition without affecting either of the two competitors directly (Bairey, Kelsic, and Kishony 2016). Such attenuation of the pairwise inhibitory effect can be density-mediated or trait-mediated, and can lead to qualitatively different community dynamics compared to pure pairwise interactions. The importance of such higher-order interactions has been recognised (Levine et al. 2017), but the singular focus of coexistence studies on average species level differences has meant that few investigations have been undertaken.

A further consequence of the focus on testing differences in species-level averages is that within-species or individual level variation has largely been ignored (Siefert 2012; Hart et al. 2016). Observations that variation within species exceeds the differences in species-level averages have prompted much theoretical and empirical research (Hart et al. 2016; Barabás, J Michalska-Smith, and Allesina 2016; Hausch, Vamosi, and Fox 2018; Barabas and D'Andrea 2016). Intraspecific variation can have both ecological and evolutionary effects on competitive interactions, which ultimately determine patterns of species coexistence. For example, intraspecific trait variation can hamper species coexistence by increasing competitive ability, niche overlap and even-spacing among species (Barabas and D'Andrea 2016), or by altering competitive outcomes through non-linear averaging of performances (Hart et al. 2016). There is equally compelling evidence that intraspecific variation promotes species coexistence, mainly through disruption of interspecific competitive abilities and obscuring the effect of strongly competitive individuals in a community (Clark 2010b; Bolnick et al. 2011). Experimental work has shown that intraspecific variation although allows a community to be resilient to invaders, creates the opportunity for competitive exclusion among strong competitors (Hausch, Vamosi, and Fox 2018). These contrasting

findings indicate the need for further investigations, particularly given that high levels of intraspecific trait variation within communities appears to be more a rule than an exception.

We notice that the importance of higher-order species interactions and of intraspecific variation on species coexistence had been investigated separately. The effect of intraspecific trait variation and eco-evolutionary dynamics on structuring large communities where both pairwise and higher-order interactions dominate a community is unknown. Purely pairwise interactions in a community lead to even trait spacing when intraspecific variation is high. Consequently, due to high intraspecific variation, competitive exclusion of inferior species in a large community becomes inevitable (Fig. 1). However, a community dominated by both pairwise and higher-order interactions could lead to less even spacing of species in a trait axis and might lead to trait clustering. This could be because with high intraspecific variation present in the community, higher-order interactions could significantly alleviate and stabilize the negative pairwise interactions that lead to distinct spacing in the first place.

Here in this study, we examine the importance of higher order interactions and intraspecific variation in structuring species coexistence and trait patterning. We do this using a modified Lotka-Volterra modelling approach, where dynamics of the whole community is mediated both by pairwise competitive interactions as well as higher-order three-way interactions. Specifically, we model a one-dimensional quantitative trait that contributes to the competitive ability of species interacting in the community. We show that in the presence of higher-order interactions, high intraspecific variation across different levels of strength in competition leads to significantly greater numbers of species coexisting in a community than when individual variation is low. We show analytically and with model simulations that intraspecific variation not only contributes to species coexistence, but also stabilizes the community to external perturbation. In addition, our analyses reveal that intraspecific

variation in a community where higher-order interactions dictates dynamics leads to stable trait clustering. Our study links the recent ecological studies of higher-order interactions with eco-evolutionary dynamics and intraspecific variation.

2. Methods and Models

2.1 Community model with pairwise interactions

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

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

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

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

Where $\alpha_{ij}(t)$ describes the pairwise competition coefficient of species *i* with species *j* at any time *t*. This competition coefficient derives directly from Gaussian competition kernel (See appendix 2). If the two species are similar to each other in terms of their average trait value *u*, then competition between them is stronger than when they are farther apart in the trait axis; h_i^2 is the heritability of species *i*, $b_i(t)$ describes the growth rate of the species *i* in the absence of any competition which is determined by where they lie in the trait axis z; $\overline{b_i(t)}$ describes the growth of the trait and $\beta_{ij}(t)$ quantifies the evolutionary pressure on the trait *z*

of species *i* due to competition with the species *j* in the community (this has been derived in Barabas et al, 2016).

2.2 Community model with higher-order interactions

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

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

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

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

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

where $\epsilon_{ijk}(t)$ gives the 3-way interactions in the sense that strictly pairwise trait-based interactions are also affected by the presence of a third species *k*; γ_{ijk} denotes 3-way interactions affecting evolutionary dynamics of mean trait *u* for species *i*. Similar to the pairwise Gaussian interaction kernel, the three way interaction remains Gaussian with a third species *k* influencing the interaction between the two species *i* and *j* given as (see appendix 2):

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

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

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

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

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

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

(2016) derived an upped bound for species richness. Accordingly, a diverse multispecies community with pairwise as well as three-way interactions will follow (appendix 3):

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

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

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

Where $\epsilon'_{ijk}, \alpha'_{ij}$ are three way and pairwise interactions without intraspecific variation, *i.e.*, $\sigma_i^2 = \sigma_j^2 = 0$ and S_{var} and S are species richness in the community with and without intraspecific variation respectively. We analyse the results from simulations of our model with this derived analytical solution of species richness, with and without intraspecific variation (see Results).

