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The impact of individual variation on abrupt collapses in mutualistic networks

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Abstract

Individual variation is central to species involved in complex interactions with others in an ecological system. Such ecological systems could exhibit tipping points in response to changes in the environment, consequently leading to abrupt transitions to alternative, often less desirable states. However, little is known about how individual trait variation could influence the timing and occurrence of abrupt transitions. Using 101 empirical mutualistic networks, I model the eco-evolutionary dynamics of such networks in response to gradual changes in strength of co-evolutionary interactions. Results indicated that individual variation facilitates the timing of transition in such networks, albeit slightly. In addition, individual variation significantly increases the occurrence of large abrupt transitions. Furthermore, topological network features also positively influence the occurrence of such abrupt transitions. These findings argue for understanding tipping points using an eco-evolutionary perspective to better forecast abrupt transitions in ecological systems.

KEYWORDS
co-evolution, eco-evolutionary dynamics, individual variation, mutualistic networks, population collapses, tipping points

INTRODUCTION

Complex ecological systems, for instance a mutualistic community, could exhibit tipping points at which such a system could abruptly shift from one state to another. Typically, this happens when environmental conditions cross a specific threshold (Dakos & Bascompte, 2014; Scheffer et al., 2001). Such tipping points are generally prevalent in dynamical systems governed by positive feedback loops, as also observed in aquatic systems of macrophytes and algae (Dakos et al., 2019), or populations with Allee thresholds (Courchamp et al., 1999; Hilker, 2010; Stephens et al., 1999). Previous research on stability of ecological systems has mainly focused

on effects of interspecific differences and interactions (Blüthgen & Klein, 2011; Ebeling et al., 2008; May, 1977; Stavert et al., 2019), ignoring intraspecific variation. Although individual variation has been documented to be widespread in such systems (Bolnick et al., 2011; Des Roches et al., 2018), their role on collapse of biodiversity has largely been unexplored.

Theoretical and empirical studies in various systems have demonstrated the ecological effects of individual variation on ecosystem functions and community structure (Barabas & D'Andrea, 2016; Cloyed & Eason, 2017; Des Roches et al., 2018; Post et al., 2008). For instance, phenotypic variation in predation can marginalise negative effects of interspecific competition among prey

species and mediate coexistence in a predator–prey community (Schreiber et al., 2011). Thus, understanding whether individual variation can have important consequences for biodiversity loss in response to changes in environmental conditions is crucial. Incorporation of individual trait variation in classical phenomenological models could potentially have consequences on ecological dynamics and thereby alter the prediction of biodiversity response to environmental change (Baruah et al., 2019).

Recent studies have called for an understanding of eco-evolutionary effects of individual variation on tipping points in ecosystems (Dakos et al., 2019; Matthews et al., 2011; Norberg et al., 2001). Various hypothesis has been put forward. One hypothesis is that trait variation could facilitate rapid trait change and thereby maintain stability of an ecological system, either by phenotypic plasticity or rapid evolution (Chevin & Lande, 2010; Gomulkiewicz & Holt, 1995). In turn, this could delay the onset of tipping points (Dakos et al., 2019), although support for this is somewhat limited. Another hypothesis is that trait variation could lead to an earlier occurrence of a tipping point (Dakos et al., 2019). This particular phenomenon could occur when environmental change imposes a directional selection on species traits that brings an ecological system closer to a tipping point, such as those observed in evolutionary suicides or fisheries collapse due to size-selective harvest (Rankin & López-Sepulcre, 2005; Walsh et al., 2006).

Mutualistic networks provide an ideal ecological system to evaluate dynamically the effects of individual trait variation on tipping points (Dakos & Bascompte, 2014; Dean, 1983; Guimarães et al., 2007; Jiang et al., 2018; Latty & Dakos, 2019; Lever et al., 2014, 2020; Pascual-García & Bastolla, 2017; Wright, 1989). These mutualistic networks have previously been shown to exhibit tipping points in response to small changes in mutualistic interaction that causes the onset of community collapse (Dakos & Bascompte, 2014; Jiang et al., 2018; Lever et al., 2014). Theoretical work on mutualistic networks has shown that changes in the external environment could have differential effects on species extinctions, contingent on the topology and the architecture of such networks (Lever et al., 2014; Staniczenko et al., 2013; Valverde et al., 2018). The architecture of such networks in turn could govern the co-evolutionary dynamics (Andreazzi et al., 2020; Guimarães et al., 2017; Jr et al., 2011; Nuismer et al., 2013; Okuyama & Holland, 2008) and could influence the stability of such ecological networks in response to gradual changes in the environment (Bastolla et al., 2009).

In this study, using hundred and one empirical plant–pollinator networks collated from the database of Web-of-Life, I explore how within-species trait variation and the architecture of plant–pollinator networks impacts the timing and occurrence of abrupt tipping points in response to gradual changes in the environment.

Reconciling quantitative genetics with classical phenomenological Lotka–Volterra equations, I model the eco-evolutionary dynamics of such mutualistic networks. First, using some example mutualistic networks, I roughly determine the parameter space where such networks could be feasible. After estimating the parameter space that could lead to feasible communities, I model the eco-evolutionary dynamics of 101 networks in response to gradual changes in the strength of co-evolutionary mutualistic interactions. I show that the presence of individual variation does not delay but promotes the onset of network transitions. Furthermore, it substantially increases the occurrence of abrupt collapses. Additionally, I demonstrate that nestedness, and community size, has a strong impact on whether a transition to collapse was abrupt or not.

MATERIALS AND METHODS

One hundred and one empirical mutualistic networks were accessed from the Web-of-Life database (www.web-of-life.es) (references in Table S1). These networks were extracted on the basis that nestedness (NODF) (Almeida-Neto et al., 2008) range should vary as wide as possible (see Figure S11). On that basis, hundred and one networks that were extracted which had total species ranging from 8 to 68 and had nestedness that ranged from 0 to 0.85. These empirical networks were next used for modelling eco-evolutionary dynamics.

