Evolution of genetic variance and its consequences on eco-evolutionary response in complex mutualistic networks

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Abstract

Climate change, especially rising temperatures, poses a threat to biodiversity and ecosystem resilience, for example, by disrupting phenological synchrony in plant-pollinator networks. These interactions, essential for ecosystem stability, are highly sensitive to temperature shifts, which can lead to mismatches in plant flowering and pollinator emergence, weakening species interactions and reducing resilience to environmental disturbances. In this study, we model species' evolutionary responses to an abrupt temperature increase, examining one-dimensional adaptation in mean temperature optimum trait versus adaptation involving both the mean and trait variance. Our results indicate that networks where species can evolve in both dimensions exhibit greater resilience, especially those species with a larger number of interactions that enhance genetic variance and exhibit evolutionary rescue under strong selective pressures. Even specialist species benefit from increased resilience through interactions with highly connected generalists, which help stabilize adaptation of entire mutualistic network to a new environmental optimum. We observed the emergence of opposing selection pressures in such complex networks which consequently promotes increased genetic variance, or "evolvability," enabling faster adaptation, and thus reducing trait lag, and boosting species survival. These findings highlights the critical role of evolving genetic variance and network architecture in mitigating the impacts of plant-pollinator phenotypic mismatches to rising environmental temperatures. This study provides valuable insights into the adaptive capacity of mutualistic networks, highlighting the importance of dynamical evolution of genetic variance in promoting resilience in the face of accelerating climate change.

1 Introduction

The increasing challenges posed by climate change, particularly rising temperatures, have been shown to have negative impacts on the life cycles of organisms (Hegland *et al.*, 2009; Opedal, 2019), leading to alterations in ecological communities. As temperatures increase, complex communities must adapt not only to the changing thermal environment (Scranton & Amarasekare, 2017) but also to shifts in the life cycles of interaction partners embedded within these complex communities (Baruah & Lakämper, 2024; Freimuth *et al.*, 2022; Hegland *et al.*, 2009). The rate of these adaptations will inevitably influence the resilience of such ecological systems (Baruah & Lakämper, 2024), spanning predator-prey relationships (Yamamichi & Miner, 2015) to aquatic ecosystems (Bolchoun *et al.*, 2017; Morgan *et al.*, 2020) and critically, plant-pollinator systems (Baruah & Lakämper, 2024; Baruah & Wittmann, 2024; Duchenne *et al.*, 2020; Hegland *et al.*, 2009). Plant-pollinator networks are especially vulnerable to changes in environmental temperatures, as abrupt temperature increases can disrupt the synchrony of phenological events (Duchenne *et al.*, 2020; Freimuth *et al.*, 2022; Hegland *et al.*, 2009; Labonté *et al.*, 2023; Trunschke *et al.*, 2024). Such asynchrony in phenological events, like insect emergence or flower blooming, can weaken species interactions and cascade across communities, posing a severe threat to essential ecosystem services and food production. Species may be able to survive these events through evolutionary adaptation, a process by which they adapt to the altered environment (Bell & Gonzalez, 2009; Klausmeier *et al.*, 2020; Opedal, 2019). However, species within complex communities face selective pressures to adapt not only to the new environment but also to changes in interactions with other species in the community. Investigating adaptation to altered environments without considering complex species interactions will provide an incomplete understanding of the process.

Plant-pollinator interactions are integral to the reproductive success of many plants and are key in maintaining biodiversity (Bascompte & Scheffer, 2023; Bascompte & Stouffer, 2009; Hegland *et al.*, 2009; Labonté *et al.*, 2023; Opedal, 2019). As temperatures rise, mismatches between plants and their pollinators can result in decreased pollination success and, consequently, diminished plant reproduction (Labonté *et al.*, 2023). This vulnerability is particularly pronounced in insect-pollinated plants, as their emergence is intricately tied to pollinators whose life cycles are directly influenced by temperature. Numerous studies (Hegland *et al.*, 2009; Menzel *et al.*, 2006; Miller-Rushing & Primack, 2008) substantiate these observations. Furthermore, climate-induced shifts in plant-pollinator phenological events can push these vital species to the brink of decline or weaken species interactions that can cause critical transition to undesirable states such as collapse of the entire network (Baruah & Lakämper, 2024). The vulnerability of plant-pollinator communities to collapse has broader implications for biodiversity, ecosystem stability, and the provision of essential ecosystem services.

Eco-evolutionary dynamics play a pivotal role in shaping the complex relationships between species, driving their co-evolution as well as adaptation to environmental changes. One important factor that plays an important role in maintaining these complex relationship in

plant-pollinator networks is variation within species (Arroyo-Correa *et al.*, 2023; Baruah, 2022; Baruah & Wittmann, 2024; Cantwell-Jones *et al.*, 2024). In the context of plant-pollinator interactions, intraspecific variation in traits such as phenology becomes evident, where individuals exhibit variation in their emergence or flowering onset (Hegland *et al.*, 2009). This variation can arise due to a genetic component As anthropogenic changes drive increases in temperatures, understanding the eco-evolutionary changes in traits impacting plant-pollinator interactions becomes paramount. The variation in these traits can significantly influence species interactions within mutualistic communities. However, there is currently no theoretical framework or understanding of how such trait variation could evolve in response to multiple selective pressures, such as shifts in local environmental optima, changes in competitive pressure from species within a guild, or alterations in mutualistic partners, all of which can change simultaneously when local environmental temperature shifts. Hypothetically, a strong directional shift in environmental optima could reduce genetic variance within species, potentially hindering adaptation to new conditions. However, this scenario becomes more complex in the context of multiple species interactions within a large plant-pollinator network. It is also possible that due to the presence of various species interactions (both positive and negative), a significant shift in environmental temperature could potentially also increase trait variance in species, also commonly known as "evolvability" (Houle, 1992; Opedal, 2019). This might occur due to conflicting selective pressures: one driving species to remain matched with their mutualistic partners, and the other pushing them to adapt to the new environmental conditions while also competing with others. These dynamics could ultimately shape the resilience of complex plant-pollinator networks in novel environments. However, these hypotheses lack theoretical support at present.

The complex relationship between the structure and function of plant-pollinator networks requires an additional focus on the consequences on the structural aspects of these interactions on species persistence. By adopting a network theory approach, one can define the connectance of a specific plant-pollinator network as the proportion of established connections between mutualistic partners in comparison to the total potential interactions. Another crucial concept inherent to plant-pollinator networks is their nestedness. This term delineates the relationship among subsets of interacting species. In the context of plant-pollinator networks, it has been observed that a limited number of hyper-generalist species exist, whose set of interaction partners encompasses the set of partners of more specialized species (Bascompte *et al.*, 2003; Bascompte & Stouffer, 2009). This relationship is often evident across multiple levels, contributing to the nested structure of the plant-pollinator networks (Guimarães *et al.*, 2017). Beyond mitigating the risk of extinction, the high number of interactions involving a generalist species appears to confer a selective advantage on their mutualistic partners including specialists (Arroyo-Correa *et al.*, 2023; Baruah, 2022; Bascompte *et al.*, 2003). The positive impact of having a greater number of mutualistic partners extends to the whole of the plant-pollinator network. Network connectance is a characteristic tied to the architecture of plant-pollinator communities, and it is crucial to consider it in addition with the total number of species. Previous studies have

demonstrated that architecture of a plant-pollinator network quantified by connectance or nestedness appears to enhance the resilience of plant-pollinator networks (Baruah, 2022; Baruah & Lakämper, 2024; Bastolla *et al.*, 2009). Taking all these considerations, the architecture of such plant-pollinator networks is bound to interact with eco-evolutionary dynamics and thereby impact species responses to increases in warming.