2.4 Simulations of the community model with higher-order interactions

We assessed the effect of different levels of intraspecific trait variation on community structure and species coexistence using data generated from simulations of our community model. We simulated both trait dynamics and population dynamics resulting from equations (3) and (4). Initial community size for the start of each simulation was 40. All the 40 species were randomly given an initial trait value within -0.5 to 0.5 in the trait axis. Outside this trait regime, fitness value of a species will be extreme and growth rate will be negative. Effectively, this strict criterion qualitatively means that outside this trait boundary resource acquisition by a species is too low to survive and have positive growth rate. We carried out 45 replicate simulations for each level of intraspecific variation. We also simultaneously tested the influence of the width of the competition kernel, which signifies the strength of pairwise interaction, using a full factorial design where all possible combinations of

intraspecific variation and strength in competition width were tested for their influence on species coexistence. In all our simulations, heritability h_i^2 of the trait for all species was fixed at 0.1.

We evolved our community for a maximum of $1x10^4$ time points, but we concluded each simulation when the community had reached a stable state. We assumed that the community attained a stable state if the ratio of minimum value of the entropy of the community given by, $-\sum N_i \log(N_i)$, at two different time points, 500 units apart ($\Delta t = 500$), remains bounded within 10^{-5}. This condition was checked when the community had evolved for more than $5x10^3$ time points. If this condition was not met, we kept the simulation going for another $5x10^3$ time points before checking for the same condition. This condition was however met at almost every simulation indicating the tendency for convergence toward stable species density values.

2.4.1 Levels of width of the competition kernel and intraspecific variation

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

2.5 Trait clustering:

Theoretical models have suggested that species coexisting together tend to spread more evenly along a trait axis than expected (Barabas and D'Andrea 2016; D'Andrea and Ostling 2016). However, empirical studies have shown that it is possible for species clusters to emerge along a trait axis (Segura et al. 2011; Vergnon, van Nes, and Scheffer 2012). Here,

we use a quantitative metric to evaluate the effect of intraspecific variation on the patterning of traits in the trait-axis. We measured trait similarity between species coexisting together by measuring the coefficient of variation (CV) of adjacent trait means (D'Andrea and Ostling 2016). High values of CV would indicate clustering of trait means of species in the trait axis while lower CV values would indicate even spacing of traits.

2.6 Stability and robustness measures of species coexistence

Stability of our community model with higher-order interactions was measured by calculating the Jacobian at equilibrium. Specifically, the Jacobian of our dynamical system at a given point is (see appendix 3):

$$J_{ij} = -\delta_{ij}N_i + (-1)N_i\alpha_{ij} + (-1)N_i \sum_k N_k\left(\gamma_{ijk} + \gamma_{ikj}\right)$$

$$= N_i\left(-\delta_{ij} - \alpha_{ij} - \sum_k N_k\left(\gamma_{ijk} + \gamma_{ikj}\right)\right)$$

where, δ_{ij} is the Kronecker delta. At equilibrium it is possible that all the species coexist, but for the community to be locally stable, the eigenvalues of the Jacobian at that equilibrium point must all have negative eigenvalues. Thereafter, we measured the average robustness of the community by taking the geometric mean of the absolute values of the eigenvalues of the Jacobian (May 1973) (see appendix 3). Average community robustness measures the mean response of the community to environmental perturbation (Barabas and D'Andrea 2016). Specifically, this quantity measures the average return times in response to environmental perturbation for each of the species in the community. For each replicate simulation of each level of intraspecific variation, we calculated the average community robustness as the measure to evaluate how intraspecific variation affected robustness of species coexistence. Here, high values of average community robustness indicate lower stability.

3. Results

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

We found that communities with higher intraspecific variation resulted in greater numbers of coexisting species than with communities that had no intraspecific variation (Fig. 2). At low levels of intraspecific variation, the ratio of species richness with and without intraspecific variation was around 1. But as intraspecific variation increased, the ratio of $\frac{S_{var}}{S}$ also increased significantly, showing that variation within species led to greater numbers of coexisting species than without intraspecific variation.

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

We found that, with increases in intraspecific variation, the numbers of coexisting species increased. At low levels of competition *w*, the effect of intraspecific variation on species coexistence was minimal, particularly for $w = 0.2$ and $w = 0.25$. But as the intensity of competition increased, we observed intraspecific variation had a stabilizing effect on species coexistence. At high levels of competition *w*, high intraspecific variation allowed a greater number of species to coexist in the trait axis (Fig. 3, Fig. 4).

3.3 Trait clustering

We measured trait clustering by quantifying coefficient of variation in the trait axis around a species' neighbourhood. We found that with increased intraspecific variation, coefficient of variation increased, indicating that traits tend to cluster together. Particularly, this result was evident only at high levels of intraspecific variation across all intensities of competition (Fig. 5).

3.4 Robustness of species coexistence

With increases in intraspecific variation, average robustness of the community increased. The community became robust to external perturbation with increasing intraspecific trait variation when compared with a community where intraspecific variation was low (Fig. 6).

4. Discussion

The importance and the consequence of intraspecific variation in community ecology is intensely debated (Clark et al. 2010; Clark 2010b; Violle et al. 2012), with contrasting findings being reported. Some studies have found that ecological and evolutionary consequences of individual variation tend to weaken species coexistence (Hart et al. 2016; Barabas and D'Andrea 2016). The nature of competitive interactions however appears to be critical in determining the role of intraspecific variation. In competition models, purely pairwise interactions place upper bounds on the numbers of coexisting species, decreasing with increases in intensity of interactions, but including higher-order interactions leads to qualitatively different dynamics (Bairey, Kelsic, and Kishony 2016; Mayfield and Stouffer 2017; Grilli et al. 2017). We investigated how intraspecific variation influences coexistence in communities with both pairwise and higher-order interactions and found strong evidence for stabilizing effects of intraspecific variation for species coexistence.