I model the eco-evolutionary dynamics of species that has individuals which vary along a uni-dimensional phenotypic trait of interest. The phenotypic distribution of the trait z of interest was assumed to be normal with mean u_i^A and phenotypic variance of σ_i^2 where the i and A stands for species i and animals, respectively. The phenotypic distribution was modelled to be in the limit of quantitative genetics, which means that variance of the trait distribution does not change in response to selection (Falconer & Mackay, 1996). Interaction between species in a mutualistic network occurs through the phenotype z they possess as in the 'trait-matching' model (Nuismer et al., 2005, 2013). Individuals belonging to different species encounter each other and their fitness was assumed to be dependent on mutualistic interactions. Fitness benefits in terms of growth rate from mutualistic interactions thus depended on the phenotypes that individuals possess and how similar they are, for example, as observed in proboscis of pollinators and corolla lengths in plant–pollinator systems (Agosta & Janzen, 2005; Santamaría & Rodríguez-Gironés, 2007). The eco-evolutionary dynamics of animal guild, for instance, then could be generally written as (see Supporting Information 1):

$$\frac{dN_i^A}{dt} = N_i^A \int r_i^A \left(\overrightarrow{N}, \overrightarrow{p}, z, t \right) p_i^A (z, t) \, dz, \tag{1}$$

$$\frac{du_i^A}{dt} = h_i^2 \int \left(z - u_i^A\right) r_i^A \left(\overrightarrow{N}, \overrightarrow{p}, z, t\right) p_i^A(z, t) \, dz.$$

We can get the population dynamics for plant species by changing the superscripts to P. Here, N_i^A is the abundance of animal species i; u_i^A is the mean phenotypic trait for a species i belonging to an animal species A; h_i^2 is the broad-sense heritability of the mean phenotypic trait; $p_i^A(z, t)$ is the phenotypic distribution of the animal trait z which is normal; $r_i^A\left(\overrightarrow{N}, \overrightarrow{p}, z, t\right)$ is the per-capita growth rate of species i. Specifically, $r_i^A\left(\overrightarrow{N}, \overrightarrow{p}, z, t\right)$ can be further broken down as (Barabas & D'Andrea, 2016; Valdovinos, 2019):

$$r_i^A\left(\overrightarrow{N}, \overrightarrow{p}, z, t\right) = b_i - \sum_j^{S_A} a_{ij}^A(t) N_j^A(t)$$
$$+ \sum_k^{S_P} N_k^P(t) \int \frac{A_{ik}\gamma(z, z\prime)}{1 + \tau A_{ik}\gamma(z, z\prime) N_k^P(t)} p_k^P(z\prime, t) \, dz\prime, \quad (2)$$

where S_A and S_P are the number of animal and plant species, respectively; b_i is the growth rate of species i that is, independent of the phenotypic trait and was fixed at -0.05. This formulation meant that species were obligate mutualists (Dakos & Bascompte, 2014), and thus were completely dependent on mutualistic interactions for maintaining positive growth rates; a_{ij}^A captured the inter- and intraspecific competition for animals; $p_k^P(z\prime, t)$ is the phenotypic distribution of the plant trait; $A_{ik} = 1$, if species i interacted with species k and 0 if they did not; τ is the handling time which in this study I fixed it at 0.25 for all plants and animal species. Species in a mutualistic network interact via their phenotypes and evolve in response to changes in trait matching. Whenever traits between two species slightly match, species benefit in terms of increases in growth rates leading to co-evolution of mean traits for both species, which could be quantified (see section 'Individual trait variation and mutualistic interactions'). $\gamma(z, z\prime)$ captures the interaction between two mutualistic individuals, which is gaussian, and was written as $\gamma(z, z\prime) = \frac{\gamma_0}{q_i^\delta} e^{\frac{-(z-z\prime)^2}{w^2}}$, γ_0 captures the average strength of mutualistic interaction when an individual with trait z from an animal species interacts with an individual $z\prime$ from the plant species; w^2 controls the width of the interaction kernel which was fixed at 0.5 to ensure that mutualistic interaction strength was medium (Figure S2). To be noted that mutualistic eco-evolutionary dynamics were modelled without the addition of noise (see Supporting Information 4 for additive and multiplicative noise). In addition, in such mutualistic networks some generalist species asymmetrically enjoy a higher number of interactions than specialist species (Bascompte et al., 2006). Hence, in order to account for asymmetries in mutualistic interactions, I used a trade-off that takes into account the number of interactions of a species and average mutualistic

strength γ_0 (Dakos & Bascompte, 2014; Lever et al., 2014) controlled by the parameter q_i^δ, where q_i is the degree of a species i in a mutualistic network, and $\delta = 1$ indicates trade-off and $\delta = 0$ indicates trade-off being relaxed. When there is a trade-off (i.e. $\delta = 1$) strength of interaction falls off as degree of the species increases. In the main-text I present the results for trade-off only but please refer to appendix Figure S5 for the case when trade-off was relaxed, that is, $\delta = 0$. These two values were chosen as they correspond to the two extreme possibilities, although in reality the trade-off strength might likely lie in between these two extremes.

Individual trait variation and mutualistic interactions

For any mutualistic network extracted from the Web-of-Life database, I randomly sampled mean trait values for plants, u_i^P, and animals, u_i^A, in the range of -1 to 1. This meant that some plant species might have mean trait values that might not be similar to other pollinators trait which could then decrease trait–trait mutualistic benefits (Nuismer et al., 2005, 2013). With that I evaluated the effects of two levels of individual variation: *high* individual trait variation, where all species belonging to either plants or animals had phenotypic variance σ_i^2 sampled from a random uniform distribution in the range of U[0.05, 0.5]. For low individual variation, phenotypic variance σ_i^2 was sampled from a random uniform distribution in the range U[0.0001, 0.001]. With this, I evaluated how individual trait variation could influence the collapse of mutualistic networks (see section 'Collapse of mutualistic networks' for details). In all our co-evolutionary simulations, heritability was fixed at 0.4.

I also evaluated how mean trait matching in mutualistic networks changes as co-evolutionary strength, γ_0, was changed (Guimarães et al., 2017; Jr et al., 2011; Medeiros et al., 2018). In the following, trait matching was defined for each network k as $\theta_{ijk} = A_{ij} e^{-\frac{\left(u_i^A - u_j^P\right)^2}{w^2}}$, where u_i^A, u_j^P are the mean phenotypic values at equilibrium for a given mutualistic network k, and w^2 controls the width of the mutualistic interaction; $A_{ij} = 0$ or 1, depending on whether there was an interaction between species i and j. Following this, I calculated trait matching for each network $\overline{\theta}_k$, which was the mean across all the interacting species i and j in the network. Next, the mean of trait matching was calculated across all networks k (Medeiros et al., 2018).