In this study, we develop a theoretical framework to assess how complex mutualistic plant-pollinator networks can undergo evolutionary adaptation through genetic evolution, despite intricate relationships with both partner species and competitors. In such mutualistic plant-pollinator interactions, phenology and variation in traits such as phenology, such as insect emergence and/or plant flowering, play a critical role in successful plant-pollinator interactions. We present a theoretical model in which we model such a trait that is dependent on environmental temperature. In addition, we model how the variation in such trait can evolve under strong selection pressures due to a shift in the local environmental temperature, and examine how such shift might influence eco-evolutionary adaptation of species.

We introduce a quantitative eco-evolutionary framework based on modified generalized Lotka-Volterra equations, allowing for the evolution of the trait mean and its genetic variance. We then compare scenarios where 1) only the mean trait evolves, 2) where both mean trait and genetic variance evolve, and 3) where species do not evolve at all, to understand their relative impacts on adaptation to novel environmental temperatures. Our analysis disentangles the roles of various eco-evolutionary factors and network architectural metrics, exploring whether a species' position within a complex community or its proximity to a super-generalist, or its closeness to local environmental optima is more critical for species survival in such complex networks. We emphasize the importance of evolving trait variance in determining the resilience of these networks, alongside the competitive pressures a species faces relative to its position in the mutualistic network, determined by its degree and distance from a super-generalist. We argue that evolutionary rescue is strongly influenced by a species' position within the mutualistic system, including whether it occupies a peripheral role, the level of competition it faces, and its distance from the environmental optimum.

2 Methods and Materials

2.1 Modelling framework: Plant-pollinator mutualistic dynamics

We model the dynamics of pollinators N_i^A and plants N_i^P in an ecologically relevant quantitative trait z that relates to its optimum temperature. Here the superscript of A, and P stands for pollinators and plants respectively. Within each plant or pollinator species i, the trait is normally distributed given by, $p_i^{(A,P)}(z,t)$, with mean μ_i and phenotypic variance ρ_i, with each individual having its own trait value z. The governing dynamical equations of population dynamics can be written with modified Lotka-Volterra equations. The per-capita growth rate of pollinator, $r_i^{(A)}(z)$, and plants, $r_i^{(P)}(z)$, can be written as modified from Baruah & Lakämper (2024);

Baruah & Wittmann (2024) (see details in supplementary appendix):

$$r_i^A(z) = \underbrace{b(z,T)}_{\text{growth rate}} - \underbrace{\alpha_{ii}^A N_i^A}_{\text{density dependence}} - \underbrace{\int \sum_{j=1, i\neq j}^{S_A} N_j^A \alpha(z,z''') p_j^A(z''',t) dz'''}_{\text{trait-based inter specific competition}} + \tag{1}$$

$$\underbrace{\int \frac{\sum_{k=1}^{S_P} \gamma(z,z') A_{ik} N_k^P(t)}{1 + H \int \sum_{k=1}^{S_P} \gamma(z,z'') A_{ik} N_k^P(t) p_k^P(z'',t) dz''} p_k^P(z',t) dz'}_{\text{trait-based mutualistic interaction}} \tag{2}$$

where, $N_i^{A,P}$ gives the density of species i belonging to either animals or plants. In this model, $b(z,T)$ denotes the temperature-dependent growth rate of a specific phenotype, independent of competitive or mutualistic advantages for both animals and plants, each exhibiting a similar dependency. This implies that individuals within a guild will experience the impact of local temperature, denoted as T. S_A, S_P are the number of pollinator and plant species respectively. H represents the handling time, while A_{ik} signifies the corresponding entry in the adjacency matrix A, with a value of 1 indicating interaction between species i and k, and 0 representing no interaction. α_{ii}^A in equation 1 refers to density dependence of species i (here pollinator), and $\alpha(z,z''')$ refers to a Gaussian pairwise competition kernel between phenotypes of different species belonging to the same guild of species i.e., either pollinators or plants. among species within their respective guild. This formulation suggests that if different pollinators have similar optimal temperatures, indicating they become active or emerge at those temperatures, the intensity of interspecies competition for resources, such as the pollen of the plants flowering at the same time, will increase. Consequently, the formulation becomes:

$$\alpha(z,z''') = \alpha_0 \exp(-\frac{(z-z''')^2}{w_c^2}) \tag{3}$$

In addition, $\gamma(z,z')$ characterizes mutualistic interactions among individuals, where z denotes the optimum temperature of a pollinator individual and z' denotes the optimum temperature of a plant individual. This function can also be modeled as a Gaussian function:

$$\gamma(z,z') = \frac{\gamma_0}{d_i} \exp \frac{-(z-z')^2}{w^2} \tag{4}$$

In this equation, γ_0 represents the average strength of mutualistic interactions, while w controls the extent of interaction between individuals. When the optimal temperatures of a plant and a pollinator are similar, mutualistic benefits are enhanced. Biologically this means that the flowering temperature of plants matches the emergence temperature of pollinators, increasing the likelihood of mutualistic interaction (Baruah & Lakämper, 2024; Guimarães *et al.*, 2011; Thompson *et al.*, 2002). Temperature strongly influences species phenology, such as plant flowering times and pollinator emergence, which are often tied to monthly temperatures. Thus, mutualistic interactions are more likely when their optima temperature trait align (Hegland *et al.*, 2009).

The temperature-dependent growth or tolerance curve is derived from a modified version of the studies by Amarasekare & Johnson (2017); Baruah & Lakämper (2024):

$$b(z,T) = \frac{g_i}{b_w} \exp\left(\frac{-(T-z)^2}{2b_w^2}\right) - k_i \tag{5}$$

In this equation, T represents the local temperature, while b_w and g_i are parameters that shape the temperature tolerance curve. The parameter b_w determines the width of the curve, and the ratio $\frac{g_i}{b_w}$ influences the height of the peak of the curve (Amarasekare & Johnson, 2017; Åkesson *et al.*, 2021). The mean trait of a species i thus is under selective pressure from changes in the local optimum temperature T and from the strength in inter-species competition.