The assumption that pairwise interactions between species are sufficient to describe competition in a community is ubiquitous in coexistence theory (Levine et al. 2017). Strong competition (e.g., for shared limiting resources) between pairs of species would drive species apart in niche space, structure communities, and maintain diversity. However, there is little evidence that the observed species-level differences in mean demographic rates or resource use are sufficient to explain species coexistence. Species may of course differ along many dimensions that are either unmeasured or unseen, and this may be evident in the high levels of intraspecific variation that is generally found (Clark 2010). Consistent with strong arguments from other studies that intraspecific variation contributes to maintaining diversity

(Clark 2010), we found a strong stabilizing effect of intraspecific variation in communities structured by pairwise and higher order competitive interactions.

In mechanistic models of competition where the underlying biology is modelled explicitly, higher-order interactions can emerge subsequently in the process (Abrams 1983). Where higher-order interactions have been explicitly modelled in phenomenological ecological models, they act as a stabilizing factor in maintaining species diversity (Bairey, Kelsic, and Kishony 2016; Grilli et al. 2017). We modelled the evolution of a trait that dictates competitive ability between species and introduced higher order competitive interactions where pairwise interactions were modulated by the density of a third species. Consistent with earlier studies on the role of higher-order interactions (Bairey, Kelsic, and Kishony 2016; Wilson 1992; Grilli et al. 2017) we found that such interactions greatly stabilize the dynamics of species in the community. Expectedly, purely pairwise interactions led to lower numbers of coexisting species as the strength of pairwise competitive interactions increased (Bairey, Kelsic, and Kishony 2016). When we introduced three-way interactions, the dynamics of the community quickly reached a stable equilibrium (Fig. 2, Fig. 3, Fig. 4). A strong competitor in the trait axis can significantly affect the growth of inferior competitor. This results in a disproportionately higher abundance for the dominant competitor compared to the competitively inferior species. However, our results suggested that with the introduction of three-way interactions, this dominance of the competitively superior species is significantly reduced due to the presence of the third similar species leading to proportionately similar densities for all the three species (Fig.1, Fig. 2). Earlier studies have studied the impact of higher-order interactions from an ecological perspective, where the evolutionary side of things was largely ignored. Our eco-evolutionary model that included higher-order interactions led to stable coexistence of all distinct phenotypes, particularly when strength in competition was low. With increases in the strength of pairwise competition, higher heritable

individual variation in the phenotypes stabilized ecological dynamics and led to higher number of species coexisting. Higher-order interactions that could emerge in species-rich competitive systems have not been well explored in the context of species coexistence (Saavedra et al. 2017). Although, empirical studies on quantifying higher-order interactions in field systems is exceedingly difficult (Mayfield and Stouffer 2017), ignoring such interactions would limit fundamental understanding of the mechanisms behind species coexistence in complex communities.

Our results show that greater levels of intraspecific variation can lead to higher species richness but this effect was more prominent when pairwise competition was strong (w >0.25) (Fig. 3, Fig. 4). Earlier studies have indicated that the numbers of species coexisting in eco-evolutionary models incorporating purely pairwise interactions are always less than the number of species coexisting in the absence of evolutionary dynamics (Edwards et al. 2018). With sufficient intraspecific variation, a species can evolve into an uninvasible phenotype that can lead to significant increases in its density. Consequently, the species with uninvasible phenotypes could easily displace other species in the community (Edwards et al. 2018; Barabas and D'Andrea 2016). However, with the incorporation of three-way higher order interactions, the increases in density of superior species with sufficient intraspecific variation is significantly limited, leading to higher number of coexisting species. With purely pairwise interactions, eco-evolutionary models with higher intraspecific trait variation would lead to greater overlap in the trait axis and species would limit other species more than they limit themselves. .Consequently, the number of species coexisting with high intraspecific variation should decrease substantially. With just pairwise interactions pervasive in a community, the optimal number of species that could coexist scales inversely to the strength of pairwise competition (Bairey, Kelsic, and Kishony 2016). With three way interactions, however, the optimal number of species that could coexist in a community scales as $\frac{1-\epsilon_{ijk}}{\alpha_{ij}}$, such that

incorporation of higher order three way interactions would lead to increases in the number of species that could coexist (Bairey, Kelsic, and Kishony 2016) when compared to a community with purely pairwise interactions. Further, with higher intraspecific variation, the strength in the three-way interaction strength decreases substantially that causes a rise in the number of species that could coexist (Fig. 4, see appendix 3).