Feasibility of mutualistic networks

Since dynamics of mutualistic communities and species coexistence would depend on initial mean trait values of species (u_i^A, u_i^P), strength and the range of interspecific

competition coefficients being sampled a_{ij}^A, a_{ij}^P, and on strength of co-evolutionary mutualistic interactions γ_0, I roughly wanted to determine the parameter set that would lead to feasible communities (Rohr et al., 2014). A mutualistic community was termed 100% feasible if all the species survived at the end of a simulation and 0% if none of the species survived with an abundance above a threshold of 0.001. In this way, I created a feasibility index that goes from 0 to 1. For the feasibility analysis, three representative networks were chosen in a way that total number of species ranged from high to low (network size were 60, 34 and 8, respectively) and nestedness ranged from high to low (0.75, 0.56 and 0.25, respectively). For each parameter combination of competition coefficients and co-evolutionary mutualistic strength γ_0, 30 sets of independent simulations were done to quantify the feasibility index. The feasibility index was then calculated as the mean across the 30 sets of simulations for each parameter set of competition coefficients, co-evolutionary mutualistic strength, and a level of individual trait variation. Initial mean species trait values were randomly sampled for each replicate from a uniform distribution ranging from −1 to 1. In all these simulations, I fixed intraspecific competition at 1 for all the species. Interspecific competition coefficients, a_{ij}^A, a_{ij}^P, randomly sampled for both plants and animals from a random uniform distribution give as: $\rho * \frac{U[0.0001, 0.001]}{n(A,P)}$, where ρ controls the average strength of interspecific competition coefficients being sampled and scaled by $n(A, P)$,

which is the total number of species involved in competition within a guild (Table 1) (*A*, *P* stands for animals and plants, respectively). I increased ρ from 50 to 7000 that subsequently controlled the strength of competition coefficients being sampled, such that when $\rho = 7000$, a_{ij}^A, a_{ij}^P were sampled from $\frac{U[0.7,7]}{n(A,P)}$. For this particular case, for instance, interspecific competition coefficients sampled could be greater than intraspecific competition. Similarly, γ_0 was varied from 6 to 0 in small steps and the feasibility index was calculated for each replicate simulation after co-evolutionary dynamics have stabilised. Growth rates were fixed at −0.05.

Collapse of mutualistic networks

Intraspecific competition was ensured to be always greater than interspecific competition in magnitude and hence was fixed at 1, and interspecific competition coefficients were drawn from a scaled random uniform distribution, $\frac{U[0.0001,0.001]}{n(A,P)}$ (Table 1). Initial population size of all species in the mutualistic network was fixed at 1.

The collapse of the mutualistic networks were done by decreasing the average mutualistic strength, γ_0, sequentially from 7 to 0 in steps of 0.15 as done similarly in (Dakos & Bascompte, 2014; Jiang et al., 2018). For each value of γ_0, I simulate the dynamics of mutualistic networks till it reached equilibrium. I discarded the

TABLE 1 List of variables and parameter values used in the model and their short descriptions

Parameters	Description	Value
N_i^A, N_j^P	Abundance of species *i* and *j* belonging to animals A, and plants P.	Variable
u_i^A, u_i^P	Mean phenotypic trait value for species *i* belonging to animal species A and plant species P.	Evolving, although starting initial mean phenotypic values were sampled from U[−1, 1].
b_i	Growth rate for species *i*. Growth rate was fixed and same for both plants and animal species.	−0.05
a_{ij}^A, a_{ij}^P	Competition coefficients belonging to animal species *A* and plant species *P*. Competition occurs within a guild of species. The competition coefficients were scaled by the number of species within a guild following (Dakos & Bascompte, 2014), i.e. $\frac{a_{ij}^A}{n(A)}$, $\frac{a_{ij}^P}{n(P)}$, $i \neq j$, where $n(A)$ and $n(P)$ are the total number of animals and plants in the network. a_{ii}^A, a_{ii}^P are fixed at 1 and ensured to be larger in magnitude than $\frac{a_{ij}^A}{n(A)}$, $\frac{a_{ij}^P}{n(P)}$.	a_{ij}^A, a_{ij}^P $\epsilon \frac{U[0.0001, 0.001]}{n(A)}$, $\frac{U[0.0001, 0.001]}{n(P)}$
A_{ik}	Adjacency matrix of plant–pollinator interactions.	$A_{ik} = 1$, if species *i* interactions with *k* or else is 0
$\gamma(z, z\prime)$	Gaussian mutualistic interaction kernel for an individual pollinator with trait *z* interacting with another plant individual with trait *z'*.	-----
τ	Handling time.	0.25
h_i^2	Broad-sense heritability of the mean phenotypic trait, u_i.	0.4
w^2	Width of the mutualistic Gaussian interaction kernel.	0.5
γ_0	Average strength of mutualistic co-evolutionary interaction	Variable
σ_i^2	Variance of trait distribution. In other words, amount of individual variation.	U[0.0001, 0.001] for low individual variation and U[0.05, 0. 1] for high individual variation

initial transient dynamics and estimated equilibrium plant and animal abundances from the last 1000 time points. The extinction threshold of species in such mutualistic networks was fixed at 0.001. As the strength of co-evolutionary interactions γ_0 decreased, loss of species occurred until the entire mutualistic network collapsed. Next, I estimated two metrics: (1) the threshold mutualistic strength at which a network collapsed, and (2) one that quantifies whether a mutualistic network went through an abrupt collapse. The threshold mutualistic strength was determined as the γ_0 at which the total equilibrium abundance of a network fell below 1. To quantify whether a network passed through an abrupt collapse, the slope of the decline of total community abundance as change in total community abundance per consecutive change in co-evolutionary mutualistic strength y_0, as, $N\left(y_0\left(i+1\right)\right) - N\left(y_0\left(i\right)\right)$ was estimated, where i is the index number. If the decline in total community abundance for each network for any two consecutive changes in y_0 was larger than 45 (i.e. $N\left(y_0\left(i+1\right)\right) - N\left(y_0\left(i\right)\right) > 45$), the community collapse was characterised as 'abrupt' and if it was smaller than 45, the collapse was characterised as 'gradual'. I used the number 45 to characterise 'large abrupt shifts' in comparison to small changes in the strength of co-evolutionary interactions, γ_0, since $\gamma_0\left(i+1\right) - \gamma_0\left(i\right) = 0.15$ (as co-evolutionary strength γ_0 was decreased in steps of 0.15). This particular method was done for all 101 empirical networks. Thus, chances of abrupt collapse were characterised by a binary value of 0 or 1, where 0 would indicate a gradual collapse (quantified by the decline in total abundance per consecutive changes in γ_0 being smaller than 45) and 1 would indicate abrupt collapse. In addition to this, I also determined the proportion of species in a network that also went through an abrupt collapse. A species in a mutualistic network was termed to go through an abrupt collapse if the change in equilibrium abundance of the species per consecutive change in γ_0 was >5.