Taking everything together, the population dynamics of animal species i can be written as

$$\frac{dN_i^A}{dt} = N_i^A \left(b_i(T) - \alpha_{ii}^A N_i^A - \sum_{i \neq j}^{S_A} \alpha_{ij}^A N_j^A + \gamma_{ik} \right), \tag{6}$$

where, α_{ij}^A, is the evolutionary impact of competition by pollinator species j, on species i based on their mean trait values, and γ_{ik} is similarly the evolutionary mutualistic impact of plant species k on pollinator i. Here, exact formulation of α_{ij}^A and γ_{ik} is given in the supplementary section 1. Similarly, an analogous equation can be formulated for the plant species with index A replaced by P. The evolutionary dynamics of the mean trait are given as:

$$\frac{d\mu_i^A}{dt} = h_i^2 \left(\bar{b_i}(T) - \sum_{i \neq j}^{S_A} \beta_{ij}^A N_j^A + \bar{\gamma_{ik}} \right) \tag{7}$$

and evolutionary dynamics of genetic variance

$$\frac{dV_i^A}{dt} = \frac{V_i^2}{2} \left(v_i(T) - \sum_{i \neq j}^{S_A} \Gamma_{ij}^A N_j^A + \nu_{ik} \right) \tag{8}$$

where, V_i is the genetic variance for trait μ_i for species i in a mutualistic community. Phenotypic variance in our modelling setup was given as $\rho_i = V_i + \epsilon$, where ϵ is the environmental variance, and ρ_i is the phenotypic variance. Thus, the broad sense heritability, h_i^2, also changes as genotypic variance evolves in response to changes in interspecific competition, mutualistic interaction, and tolerance to temperature. Here, $h_i^2 = \frac{V_i}{\rho_i}$ for a species i in question, $b_i(\bar{T})$ is the evolutionary impact of temperature on changes in the mean trait μ_i, β_{ij}^A is the evolutionary impact of competition on change in mean trait of species i, $\bar{\gamma_{il}}$ is the evolutionary impact of mutualistic trait-based interaction on changes in mean trait, $v_i(T), \Gamma_{ij}, \nu_{ik}$ are the environmental temperature, competition and trait-based mutualistic interaction on changes in the genetic variance of species i respectively.

3 Plant-pollinator networks and eco-evolutionary dynamics:

To capture rapid declines in the fitness of species within a plant-pollinator network as a consequence of a shift in the environmental optimum, we modeled the environmental optimum change as a press perturbation, representing a permanent shift in the environmental optimum, T. A qualitative overview of the modeling framework is presented in Figure 1.

To begin, we assembled 65 empirical plant-pollinator networks and their corresponding adjacency matrices, $\mathbf{A}$ (indicating species interactions), sourced from the web-of-life database. These networks varied in size, containing between 8 and 105 species, and exhibited a range of network metrics such as connectance.

After assembling these plant-pollinator adjacency matrices, we simulated the evolution of these networks under a constant optimum temperature, (T), set at 20, over a period of (10^3) time points. The initial conditions for the simulation included assigning random mean trait values to both plant and pollinator species, (μ_i), drawn from a uniform distribution $(U[15, 30])$. The environmental variance (ϵ) for all species was fixed at 0.1, and the initial genetic variance (V_i) was randomly sampled from a uniform distribution $(U[0.05, 0.1])$. All species started with an initial density of 1, and extinction threshold was fixed at $10 - 6$, and species falling below this density were fixed at 0. Additional parameter values used to simulate the communities to reach eco-evolutionary equilibrium are detailed in Table 1.

First we simulated the eco-evolutionary dynamics of plant-pollinator communities with constant genetic variance, and only the mean trait evolved in response to changes in competitive pressures and mutualistic benefits. This means that the right-hand side of Equation 10 was set to 0, keeping genetic variance constant at its initially assigned random values. This was done to let species adapt to the local environmental temperature as well as to their partners, without the erosion of genetic variance which could happen due to stabilising selection on the mean trait. Thus, sing Equations 6 and 7, we simulated the eco-evolutionary dynamics of 65 plant-pollinator communities until 10^4 time points. By this time, the plant-pollinator networks had reached a quasi-eco-evolutionary equilibrium. Subsequently, we used the final species densities and mean trait values at $t = 10^4$ as the starting point for the evolutionary rescue experiment.

4 Shift in optimum temperature and evolutionary response:

We aimed to evaluate the distinct effects of mean trait value evolution and trait variance evolution on the evolutionary rescue of complex plant-pollinator networks, comparing these outcomes to scenarios where only mean trait evolution occurs or where neither mean trait nor genetic variance evolves. Additionally, we sought to determine whether strength of trait-based competition exerts a positive or negative influence on evolutionary rescue and to identify the networks most susceptible to these effects. Furthermore, we investigated how a species' role within a network influences its likelihood of evolutionary rescue following an abrupt shift in environmental temperature, specifically examining whether being closely connected to a super-generalist or

Table 1: Parameters and their values with the description used in the study. $U[a, b]$ is the uniform distribution between a and b.

Symbol	Description
V_i	Genetic variance of species i.
h_i^2	Heritability of species i's trait which is $\frac{V_i}{\rho_i}$.
g_i	modulates the peak of temperature-dependent growth rate which was fixed at 1.5 for all species.
b_w	modulates the trade-off between temperature-dependent growth rate width, and peak, which was fixed at 2 for all species.
$\alpha_{ij}^{(A,P)}$	pairwise inter- and intraspecific competition. Intraspecific competition α_{ii} was fixed at 1 for all species, whereas interspecific competition α_{ij} was derived from equation 2.
d_i	degree of species i.
γ_0	average mutualistic interaction strength which was fixed at 1.5.
w^2	width of mutualistic Gaussian interaction kernel fixed at 1.
w_c	width of the Gaussian competition kernel fixed at 0.5.
k_i	mortality from the temperature tolerance curve fixed at 0.2 for all species.
T	Average local environmental temperature, which shifted from $22°C$ to $27°C$.
μ_i	Mean phenological trait values of species with units of degree Celcius. Their initial values are sampled from $U[20, 25]$.
N_i^A N_i^P	Population density of animal and plant species. Their initial value was 1 for all species.
ϵ	environmental variance which was randomly sampled for all species from $U[0.01, 0.05]$.
H	Handling time of species fixed at 0.25 for all species.

occupying a peripheral position within the network confers greater resilience.

We assessed the impact of an abrupt shift in temperature on the evolutionary rescue of species within plant-pollinator networks. Species in these networks are adapted to both their interacting partners and the local temperature. Before we describe the metrics that we quantified, we introduce two notations t_0 and t_{max}, where t_0 is the time point at which the local environmental temperature shifts, and t_{max} is the final time point of our simulations. Following a shift in temperature, as illustrated in Fig. 1, four potential outcomes may arise: 1) *Rescue*: rescue: species initially experience a decline due to maladaptation but may eventually adapt to the new temperature and recover, exhibiting a U-shaped population trajectory ($min(N_i(t)) < N_i(t_0); min(N_i(t)) < N_i(t_{max}), N_i(t_{max}) > 0$). 2) *Extinction*: certain species, due to specific eco-evolutionary factors, may decline and fail to recover, ultimately going extinct ($N_i(t_{max}) < N_i(t_0) < 10^{-3}$). 3) Stasis: some species might remain stable in their population size, showing no significant decline or increase despite the shift in temperature ($N_i(t_0) \sim N_i(t_{max}) \sim min(N_i(t))$). 4) Growth: certain species may experience an increase in population density if these species are adapted better to the new temperature than the one before ($N_i(t_{max}) > N_i(t_0); min(N_i(t)) \geq N_i(t_0)$)). Each of these metrics were binomial in nature for a species that fulfilled any of these criteria. In other words, for instance, if a species went extinct, then the extinct metric for that species was 1, and all other metrics thus would be zero.