Clustering of species in a trait axes has been documented in nature particularly in aquatic beetles, and freshwater algae (Scheffer and van Nes 2006; Holling 1992; Vergnon, van Nes, and Scheffer 2012). Trait variation within populations in a community is a widespread phenomenon in nature, however the implication of such trait variation on patterning of traits is still debated. Trait patterning varies widely, often conforming to even spacing or sometimes displaying extensive overlap (Vergnon, van Nes, and Scheffer 2012; Siefert 2012). In our eco-evolutionary model, where competition between species is includes both pairwise and three-way interactions, increases in trait variation led to significant of trait clustering (Fig. 5). Lotka-Volterra models dominated by pairwise interactions generally support the idea that species tend to distribute more evenly along a trait axis than expected by neutral evolution for the given trait (Barabas and D'Andrea 2016; Barabás, Meszéna, and Ostling 2012). This is mostly because of the underlying competition kernel. Usually the competition kernel is formulated in a way that species with similar phenotypes compete more than species with dissimilar phenotypes. In such a case, naturally, when two species, for instance, are placed in a trait axis (see Fig. 1) in way that they are very similar, initially there would be strong pairwise competitive interactions between the species. In the presence of evolutionary dynamics, both species would displace themselves in order to minimize the negative effect of competition on each other's fitness. This leads to less of a trait overlap and more of a trait divergence. However, the scenario changes when higher order interactions come into play, such that the trait divergence due to strong pairwise competition is stabilized,

and species evolve to have more overlap in the trait axis. In other words, with the addition of three-way higher-order interactions, the even spacing is decreased because the third species attenuates the inhibitory or the displacing effect of the dominant species in the pairwise interaction community, thereby maintaining stable coexistence and more trait overlap (and thus overhauling the 'limiting similarity principle') (Bairey, Kelsic, and Kishony 2016). When high-intraspecific variation is introduced to such a community, this pattern of trait clustering becomes more evident as species tend to converge in the trait axis (Tobias et al. 2014).

Our modelling results suggest that higher intraspecific variation leads to robust and stable species coexistence (Fig. 6). This means, that with higher intraspecific trait variation, communities become more stable to external environmental perturbation (Barabas and D'Andrea 2016). Local stability of a community at eco-evolutionary equilibrium will be guaranteed if the community matrix or the Jacobian has all negative eigenvalues. This however is not guaranteed in all dynamical systems at equilibrium (Barabás, Meszéna, and Ostling 2012). Our results suggest that's high intraspecific variation in a community dominated by pairwise as well as higher-order interactions, are significantly more robust and stable than communities with low intraspecific variation. This stabilizing effect of intraspecific variation is due to the fact that traits of species evolved into locations in the trait axis that was advantageous to average community robustness. Moreover, with high intraspecific variation, species could quickly recover and evolve to new trait means after an external perturbation. Consequently, high variation and evolutionary dynamics could greatly stabilize community responses to external perturbation (Dakos et al. 2018). Similar studies also reported the stabilizing effect of higher intraspecific variation on community robustness (Barabas and D'Andrea 2016) . Further earlier studies have examined the effect of intraspecific variation on robustness of species coexistence in a competitive community

dominated by pairwise interactions (Barabas and D'Andrea 2016; Barabás, J Michalska-Smith, and Allesina 2016). These studies suggest that intraspecific variation however does promote species coexistence in a community with purely pairwise interactions. With the introduction of higher-order interactions in a community, the number of species that could coexist in a large community increases substantially (Grilli et al. 2017), where diversity scales differently with different order of interactions (Bairey, Kelsic, and Kishony 2016). Incorporating three-way higher order interactions alongside pairwise interactions in a competitive community, we showed that intraspecific trait variation could significantly stabilize and promote species coexistence in a large community.

In conclusion, we showed that intraspecific variation could promote species coexistence in a competitive community provided pairwise competitive interactions and three-way higher order interactions contributed to the dynamics of the species and trait patterning. Our work demonstrates the importance of within species variation in a classical competition framework that focuses on species-level differences. We show that intraspecific variation promotes species coexistence, particularly when competitive interactions include higher-order interactions and are of higher intensity. Furthermore, high intraspecific variation not only promotes stable and robust species coexistence but also leads to trait convergence, a non-intuitive result that has been found in other studies. An important next step would thus be to characterize higher order interactions as well as individual variation in relation to capturing variation in fitness in a diverse species community.

Author contributions

GB conceived the study, developed the model framework and did the analyses with feedback from RJC; GB and RJC both contributed equally to writing the manuscript.

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

Parameters/variables/functions	**Description**	**Value**
$\boldsymbol{N_i}$	Density of species *i*	….
$\boldsymbol{\theta}$		0.5
$\boldsymbol{b_i}$	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
$\boldsymbol{\alpha_{ij}}$	Competition coefficient between	$\frac{w}{\sqrt{2\sigma_i^2+2\sigma_j^2+w^2}}\exp\left(-\frac{(u_i-u_j)^2}{2\sigma_i^2+2\sigma_j^2+w^2}\right)$

	species *i* and *j*	
$\boldsymbol{\epsilon_{ijk}}$	Three-way interaction : competition between species *i* and *j* is influenced by species *k* (a tensor of size SxSxS)	As given in equation
$\boldsymbol{u_i}$	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]
$\boldsymbol{\bar{b}_i}$		$\frac{1}{\sqrt{2}\pi\sigma_i}[\exp\left(\frac{-(\theta+u_i)^2}{2\sigma_i^2}\right)-\exp\left(\frac{-(\theta-u_i)^2}{2\sigma_i^2}\right)]$
$\boldsymbol{\beta_{ij}}$	Evolutionary pressure by species *j* on species *i's* mean trait value u_i	$\frac{2w(u_j-u_i)}{\sqrt{(2\sigma_i^2+2\sigma_j^2+w^2)^3}}\exp\left(-\frac{(u_i-u_j)^2}{2\sigma_i^2+2\sigma_j^2+w^2}\right)$
$\boldsymbol{\gamma_{ijk}}$	Evolutionary pressure on	As given in equation