For each of the empirical networks I estimated the common topological network properties such as connectance and nestedness. Connectance was measured as the number of interaction links divided by the square of total species. For nestedness I calculated a commonly used method known as NODF. The NODF measure has been suggested to be problematic in accurately measuring nestedness as it could correlate with other network measures (Ulrich et al., 2009) such as number of species interactions and total number of species (Lever et al., 2014). Thus, the traditional nestedness measure (NODF) could be scaled with connectance and total number of species (Song et al., 2017). However, to compare with earlier studies, I used the traditional NODF measure for nestedness. I also estimated the network size which would be the total number of plant and animal species present in the community at equilibrium.

Next, I used a generalised linear model with chances of abrupt collapse as the response variable, nestedness, individual variation, connectance and network size as predictor variables to evaluate whether topological features of mutualistic networks and individual trait variation impacted the occurrence of abrupt network collapse.

RESULTS

Nestedness (NODF) varied from as low as 0 to as high as 0.85 for the empirical networks. Connectance for the empirical networks ranged from 0.08 to 0.64. Community size of the mutualistic networks also ranged from as low as 8 species to as high as 68 species. Eco-evolutionary dynamics of an example mutualistic network are shown in Figure 1.

Feasibility of the example networks differed with respect to levels of individual trait variation and network size. In the case of the large mutualistic network (Figure 2a), feasibility was possible when the range of competition coefficients sampled were medium to weak, i.e. log (ρ) < 6, or in other words when interspecific competition coefficients were sampled from $\frac{U[0.0001, 0.001]}{n(A.P)}$, also conditional on the strength of co-evolutionary mutualistic interaction γ_0. High individual trait variation slightly increased the feasibility range for the same range of interspecific competition coefficients and γ_0. In the case of mutualistic network that was small in size (Figure 2c), feasibility range was also limited to strength of competition and γ_0. In addition, high individual trait variation increased the range of parameter space where feasibility was possible in comparison to when species had low trait variation.

When $\delta = 1$(when there is a trade-off), 78% of the mutualistic networks exhibited sudden abrupt collapse when species had high individual variation, whereas when species had low individual trait variation only 0.9% of the networks exhibited abrupt collapse (Figure 3b). On average, 17% of species (17% ± 2.3%) in a mutualistic network exhibited sudden abrupt collapses when they had high phenotypic variation. In contrast, 0% of species in a mutualistic network exhibited abrupt collapses when they had low phenotypic variation (Figure 3c).

When $\delta = 0$ (trade-off was relaxed), 86% of the mutualistic networks where species had high individual variation exhibited abrupt collapses, whereas now 33% of the networks exhibited abrupt collapses when species had low individual variation (appendix Figure S5). On average, 17.1% (17.1% ± 2.3%) of species in a mutualistic network still exhibited abrupt collapses when they had high phenotypic variation, but only 3.36% (2.96% ± 0.7%) of species in a network showed abrupt collapses when they had low individual phenotypic variation (Figure S5c).