Consequently, all four metrics are inherently dependent on each other in some way or another. Thus, following the temperature shift, we thus quantified each of these four metrics as shown in Fig. 1 and evaluated how such metrics were impacted by three models of only mean trait evolution, both mean trait and genetic variance evolution and no evolution.

In addition, we further evaluated how strength of interspecific competition, and a host of other variables such as network nestedness, network size, network connectance, modularity, species degree, species proximity to a super generalist, species trait lag, average strength of competition faced by a species before the shift in local environment influenced species response to abrupt environmental change. Species proximity to a super generalist was measured as the minimum number of edges that leads to the super generalist i.e., the species with the highest number of interactions. Species trait lag before the shift was calculated as the difference between the local environment and species mean trait before the environment shifted. Connectance was quantified as the total number of species links divided by the square of the number of species. To assess nestedness,employed the commonly used NODF method (Almeida-Neto *et al.*, 2008; Song *et al.*, 2017). However, the NODF measure has been criticized for its potential inaccuracies in reflecting true nestedness, as it may correlate with other network metrics, such as the number of species interactions and the total number of species (Lever *et al.*, 2014; Ulrich *et al.*, 2009). Consequently, the traditional NODF measure might need to be scaled according to connectance and the total number of species (Song *et al.*, 2017), which we used here. Modularity captures how clustered a mutualistic network is. Networks with high modularity will have groups of species that have more links among group members than with species outside these groups. Network modularity was from the R package *bipartite* (cite). However, these network metrics such as nestedness, connectance, network size and modularity are highly correlated (Baruah & Wittmann, 2024; Guimarães *et al.*, 2017). We thus used Principal Component Analysis (PCA) of the four network metrics to obtain two axes of structural variation which were the first two principal components (PC1 and PC2). We then used scores of PC1 as it correlated with high nestedness and connectance and low modularity values (see Fig S2-S3). PC2 was correlated with network size and we also evaluate the impact of network size on species eco-evolutionary response to abrupt environmental change.

To identify which explanatory variables might be significant in explaining evolutionary rescue based on the high-dimensional simulation data, we employed multivariate random forest regression. This method was well-suited to our analysis, as it accommodates categorical, non-linear, continuous, and transformation-invariant explanatory variables. We constructed 500 regression trees to assess the importance of these variables derived from our eco-evolutionary simulations. The multivariate response variable included the four outcomes we quantified: *Rescue*, *Stasis*, *Growth*, and *Decline*, all of which are binomial in nature. The explanatory variables were detailed in the previous paragraph. The importance of each explanatory variable was determined by permuting out-of-bag data. Given the multivariate nature of our response variable, we utilized a Mahalanobis distance splitting rule that accounts for correlations between the different

responses when constructing the regression trees. The multivariate random forest regression was performed using the R package *RandomForestSRC*. The multivariate random forest was used to obtain the variables which explained the most variation in the metrics that we quantified.

5 Results:

5.1 Eco-evolutionary response to abrupt change in temperature: role of evolution of mean and genetic variance

We used 66 empirical plant-pollinator networks, which have connectance values ranging from to 0.08 to 0.7. A sudden change in local temperature led to collapses of the entire plant-pollinator networks, particularly when neither the mean phenotype nor genetic variance can evolve, indicating that plant-pollinator networks may lack resilience to local temperature shifts without any evolutionary dynamics (Fig. 2A). However, when the mean phenotype evolves in response to abrupt temperature change, a number of species could adapt to the new environmental conditions, leading to higher resilience in comparison to when species do not evolve.

When genetic variance evolves in response to a shift in local temperature, both the mean phenotypic value of species and the constraints imposed by a fixed genetic variance are altered. This allows genetic variance to either increase or decrease in response to environmental changes. In this scenario, a large temperature shift induces a selection pressure to adapt to the temperature, while also maintaining trait matching with mutualistic partners. As a result, for instance as shown in Fig S1, just after the local environmental temperature shifts there are multiple regions on the trait axis where there are two significant peaks of high growth rates connected by a valley of very low growth rates, indicating the emergence of disruptive selection transiently (Fig. S1). For instance in Fig. S1, just after the local temperature shifts to 27 degrees, plant and pollinator density declines considerably and the per-capita growth rate has two peaks, one with the new optimum at 27 degrees and the other dictated by the super generalist species around 22 °C. Due to this reason, such a fitness landscape will lead to increase or decrease in trait density in those regions of the trait axis. However, due to our formulation and random mating trait distributions will remain normal, but it will have an effect of increasing trait variance. Eventually, this increase in trait variance will allow for faster evolution of the mean trait of these species. Consequently, adaptation to the new environmental temperature occurs faster. Once the species adapt to the new environmental temperature, stabilising selection on the mean phenotype causes species to lose the extra genetic variance they gained (Fig. S1 G-H), and they are only left with environmental variance given by ϵ.

We now investigate whether the number of species surviving, declining, or exhibiting evolutionary rescue, growth or stasis (Fig. 1) was impacted by inter-specific competition faced by a species, whether a species is a super-generalist or connected to a super-generatlist, or trait-lag to the environmental optimum.

5.2 Impact of competition, trait-lag, and species interaction

From the analysis of our multivariate random forest model we found that species competition, trait-lag, species degree, minimum path to super generalists are important metrics explaining our multivariate binomial response (Fig. S7). We thus present our results of all the metrics below in detail.

Without evolutionary dynamics of either the mean trait or the genetic variance, the number of species surviving a large shift in environmental temperature in the presence of moderate competition $\omega_c > 0.1$ is less than 25% overall. With evolutionary dynamics in mean trait only with strong competition $\omega_c > 0.3$ and large temperature shift > 7, the proportion of species that survived is less than when both the mean and genetic variance evolve. This was more evident in one plant-pollinator network (Fig. 3B) than in the other (Fig. 3A). Overall at low competition strength $\omega_c < 0.2$, even at large temperature shift > 8 more than 70% of species survive when both the mean and the genetic variance evolves in comparison to only the mean trait evolving in response to large temperature shift. Thus, competition strength had a profound impact on a species' evolutionary response to a shift in temperature.

We found that when there is no evolution, the proportion of species that survive and the proportion of species exhibiting evolutionary rescue were the lowest when compared with cases where the mean trait evolves, or where both the mean and the genetic variance evolve (Fig. 4A). In general, when the mean and genetic variance evolve the proportion of species surviving is greater than when only the mean trait evolves (Fig. 4A), while the proportion of species declining was similar when the mean trait evolves and when the mean and the genetic variance of the trait evolves. In addition, the proportion of species exhibiting evolutionary rescue was similar in the models of when the mean trait evolves and when the mean and the genetic variance evolves. We also observed that the proportion of species exhibiting increases in species density after a temperature shift of $6°C$ was slightly higher when the mean and genetic variance of the trait evolved (Fig. 4A). The proportion of species exhibiting stasis was very low (< 1 %) in all the three different models.