	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)	
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	40

	community	
w	Width of the competition kernel signifying the strength in competition	Various- 0.2,0.25,0.3,0.35,0.4,0.45

List of figures:

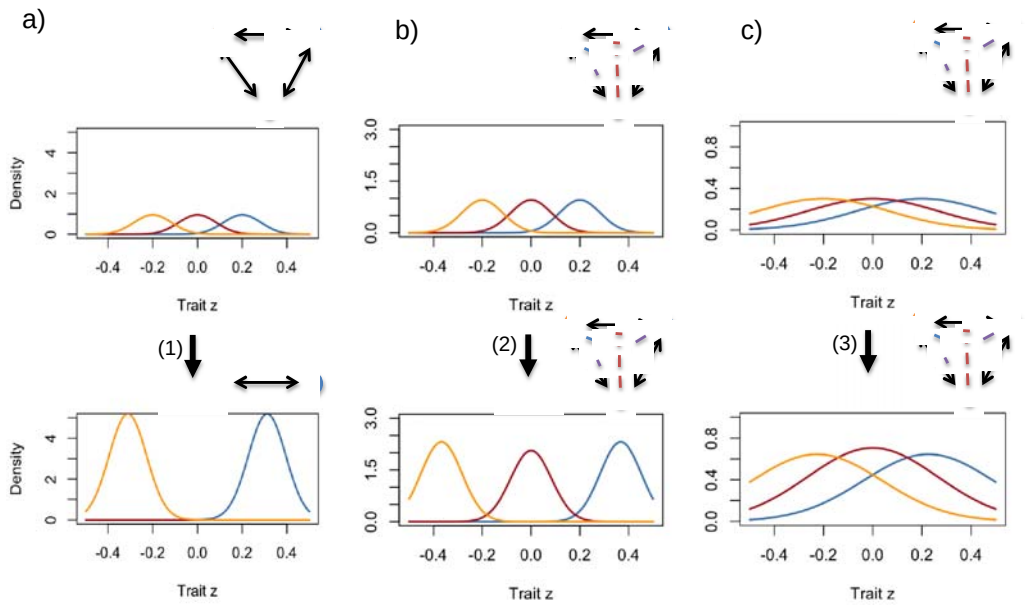

Figure 1. An example image of how intraspecific trait variation in communities with (a) pairwise competitive interactions (black arrows) and (b), (c) higher-order interactions (dashed-arrows) can affect trait patterning and coexistence. (a) Three different species (Red, blue and orange) are spaced along a trait axis with high variation. Interactions between the three species are inherently pairwise. Starting with purely pairwise competitive communities' initial high intraspecific variation will

ultimately eventually lead (1) to competitive exclusion of the red species. In addition, the other two remaining species (blue and orange) will space themselves far apart minimizing trait overlap and leading to the emergence of what is called the 'limiting similarity' principle. However, with the introduction of higher-order interactions, low levels of intraspecific variation (b) will also lead to (2) species minimizing trait overlap but leading to all species coexisting. However, (c) high intraspecific variation and with higher-order interactions will lead to (3) more trait overlap as well as coexistence of all the three species.