Irrespective of strength in competition, high individual trait variation promoted abrupt collapses in comparison to when species had low individual variation (although the
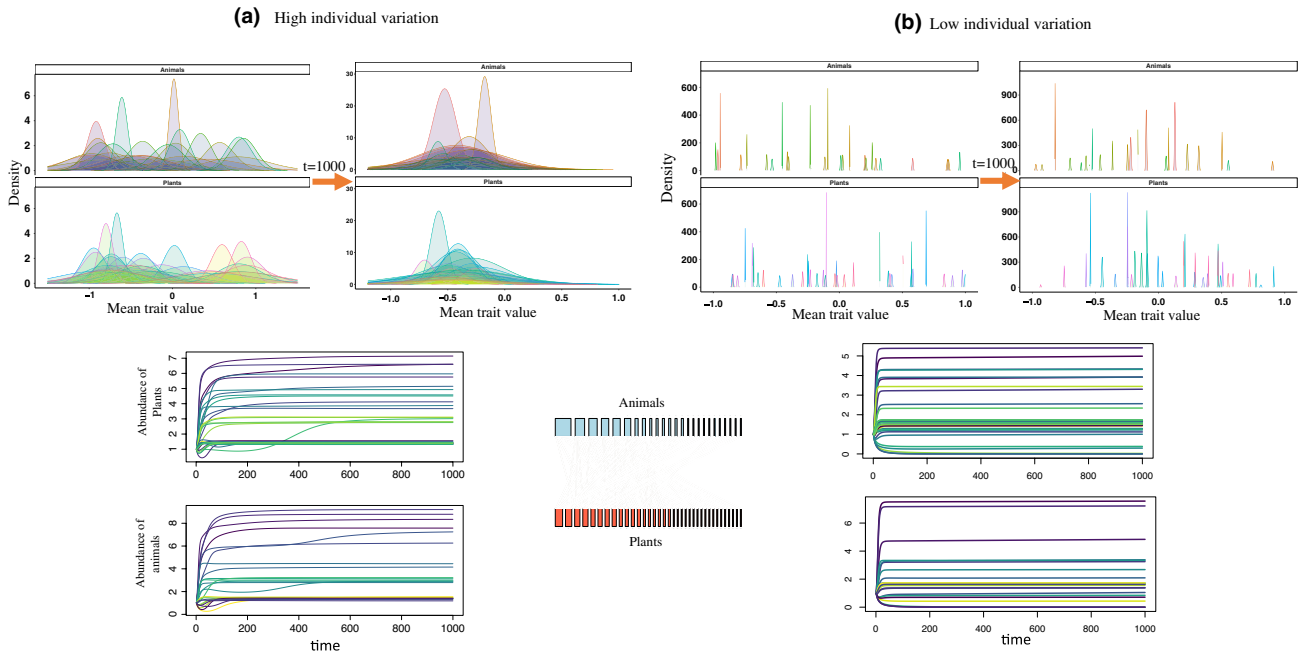
FIGURE 1 Example co-evolutionary dynamics of a plant–pollinator mutualistic community for two levels of individual variation. High individual trait variation (a) leads to different eco-evolutionary dynamics in comparison to when the same plant–pollinator network exhibited low individual trait variation (b). Initial mean trait values were sampled from U[−1,1] and heritability h^2 was fixed at 0.4. Trait variance was (a) sampled from random uniform distribution U[0.05, 0.5] and for (b) sampled from U[0.0001, 0.001] and interspecific competition for both plants and pollinators were sampled from random uniform distribution as in Table 1. The total number of species in the example plant–pollinator network was 61
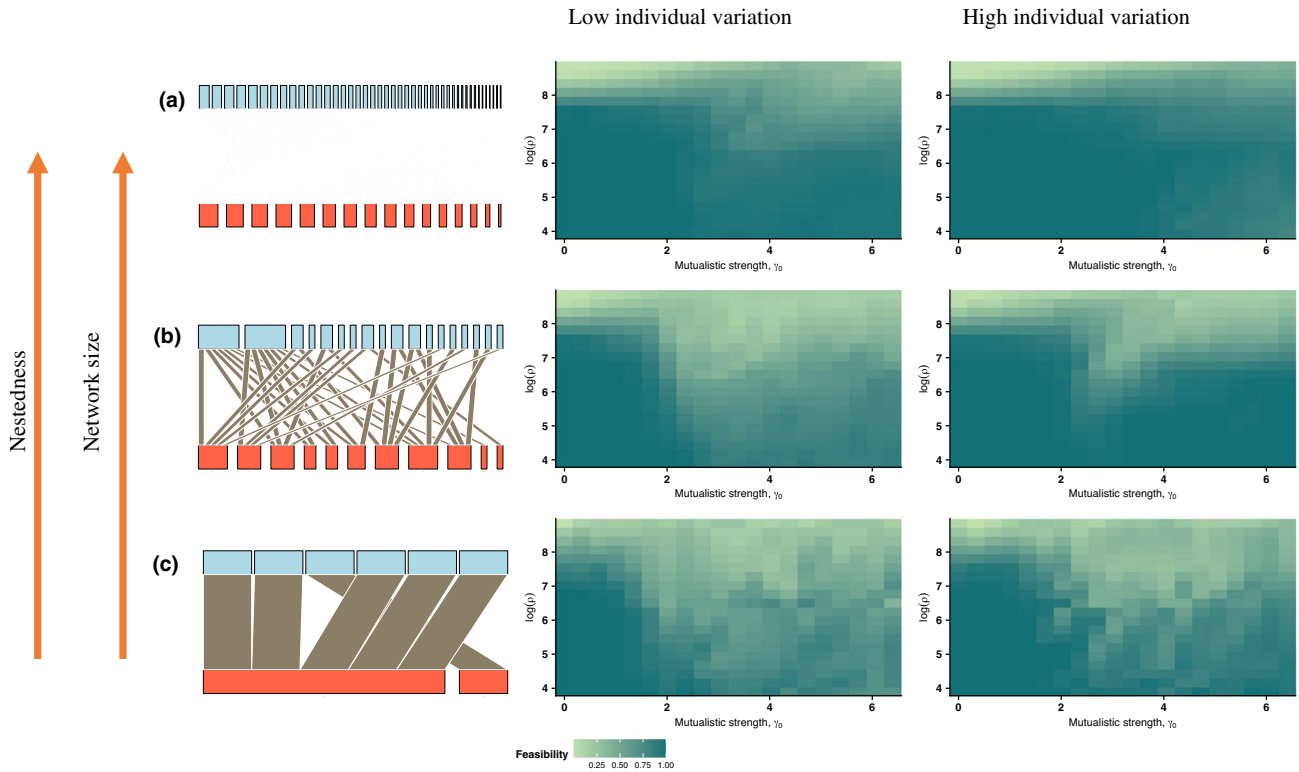

FIGURE 2 Feasibility for three example plant–pollinator networks of different sizes for two levels of individual trait variation. $\log(\rho)$ Quantified the range of interspecific competition coefficients being sampled, with high $\log(\rho)$ values indicating stronger interspecific competition for a given strength of co-evolutionary interactions γ_0. Network size in (a) was 61, in (b) was 40, and (c) was 11. Heritability in the feasibility analysis was fixed at 0.4 and initial mean trait values were sampled from a random uniform distribution ranging U[−1, 1]. (Note that in the depiction of mutualistic networks the line thickness describing interactions between plants and animals decreases as network size increases in order to accommodate the increasing number of interactions)
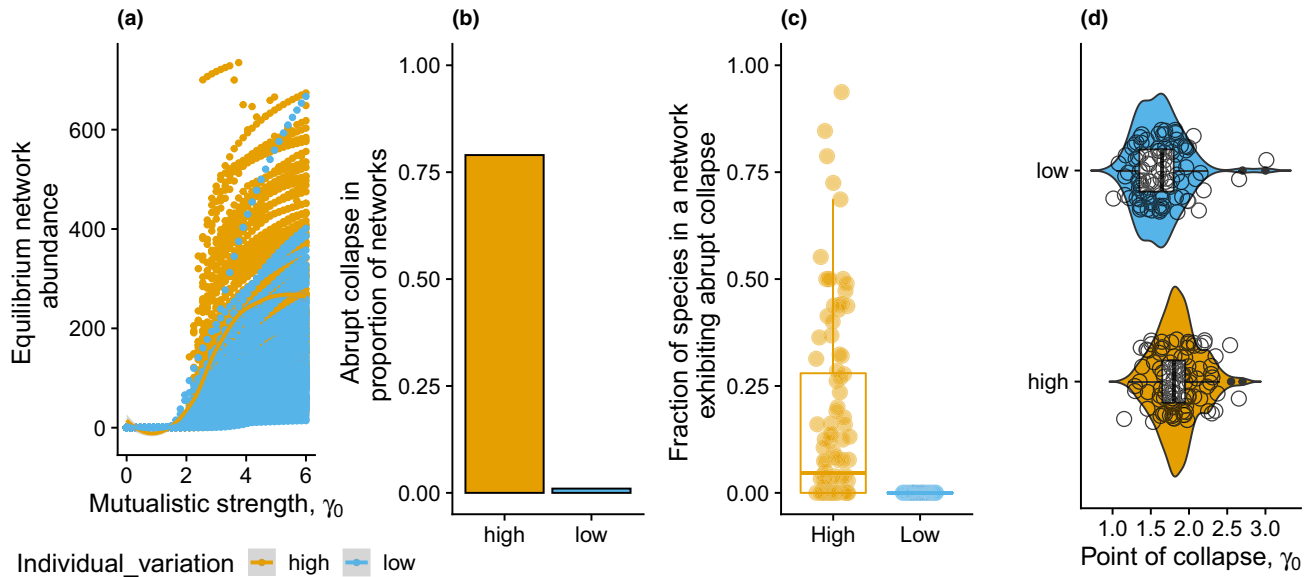
FIGURE 3 Individual trait variation on the abruptness of network collapses. (a) Total equilibrium community abundance for 101 plant–pollinator networks for each value of co-evolutionary mutualistic strength γ_0 and for two levels of individual trait variation. (b) Proportion of networks that collapsed abruptly when species had high individual variation (78%) and when species had low individual variation (0.9%). (c) Fraction of species in a network that exhibited the occurrence of abrupt collapse in the presence of high (mean ± SD error = 17% ± 2.3%) versus low individual variation (mean ± SD error = 0% ± 0%). (d) Violin plots for point of collapse, i.e. the mutualistic strength γ_0 at which the networks collapsed, for two levels of individual phenotypic variation (high and low)