We observed that in all three models competition faced by a species was a strong driver for species decline (Fig. 4B). In addition, initial species trait lag when the environmental temperature shifts influenced the chances of species decline, evolutionary rescue, and species growth strongly. Higher trait lag led to more chances of species decline, which was similar across when species trait evolved or when both mean trait and genetic variance evolved. As species trait lag increased, chances of evolutionary rescue declined more steeply when species mean trait evolved in comparison to when both mean and genetic variance evolved. Furthermore, only when species had mean and genetic variance evolve, there was a high chance of species density growing particularly when species had low trait lag. We found that a species' position within the network influences its chances of undergoing evolutionary rescue or facing decline in response to an abrupt temperature shift. Specifically, species with a higher number of interactions (a higher degree) are less prone to decline and have a greater chance of exhibiting evolutionary

rescue, regardless of whether only the mean trait evolves or both the mean and genetic variance evolve (Fig. 4D). When genetic variance evolves, species experience fewer constraints on how much their mean trait value can shift, as observed in comparisons across the three models (Fig. S3), which is consequently associated with both evolutionary rescue and species decline (Fig. S4). Finally, a species proximity to super-generalist species can also aid in survival as well as evolutionary rescue chances (Fig. 4E).

5.3 Impact of network metrics on metrics of evolutionary response

Since network architecture metrics like nestedness, modularity, connectance, and network size are correlated, we used PCA to reduce them to two axes of variation. PC1 and PC2 together explained 99% of the variation, with PC1 being positively correlated with nestedness and connectance and negatively with modularity, while network size was negatively correlated with PC2 (Fig. S2). We found that the proportion of species undergoing evolutionary rescue was positively associated with network connectance and nestedness and negatively with modularity (PC1) (Fig. 5A). The proportion of species that exhibited growth following an abrupt environmental temperature shift was significantly higher when species evolved in both trait mean and genetic variance but showed no association with PC1. However, the proportion of species that declined was negatively correlated with PC1, indicating that higher nestedness and connectance could lead to fewer species declines in response to abrupt temperature shifts (Fig. 5B).

6 Discussion:

Rising environmental temperatures pose significant threats to biodiversity and the resilience of complex ecosystems, such as plant-pollinator networks. These networks are particularly susceptible to temperature fluctuations, as changes in local temperatures can disrupt plant-pollinator interactions, weakening community resilience (Freimuth *et al.*, 2022; Hegland *et al.*, 2009; Trunschke *et al.*, 2024). Such a decrease in resilience can trigger cascading effects that may ultimately lead to ecosystem collapse (Baruah, 2022; Lever *et al.*, 2014). The potential for these communities to adapt to new temperature conditions remains uncertain, especially given that these networks rely on temperature-dependent interactions. In this study, we aimed to understand how these complex communities respond to sudden temperature shifts by modeling evolutionary dynamics of a quantitative trait that determines species' response to temperature, akin to species phenology. We explore how evolutionary responses in species within these networks vary depending on whether traits influencing interactions evolve in both mean and genetic variance. Our findings indicate that species constrained to evolve solely in the mean show weaker adaptive responses compared to when both mean and genetic variance can evolve. Additionally, a species' position within the network and its association with the most generalist species influences its capacity for evolutionary resilience in response to abrupt changes. Finally, our results reveal that certain complex networks exhibit greater adaptive resilience than others in the face

of environmental change.

When environmental temperatures shift suddenly, species can respond in several ways: they may decline in numbers, increase in numbers, remain stable, or be "rescued" through evolutionary adaptation (Fig.1). Whether a species can survive such temperature shifts depends on whether it can maintain positive population density through growth, stability, or adaptation via evolutionary rescue. A critical factor in species adaptation to changes in temperature is genetic variance, as higher genetic variance enables quicker adaptation to new conditions (Baruah *et al.*, 2019; Lande, 2009; Reed *et al.*, 2010). In response to environmental change, species could often change in different ways, including changes in mean quantitative traits and genetic variance, as new selection pressures could favor phenotypes suited to the new environment. Our findings show that when genetic variance was allowed to evolve, more species successfully adapted to novel conditions compared to scenarios where genetic variance remained fixed (Fig. 3-4).

6.1 Evolution in two dimensions and species interactions

Due to a sudden increase in the environmental temperature, selection acting on species' mean trait to adapt to the new environmental optimum is generally directional in nature. Such directional selection reduces genetic variance (Lynch & Walsh, 1998; Roughgarden, 1972; Taper & Chase, 1985), and thus should potentially hinder adaptation of species in such networks. However, we observed an increase in genetic variance in most species, also known as "evolvability" (Houle, 1992; Opedal, 2019). This increase in genetic variance was largely due to complex inter-species interactions. For example, before the environmental temperature shifted to a new value, stabilizing selection maintained a single optimal trait peak, which could reduce the genetic variance of species in a plant-pollinator network (Fig. S1A). In our study, however, we ensured that genetic variance did not evolve prior to the environmental shift. This was done to enable species to adapt to their partners while also aligning with the local environmental temperature. Following the environmental temperature shift, some species exhibited substantial increases in genetic variance. These species experienced significant trait lags and intense interspecific competition. Immediately after the environmental shift, there is a transient phase in the evolutionary dynamics, characterized by a lag in the response of species, as shown in Figure 2. During this phase, certain groups of plants or pollinators initially resist shifting their mean trait values. This resistance arises because their positive growth rates are sustained by their partners, who also remain near the same trait region. At the same time, the new environmental temperature creates an additional fitness peak, exerting strong selective pressure for species to shift toward it. The opposing selection pressures—one to remain at their current trait values due to their partner species, and another to adapt to the new environmental peak—result in transient disruptive selection, leading to an increase in genetic variance. Higher the trait lag, higher the selection pressure and thus the higher the increase in genetic variance. This, although, happens very transiently. This transient increase in genetic variance does not gaurantee survival as species could already have low equilibrium density (due to species being specialist for

instance) before the environment shifted, or due to strong competition which could drive them to extinction despite strong selection pressure to increase genetic variance (Fig. S1D). Eventually, the shift toward the new environmental temperature became stronger, resulting in a return to a single peak in the per-capita growth rate as more species reached the new equilibrium.

The lag in species traits significantly influenced whether they could survive the shift to a new environmental optimum, as shown in Figure 4C. When species experienced a greater initial trait lag, they could not adapt and match the new optimum. With evolutionary dynamics occurring in mean trait and genetic variance, species retained a positive chance of evolutionary rescue and thus survival even under maximum trait lag, in comparison with scenarios where only the mean phenotype evolved (Fig. 4A). Thus adaptation in mean and genetic variance led to a higher overall survival among species across all plant-pollinator networks (Fig. 4A). The likelihood of evolutionary rescue was also greater for species with a larger number of interactions, such as hyper-generalists, or for species that interact with such generalists (Fig. 4). Thus species, despite their few interactions, could also survive if they were interacting with these few super-generalist species. Thus, these super-generalist species indirectly contribute to species survival through evolutionary rescue. These super-generalists play a crucial role in mutualistic systems not only due to the role they play in increasing community robustness against external perturbation but also their critical role in aiding recovery when communities transition to less favorable states, as observed in both empirical and theoretical studies ((Baruah, 2022; Baruah & Wittmann, 2024; Bascompte & Jordano, 2013; Bascompte & Scheffer, 2023; Kaiser-Bunbury *et al.*, 2017, 2014; Lever *et al.*, 2020).