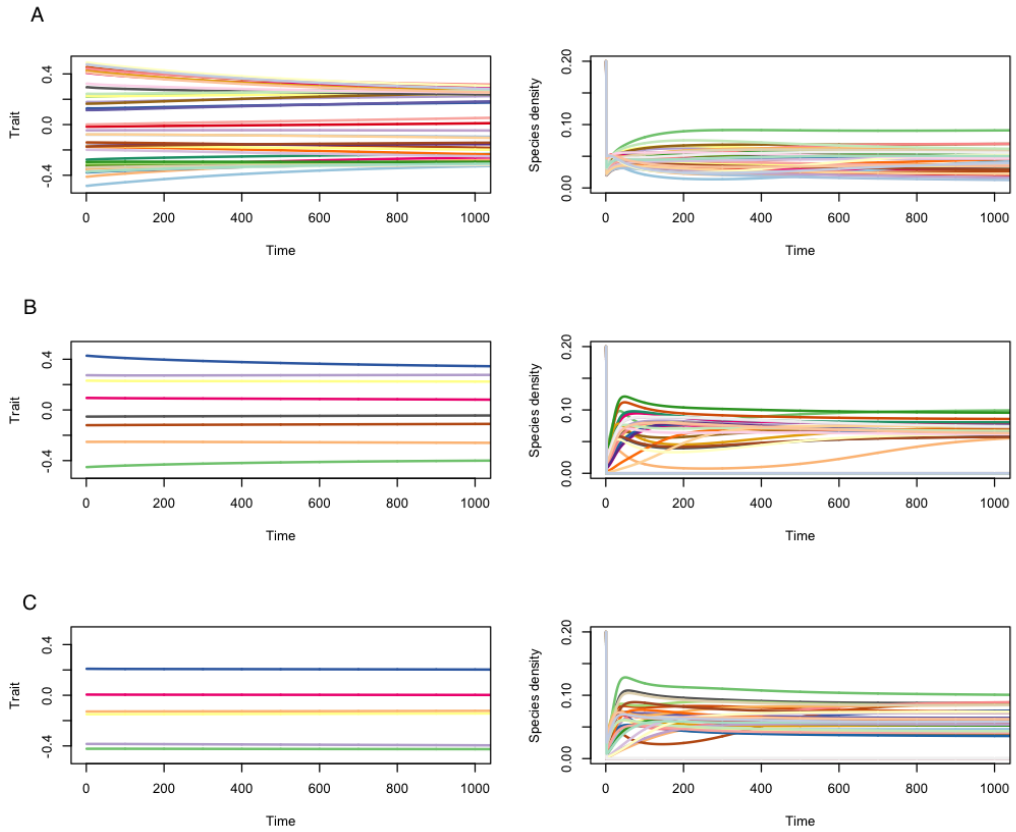

Figure 2. Example dynamics of trait and species density over time for three levels of intraspecific variation for a particular $w = 0.3$. (A) High intraspecific variation; (B) Medium intraspecific variation; (c) low intraspecific variation. Different colors represent different species.

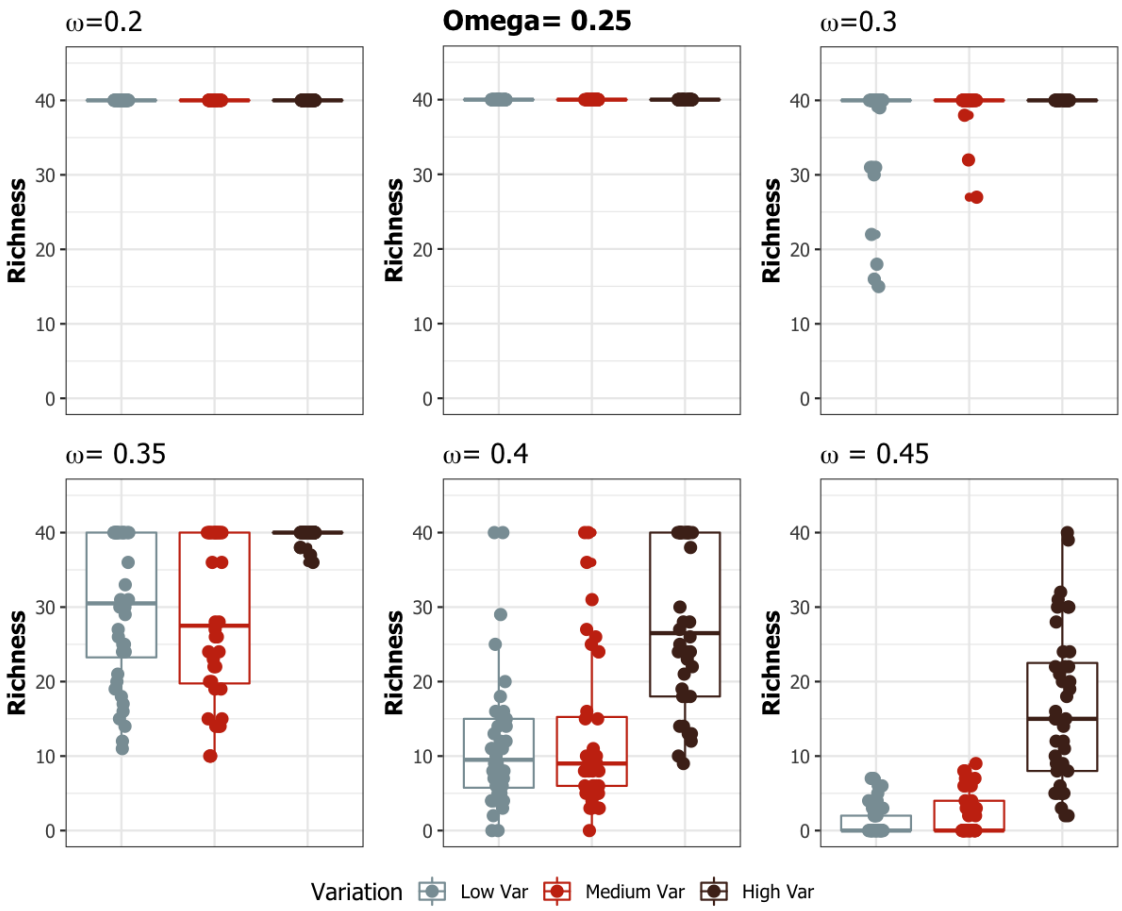

Figure 3. Effect of intraspecific trait variation on species richness. Boxplots denote the total number of species that coexisted at the end of the simulations for different levels of competition denoted by *w* levels. Grey colour indicates low individual variation; red colours represent medium intraspecific variation; brown colour denotes high level of intraspecific variation.