proportion differed slightly, appendix Figure S3). In addition, presence of either multiplicative or additive noise did not significantly alter the overall results, although the proportion of abrupt collapses differed in the presence of noise (appendix Figure S6–7). Furthermore, different sampling distribution for competitive coefficients also did not influence the overall results (appendix Figure S8).

Although, mutualistic networks differed in terms of whether collapse was abrupt or not, the co-evolutionary mutualistic strength at which they collapsed slightly differed (Figure 3d). When both plants and animal species had low individual variation, mutualistic networks collapsed at strength of 1.62 ± 0.059 (mean ± 95% CI); and when species had high individual trait variation, mutualistic networks collapsed on average at strength 1.85 ± 0.053 (mean ± 95% CI). When trade-off was relaxed (i.e. $\delta = 0$), network collapse for species exhibiting high and low individual variation occurred at 0.416 ± 0.038 and 0.374 ± 0.0360, respectively (Figure S5).

When species had high individual phenotypic trait variation, mean trait matching among species interacting in mutualistic networks increased in comparison to when species had low individual trait variation (Figures 1 and 4a). When species had low individual trait variation, mean trait matching was low and remained unaffected as strength in mutualism decreased gradually (Figure 4a). The result was similar for when trade-off was relaxed (Figure S5e).

Network connectance was positively correlated to nestedness (NODF) and negatively to network size with Pearson correlation coefficient of 0.54 and −0.51, respectively. Nestedness was, however, not correlated with

network size (Pearson correlation coefficient of −0.043). Since connectance was correlated with nestedness and network size, it is difficult to disentangle the effect of one from the other, unless networks are artificially created holding nestedness or connectance constant. Hence, connectance was subsequently dropped from the analysis. Generalised linear model results indicated that as nestedness in mutualistic networks increased, the chances of abrupt collapses increased significantly (Figure 4b, Figure S4). Similarly, with increases in network size, which quantified total number of species present in a mutualistic network, the chances of abrupt collapse also increased as mutualistic strength was decreased (Figure 4c).

DISCUSSION

Little is known about how individual trait variation influences eco-evolutionary dynamics and in turn impacts the occurrence and timing of abrupt shifts to alternative stable states (Dakos et al., 2019). The results indicated that higher amount of individual variation, surprisingly, did not delay but slightly promoted the earlier occurrence of tipping points. In addition, individual variation also promoted the occurrence of abrupt collapses of mutualistic networks.

Higher amount of trait variation could lead to faster changes in trait distribution and thereby influence the trajectory of how an ecological system responds to changes in the external environment (Bell & Gonzalez, 2009; Chevin & Lande, 2010; Gomulkiewicz & Holt,
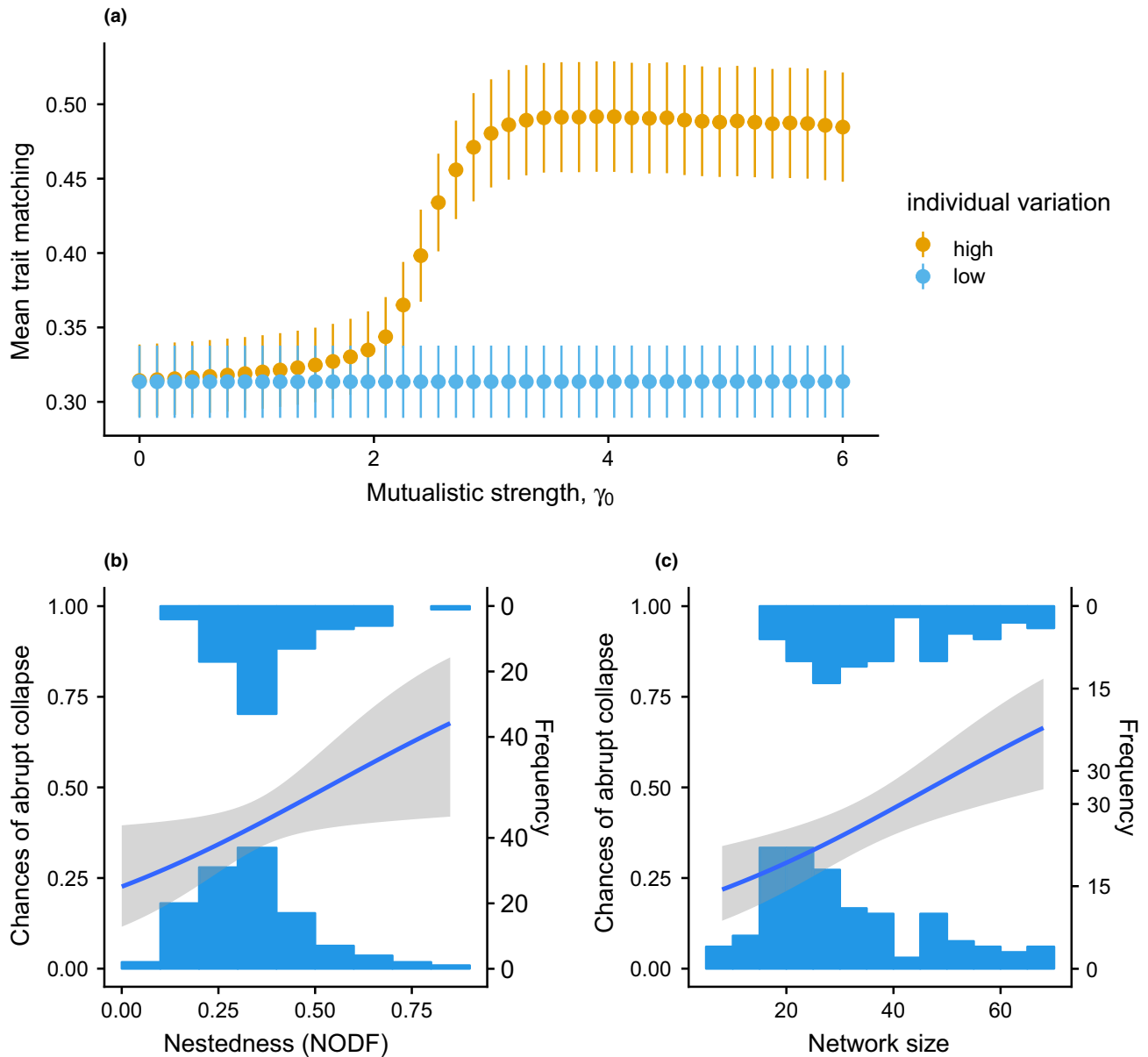
FIGURE 4 (a) Mean trait matching for mutualistic networks for two levels of individual variation. Point estimates of mean trait matching across 101 mutualistic networks as mutualistic strength γ_0 decreased when species had low versus when species had high individual variation. The error bars represent 95% CI. As mutualistic strength decreased gradually, mean trait matching decreased Network topology on chances of occurrence of abrupt collapses: (b) Nestedness (NODF) and (c) network size. Increase in nestedness had a positive influence on occurrence of abrupt collapse. Network size also influenced the occurrence of abrupt collapse of mutualistic networks. Network connectance was highly correlated to both nestedness and network size and hence was dropped from the analysis