However, specialist species can also survive abrupt temperature changes, contingent on whether their genetic variance is subject to evolutionary change. Our results reveal that when species evolve in mean trait and genetic variance, increases in genetic variance was not determined by whether a species was a generalist or a specialist (Fig. S5 B-C). Instead, strong increases in genetic variance was strongly positively correlated with initial trait lag and the intensity of interspecific competition (Fig. S5 D-E). This suggests that high interspecific competition and substantial trait lag promoted strong increases in genetic variance. As a consequence, as species genetic variance rises, species exhibit enhanced evolutionary adaptability, allowing significant shifts in mean trait values (Fig. S5 F). These shifts in mean traits are closely linked to evolutionary rescue, as illustrated in Fig. S4. Thus we observed a positive link between maximum genetic variance reached for a species and chances of evolutionary rescue (Fig. S5 A). However, we also observed that maximum genetic variance achieved by a species was also positively associated with chances of population decline (Fig. S5A). This pattern arises because maximum genetic variance is also linked to competition (Barabás *et al.*, 2022) and initial trait lag — factors that concurrently also drive increase in genetic variance (Fig. S5A) and species decline (Fig. 4B-C). On one hand, higher increase in genetic variance facilitates flexibility in large mean trait shifts, enhancing evolutionary rescue, but on the other hand, the conditions driving increase in genetic variance—intense competition and significant trait lag — simultane-

ously heighten extinction risk of species. Nevertheless, we believe increase in genetic variance still is beneficial for species evolutionary survival as without it species have a higher likelihood to decline as we observe in figure 4A.

6.2 Effect of species competition on evolutionary response

Interspecific competition thus had non-zero impact on species increase in genetic variance. We modelled a quantitative phenotypic trait that depended on temperature. If multiple pollinators interacting with one particular plant had similar phenotypic values, for instance, having similar temperature at which they emerge, these pollinators would thus compete among each other, with the pollinator species having a higher density benefiting more from interacting with the particular plant species than others, resulting in additional mutualistic benefits. As a result of, certain pollinator species will be more adapted to match the optimum phenotypic trait of certain plant species than others. Indeed species competition has been suggested to impact species trait variance positively, which consequently impacts the relationship between species diversity and functional trait diversity (Barabás *et al.*, 2022). Competition could increase disruptive selection among competing species which consequently could increase species trait variance (Barabás *et al.*, 2022). In our study, among other factors such as species trait lag, species competition was positively correlated with maximum trait variance reached by species. Thus, a combination of trait-lag, i.e., selection to match the new environmental temperature, interspecific competition, and selection to match intergroup partner's phenotypic trait led to increases in species genetic variance, which had a positive impact on species survival and evolutionary rescue.

6.3 Effect of network architecture on evolutionary response

Previous studies have demonstrated that complex network architecture significantly influences the feasibility (Arroyo-Correa *et al.*, 2023; Baruah, 2022; Bastolla *et al.*, 2009), resilience, and stability of mutualistic networks (Baruah & Wittmann, 2024; Saavedra *et al.*, 2017). Moreover, evolutionary dynamics interact with network architecture to determine when complex mutualistic networks collapse under increasing temperatures (Baruah & Lakämper, 2024). Our study contributes to this growing body of literature by exploring how network architecture affects various aspects of species' evolutionary responses to abrupt temperature changes. We found that network features such as nestedness and connectance positively influence the likelihood of evolutionary rescue, ultimately increasing the proportion of species that survive. Nestedness in complex mutualistic networks refers to hierarchical structures where a few species have numerous interactions, and specialist species interact with subsets of species linked to super-generalists. Thus, in the event of an abrupt increase in temperature, if a super-generalist was able to adapt to a novel environmental, it is likely going to translate into survival of almost all other species that are interacting with such a super-generalist species. However, in a less nested network, there are many different species which could have similar number of interactions, and survival of many different species will be interlinked with survival of other species. Similarly,

networks with high connectance—indicating a greater number of intergroup (e.g., plant-animal) interactions—showed a positive correlation between evolutionary rescue and species survival. This is likely because a higher number of intergroup interactions translates to more positive interactions, fostering higher number of species survival (Baruah, 2022; Cantwell-Jones *et al.*, 2024).

Conversely, modularity, which reflects the presence of distinct species clusters within a network, was negatively correlated with evolutionary rescue. This aligns with prior findings showing that modularity can be beneficial under certain environmental conditions (Bascompte & Stouffer, 2009; Garay-Narváez *et al.*, 2014; Olesen *et al.*, 2007) but detrimental under others (Gilarranz *et al.*, 2017). For example, in highly modular networks, localized perturbations—such as the extinction of a species—are less likely to propagate beyond the affected module (Gilarranz *et al.*, 2017). However, in our study, modularity was detrimental to evolutionary rescue and overall survival. This is likely because the temperature shift impacted all species in the network uniformly, rather than being localized. Under such conditions, evolutionary shifts in mean trait of species may be constrained, as localized clusters of mutualistic interactions can hinder species from rapidly adapting to new environmental temperatures.

A previous study theoretically proposed that mutualistic interactions could reduce the likelihood of evolutionary rescue in two-species mutualistic systems (Goldberg & Friedman, 2021). This is attributed to their mutual dependence, which, combined with competition, could increase the risk of extinction rather than facilitating evolutionary rescue. Mutualistic systems, such as plant-pollinator networks and those we modeled, ranged in complexity from as few as eight species to as many as seventy. Our findings reveal a negative correlation between the proportion of species exhibiting evolutionary rescue and the size of the network (see Fig. S6). This suggests that larger networks with more species are less likely to exhibit evolutionary rescue, similar to what was observed in the two-species system of Goldberg & Friedman (2021). Network size, however, is not an indicative parameter to accurately capture the strength of mutualistic systems as it captures within-guild competition in addition to between-guild positive interactions. Connectance, which quantifies the number of inter-guild mutualistic interactions (or nestedness), is a true indicator of mutualistic systems in a way that as connectance between inter-guild plants and pollinators increases, so does the overall strength of positive interactions in such systems. Indeed, as connectance and nestedness increases, the proportion of species exhibiting evolutionary rescue indeed increases. Consequently, our study does not support the notion that mutualistic interactions hinder evolutionary rescue (Goldberg & Friedman, 2021). On the contrary, they appear to promote it, particularly when species evolve along the mean and the genetic variance, and as the number of species in such system increases. This genetic variance increased due to interspecific competition and trait lag, thereby enhancing the likelihood of evolutionary rescue. In addition, we also incorporated the evolution of species' genetic variance in our model (Feiner *et al.*, 2021). The differences in our results occur because Goldberg & Friedman (2021) system comprised of only two species which were dependent on each other

both in terms of mutualistic interaction and also competition.