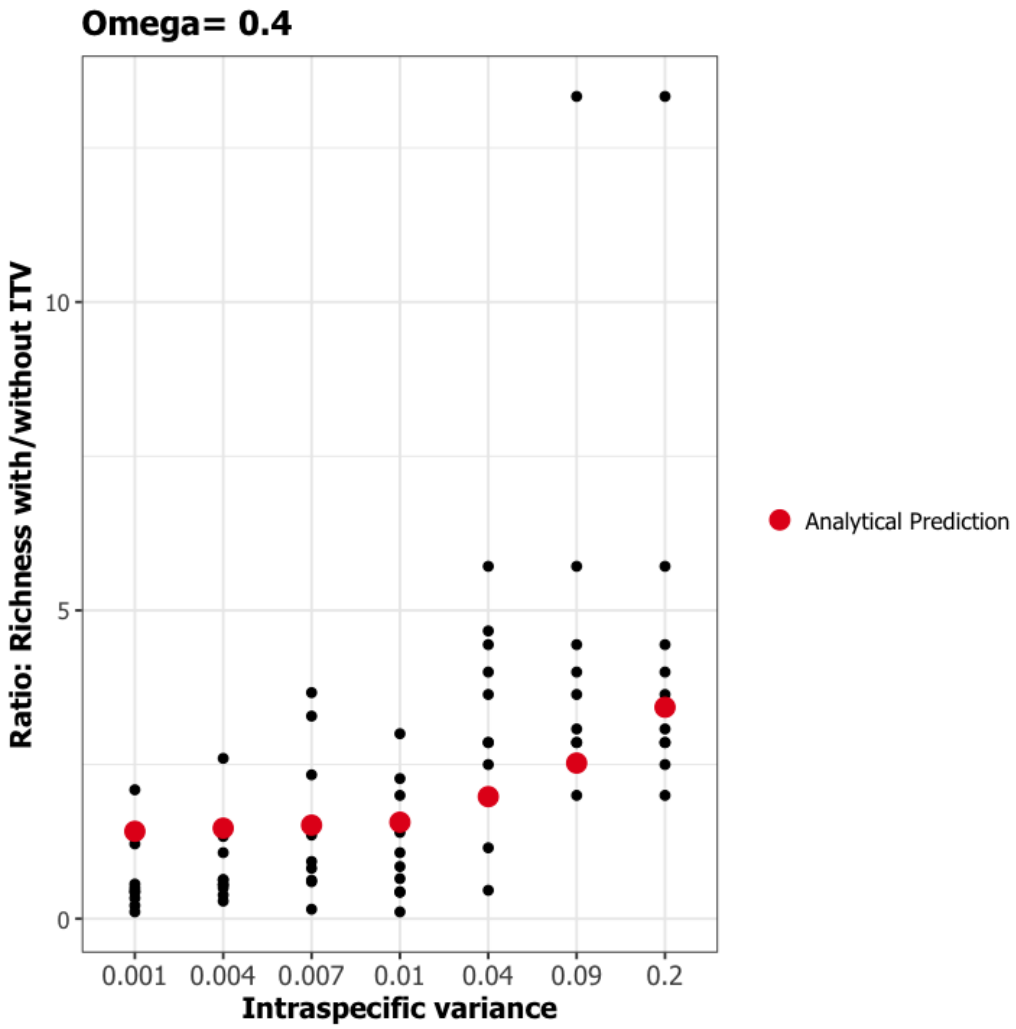

Figure 4. Effect of intraspecific trait variation on ratio of species richness with and without intraspecific variation. Red color dots denotes the analytical prediction of the model as given by equation (5). Black dots represent replicate model simulations for each level of intraspecific variance. Note that there is a shift in the ratio of species richness with to without intraspecific variation (ITV) once intraspecific trait variation increases above 0.01. This denotes that number of species coexisting increases significantly after intraspecific variation increases above the threshold of 0.01. This simulation and analytical prediction were shown for $w = 0.4$.