1995). Thus, trait variation could delay a dynamical systems trajectory to reach the threshold at which it could switch to a pre-collapse state. Contrastingly, it is also possible for individual trait variation to cause a system to reach a tipping point early (Dakos et al., 2019; Latty & Dakos, 2019). This is possible when trait variation leads to a faster evolutionary response that causes a population to reach dangerously low numbers, thereby increasing the chances of extinction from demographic stochasticity (Matsuda & Abrams, 1994). Seventy-eight per cent of the mutualistic networks in this study exhibited abrupt collapses when species exhibited high

individual variation (Figure 3b). However, irrespective of whether species had high or low individual trait variation, the threshold strength at which mutualistic networks collapse were similar (Figure 3d). This was also evident from Box 1 two-species example: individual variation does not alter the extinction equilibrium point but only alters the positive equilibrium as co-evolutionary strength decreases. However, networks exhibiting high individual trait variation could collapse significantly much earlier in comparison to when species had low individual variation, provided strength in competition was high (Figure S3h). When strength of competition was

Box 1   Analysis of how individual trait variation could influence tipping points in two species plant–pollinator system

For two species plant-pollinator system, the steady state population dynamics of a plant P' and a pollinator N' in the presence of individual variation can be written as:

$$r_1(N', P', z, t) = N'b_1 - a_{11}^A N'^2 + \phi^A N' = 0, \tag{3a}$$

and for plants,

$$r_2(N', P', z, t) = P'b_2 - a_{11}^P P'^2 + \phi^P P' = 0, \tag{3b}$$

where, N', P' pollinator and plant abundances at equilibrium respectively, and $\phi^A = \iint \frac{\gamma_0 e^{\frac{-(z-z')^2}{w^2}} P'}{1 + \tau \gamma_0 e^{\frac{-(z-z')^2}{w^2}} P'} p_1(z', t) p_2(z, t) dz\ dz'$, and $\phi^A = \iint \frac{\gamma_0 e^{\frac{-(z-z')^2}{w^2}} N'}{1 + \tau \gamma_0 e^{\frac{-(z-z')^2}{w^2}} N'} p_1(z', t) p_2(z, t) dz\ dz'$.

The double integral is analytically unsolvable but one can numerically solve to understand the impact of individual trait variation on occurrence of a tipping point. $p_1(z', t)$ and $p_2(z, t)$ are phenotypic distribution of the animal and the plant species. Solving the above two equations, one could estimate the equilibrium states for the plant-pollinator system as:

$$N' = 0, N' = \frac{1}{a_{11}^A}\left(b_1 + \phi^A\right), \tag{4a}$$

$$P' = 0, P' = \frac{1}{a_{11}^P}\left(b_2 + \phi^P\right). \tag{4b}$$

One can now analytically plot equilibrium animal abundance N' against changes in co-evolutionary strength γ_0 and evaluate the impact of individual variation on occurrence of tipping points. From the simple two species plant-pollinator system (Figure S9), one can observe that individual variation can act as a 'double-edge sword' whereby it can increase the overall equilibrium abundance, but at the same time could lead to an abrupt transition when co-evolutionary strength falls below a threshold. However, the co-evolutionary strength at which the transition occurs remains same irrespective of whether the system exhibited high or low individual variation. One can see from Equations 4a and 4b that individual variation term ϕ^A, ϕ^P only appears to influence the positive equilibrium state and does not influence the extinction equilibrium i.e., $N' = P' = 0$. Hence, increases in individual trait variation should not shift the point of collapse of a plant-pollinator mutualistic system significantly. This particular example does not involve any trade-off as species degree is 1.

Indeed, plotting steady state abundance of N' as a function of change in γ_0, one can see that transition to collapse state occurs at the same co-evolutionary strength γ_0 irrespective of whether there was high or low individual variation. (Figure S9). However, the collapse becomes more abrupt in the case of high individual variation as high individual variation significantly increases positive equilibrium state for a given positive γ_0 (Figure S9).

high, strong negative feedbacks further aggravated the occurrence of earlier collapses.