It is important to acknowledge certain limitations in our modeling framework. Notably, we did not incorporate mutation, which could arise under varying selection pressures (Alekseeva *et al.*, 2020; Wahl & Campos, 2023). Mutational variance, which we excluded, could further contribute to increases in genetic variance of species' mean traits. This increase in genetic variance, often called as evolvability, could be primarily driven by mutations, facilitating species adaptation to novel environments (Bell & Gonzalez, 2009; Klausmeier *et al.*, 2020). Additionally, our framework did not account for demographic stochasticity (Peniston *et al.*, 2020), environmental fluctuations (Draghi *et al.*, 2024), or their interactions, all of which could significantly influence species responses to environmental temperature shifts. Depending on the nature (or "color") of stochasticity in environmental fluctuations, these factors might either enhance or hinder evolutionary adaptation to novel environments (Draghi *et al.*, 2024; Peniston *et al.*, 2020). We did not model these in our framework and thus they represent avenues for future research.

7 Acknowledgements

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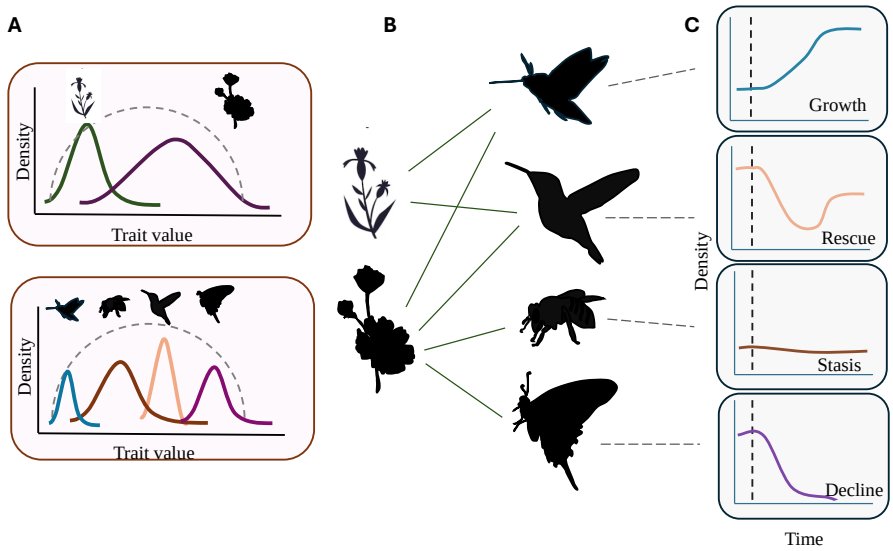

Figure 1: Example graphic of our modelling setup of an example plant-pollinator community of six species, two plants and four pollinators in response to a change in temperature. A) Species optimum trait distribution of plants and pollinators at equilibrium before an abrupt environmental shift, with dashed curved lines indicate the tolerance of species to temperature, or region in trait space where species have positive rate of growth. (B) Example plant-pollinator network before the onset of large temperature change, where some species have high number of interactions than others. (C) As the environment (temperature) changes suddenly after a certain time point shown by the dashed vertical line, the four pollinators belonging to the community could exhibit four different dynamical behaviors namely 1) Growth: where a pollinator could show an increase in density after the onset of the environmental change, 2) Rescue: another pollinator for instance could exhibit firstly a decrease in density and then an increase following adaptation to the new local environmental temperature, 3) Stasis: another pollinator could on the other hand not exhibit any change in density despite a shift in the local environmental temperature, 4) Decline: finally a pollinator either due to structure of the network, or due to eco-evolutionary factors, or due to maladaptation could decline and go extinct in response to a shift in the environment. We quantify all the four outcomes and examine how these outcomes are impacted by three different models namely when species do not evolve, when only the optimum mean trait evolve, and when both the mean trait and the genetic variance evolves in response to a shift in optimum.

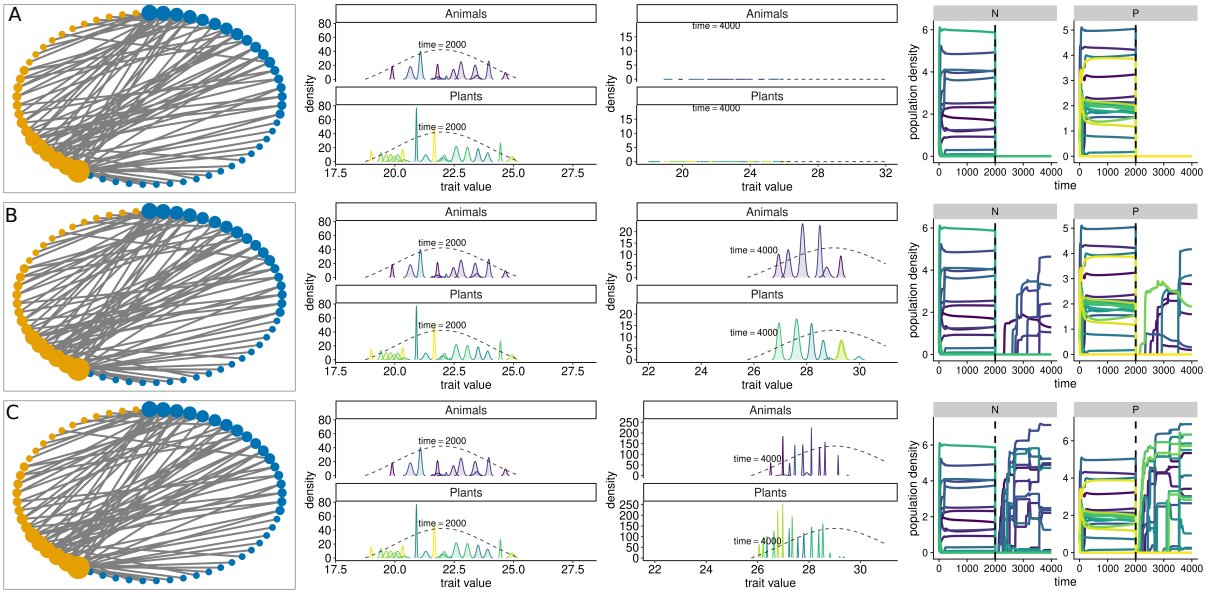

Figure 2: Example eco-evolutionary dynamics of a 86 species plant-pollinator network in response to a large shift in optimum environment for three different models: no evolution (A), evolution of mean trait (B) and evolution of mean and genetic variance (C). Initially we first allow all species to adapt to local environmental temperature of 22^0C by letting species evolve in their mean trait with constant phenotypic variances. We randomly sample mean trait values of all species from a random normal distribution with a mean of 22 and variance of 2, and density of all species were fixed at 1 at t=0. Genetic variance at t=0 was fixed at 0.1 and environmental variance was also fixed at 0.1. In A,B,C for the first 2000 time points all conditions are the same. At time point of 2000, the local temperature then shifts to 27^0C. In A) mean and genetic variance of trait does not evolve. As a result all species go extinct. In B) we let the mean trait evolve in response to abrupt shift in local temperature, and some species mange to survive and adapt to the new environment. In C) both mean and genetic variance evolve and some species do survive and adapt to the novel environment. Parameters are as in Table 1.