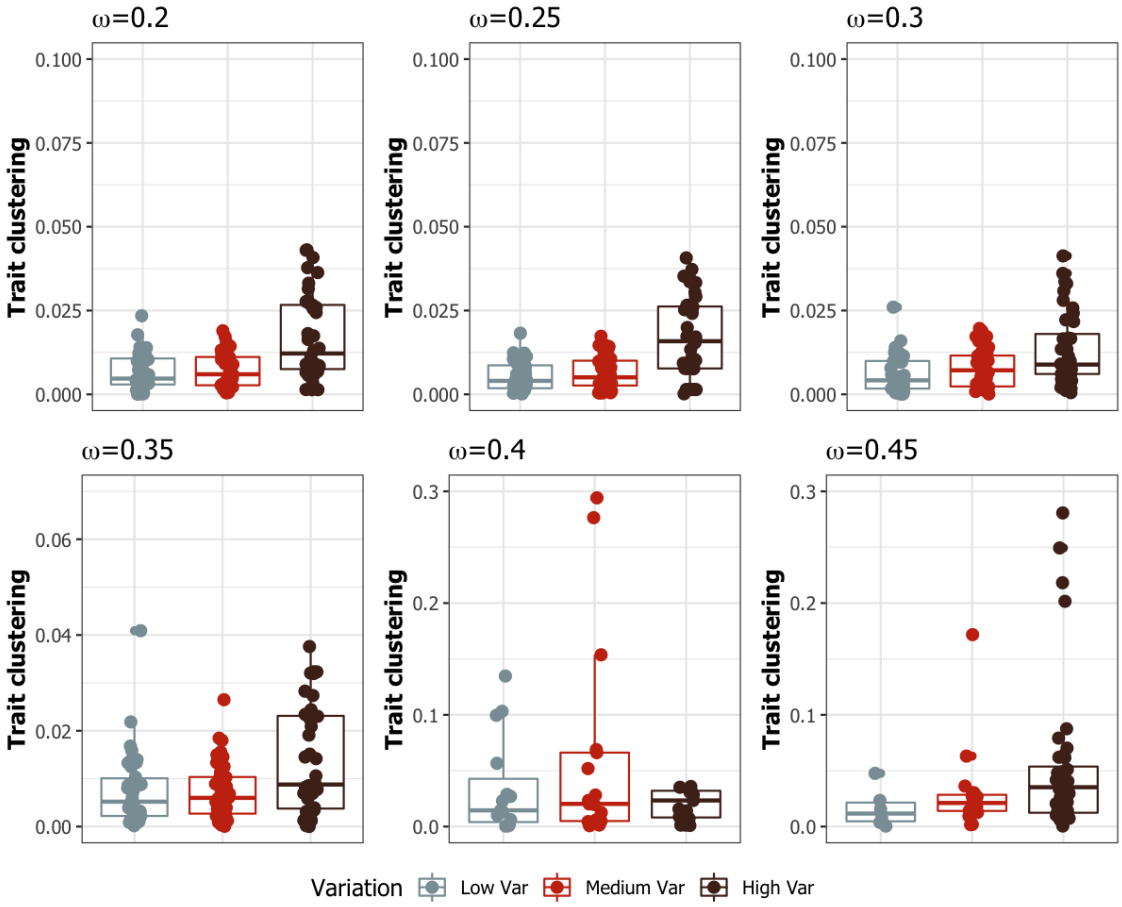

Figure 5. Effect of intraspecific variation on trait convergence for different levels of strength in competition, *w*. Note that trait convergence increases substantially with increasing levels of intraspecific variation across different *w*. Grey colour indicates low individual variation; red colours represent medium intraspecific variation, brown colour denotes high level of intraspecific variation.

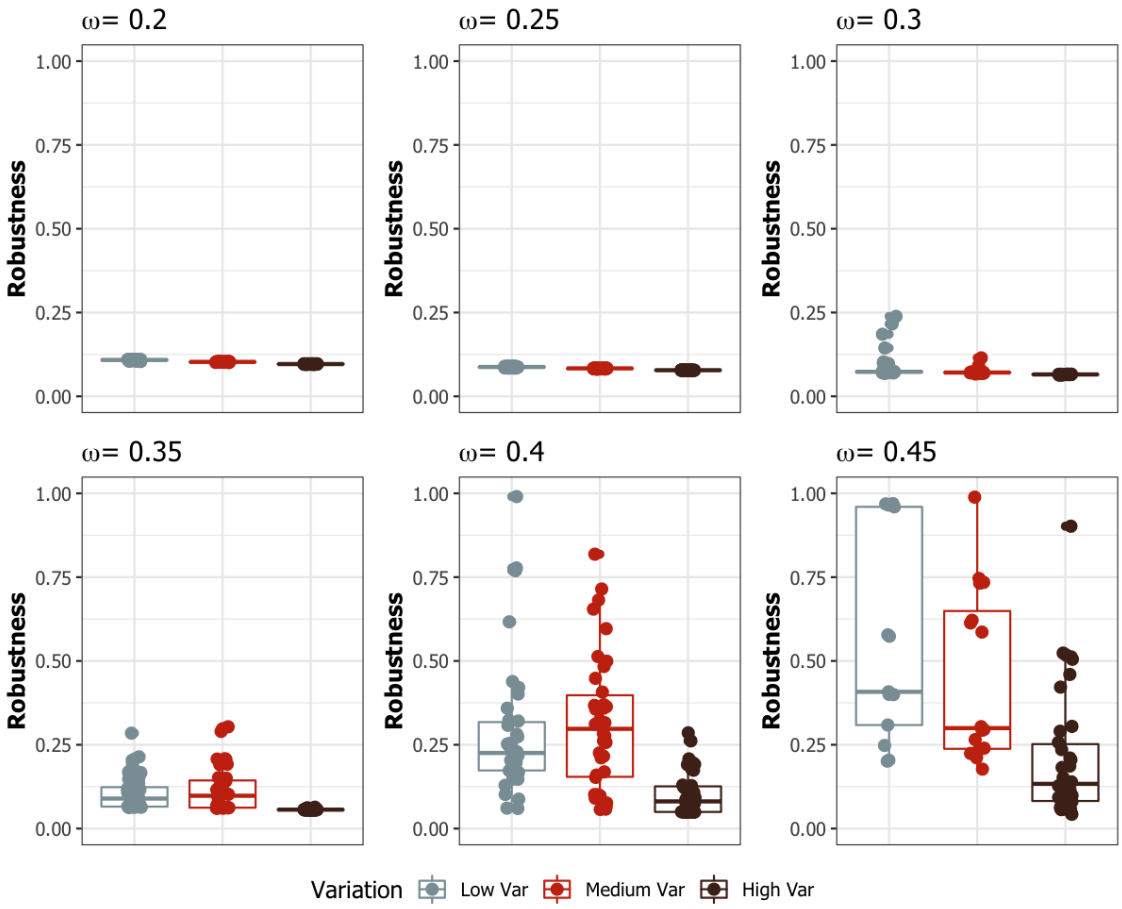

Figure 6. Effect of intraspecific variation on average community robustness for different levels of competition strength, *w*. Note that lower value of average robustness signifies greater community stability. With increases in intraspecific variation, average community robustness increased significantly across different levels of strength in competition, *w*. This indicates that communities where intraspecific variation is high, they are more stable to external perturbations.