Higher amount of individual trait variation for a given strength of co-evolutionary mutualistic interaction allows for wider range ecological niche to be available for both the plants and the animals. As individual trait variation increases, the potential for increases in growth rates, even when there could be mismatch in traits among species, increases substantially (Figure 1). Thus, for a given strength in co-evolutionary mutualistic interaction, average trait matching across all the mutualistic networks was subsequently higher when species had higher individual variation, irrespective of whether there was a trade-off between the number of interactions and strength of interaction (Figure 4, Figure S5). When individual trait variation was high, increases in growth rates from imperfect trait matching would also be high (Jr et al., 2011). This also happens because some extreme phenotypes would be able to gain mutualistic benefits from the other guild of species due to the presence of high individual variation, given the trait-matching model. This results in stronger positive

feedback. With higher average mutualistic strength, γ_0, among plants and animals, higher individual trait variation then results in overall increases in equilibrium community abundance (Box 1, Figure 3a). Since mutualistic networks collapsed around the same mutualistic strength irrespective of whether species exhibited high or low individual trait variation (Figure 3d), the slope of change in community abundance was steeper and more abrupt for mutualistic communities exhibiting high individual trait variation. As a result, sudden and more abrupt collapses were observed in most of the mutualistic networks exhibiting high individual trait variation.

Nestedness is a property observed in such networks, as generalists interact with both specialists and generalists, while specialists only interact with generalists. Nestedness property in ecological networks has been suggested to promote biodiversity in mutualistic networks (Andreazzi et al., 2020; Bascompte et al., 2003, 2006; Bastolla et al., 2009; Nuismer et al., 2013; Pascual-García & Bastolla, 2017). While assembling a mutualistic network, a species entering a community would be most successful and face less effective competition if it interacts with generalists, thereby leading to an overall nested network structure. In this way, a nested network structure could promote high biodiversity (Bastolla et al., 2009). Similarly, in conjunction with nested network structure, it might be possible that high individual variation might also lead to high biodiversity. This is because species having higher individual trait variation could disproportionately enjoy higher mutualistic benefits (higher trait overlap) for a given effective competition they face, in comparison to species having low individual variation. In turn, a nested network structure and high individual variation could lead to high biodiversity.

However, mutualistic networks that are nested are generally less stable than those networks that are minimally nested (Allesina & Tang, 2012; Staniczenko et al., 2013). I found that abrupt collapses, when strength of co-evolutionary interactions decrease, were predominantly also observed in highly nested networks and networks with higher number of species (Figure 4b). This particular result, however, did not indicate that such mutualistic networks were unstable, but rather, such nested networks were more prone to abrupt collapses (Lever et al., 2014). When networks were highly nested, the number of mutualistic interactions for some species were disproportionately larger than others. As a result, growth rates from such disproportionate number of interactions for some species increased more than others in such nested networks. Similarly, with increases in network size, which quantified total number of species present in a mutualistic network, the chances of abrupt collapse also increased as mutualistic strength was decreased gradually (Figure 4b).

Earlier studies have explored the persistence of mutualistic communities in response to increases in pollinator mortality rates or decrease in mutualistic strengths (Dakos & Bascompte, 2014; Jiang et al., 2018; Lever et al., 2014, 2020). In these studies, sudden collapses were observed as changes in environmental conditions crossed a certain threshold. Coevolutionary dynamics, however, were not modelled in these studies. I explicitly modelled evolutionary dynamics of a phenotypic trait that was central to a species interaction with others. Hence, the presence of abrupt collapses in response to gradual changing environmental conditions was also dependent on how individual variation and/or heritability influenced the direction of change in the mean phenotypic trait. Since heritability was fixed in the model, high individual variation led to high trait matching which consequently led to high equilibrium community abundances. This indirectly increased the chances of larger abrupt collapses. In contrast, the occurrence of abrupt collapses was diminished when individual variation was low, as co-evolutionary dynamics became impaired.

Rapid changes in the environmental conditions, such as shifts in phenology (Wolf et al., 2017; Duchenne et al. 2020), that directly impacts mutualistic interactions would lead to rapid changes in selection pressures among species mean traits (mismatch in traits for instance). Having higher individual trait variation in conjunction with non-zero heritability would directly contribute to rapid co-evolutionary dynamics thereby aiding ecological processes and rapid adaptation (faster trait matching) (Jr et al., 2011; Thompson, 1998). However, results from this study depicts that individual variation can also act as a 'double-edge sword', whereby if environmental conditions cross a certain threshold, high individual trait variation could lead to abrupt collapses to the point of no recovery.

Abrupt transitions, as observed in this study, are a manifestation of global perturbation that impacts the whole network (Bascompte & Stouffer, 2009; Lever et al., 2014, 2020). However, perturbation can be localised too, that impacts one species and propagates through the entire network (Hens et al., 2019; Suweis et al., 2015). In such localised perturbation, response of the network as the perturbation propagates would have distinct regimes that depend largely on the degree distribution and the interaction network (Hens et al., 2019). Thus, prediction of a species response to such localised perturbation, for instance in a mutualistic network, could easily be assessed by understanding the topology of the network and the degree of the focal species (Hens et al., 2019). It is possible that evolutionary response to such localised environmental perturbation could stabilise the propagation of such perturbation before eventually reaching a tipping point. However, further research is warranted in understanding the evolutionary response times of species to localised perturbations.

Abrupt collapses, such as those observed in this study, could be predicted with phenomenological signals called 'early warning signals', although the utility of such signals in forecasting collapses have been widely debated (Arkilanian et al., 2020; Baruah et al., 2020).

Environmental perturbations are likely going to re-shape such co-evolutionary interactions by influencing strength of mutualistic interactions as well as by perturbing the network architecture. While individual trait variation could be beneficial in adapting to changes in the external environment, or strengthening evolutionary robustness of communities to perturbation (Barabas & D'Andrea, 2016), the results from this work indicates that such variation could also lead to sudden collapses, leading to drastic changes in ecosystem services and functions provided by such mutualistic networks.

AUTHOR CONTRIBUTIONS
GB conceptualised the study, did the mathematical analysis, analysed the data and wrote the manuscript.

PEER REVIEW
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OPEN RESEARCH BADGES

This article has earned Open Data, Open Materials and Preregistered Research Design badges. Data, materials and the preregistered design and analysis plan are available at: https://github.com/GauravKBaruah/Individual_variation_and_tipping_points.

DATA AVAILABILITY STATEMENT
See Github repository for R-scripts and empirical networks https://github.com/GauravKBaruah/Individual_variation_and_tipping_points or Zenodo https://doi.org/10.5281/zenodo.5495586. The empirical networks were downloaded from www.web-of-life.es. Or see appendix Table S1 for references.

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