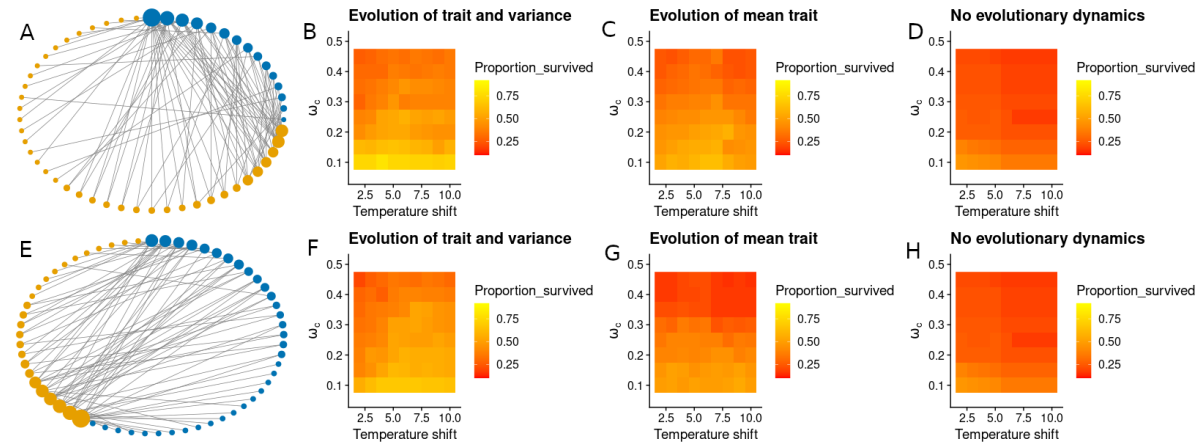

Figure 3: Parameter space for strength in species competition ω_c and the magnitude of temperature shift on final survival of species, for three models and two contrasting plant-pollinator networks. (B,F) When mean trait and genetic variance evolves, at higher strength of interspecific competition and higher temperature shift, the proportion of species that survive is higher in comparison to the other two models (C,G) evolution of only mean trait, and (D,H) no evolution, across the two different networks. Even during an unrealistic large temperature shift of 10^0 C at low competition strength $\omega_c = 0.1$, we observe almost 60% survival of species when both mean trait and variance evolves. Parameters as in table 1.

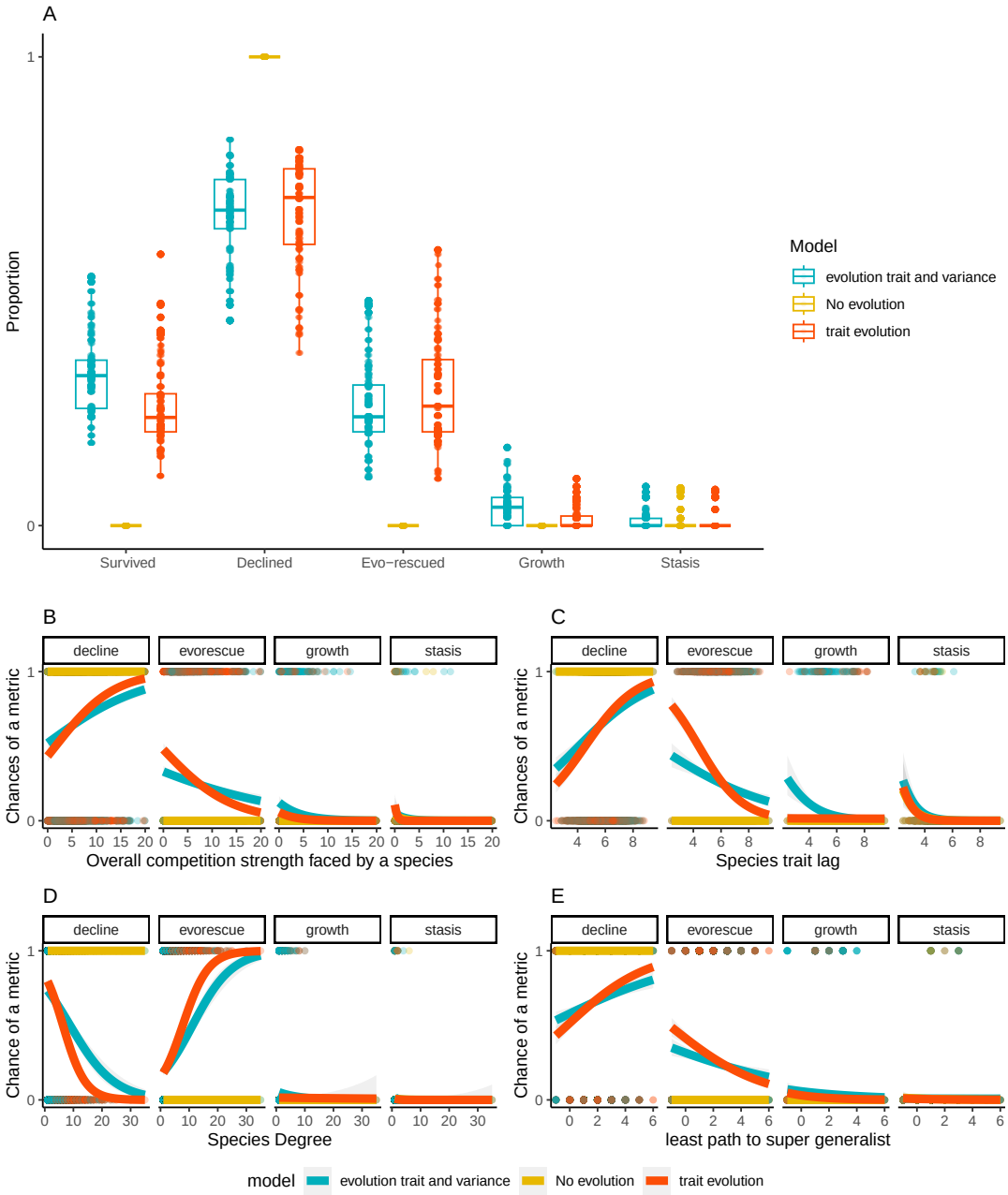

Figure 4: Proportion of species that (A) survived, declined, showed evolutionary rescue, growth or stasis for the three different models after the shift in the environmental temperature, (B) against net competition faced, (C) species trait lag, (D) species degree, (E) minimum path to a super generalist. (A) A higher proportion of species survived or exhibited growth in the models where both the mean and genetic variance evolved, compared to the other two models. The proportion of species that declined was highest when there was no evolution of either the mean trait or the genetic variance. The proportion showing evolutionary rescue was similar in both the model where only trait evolution occurred and the model where both trait and variance evolved. (B) As net competition increased, the likelihood of evolutionary rescue or growth decreased, but the decrease was steeper when only the mean trait evolved, and less pronounced when both the mean and genetic variance evolved. (C) Likewise, greater species trait lag resulted in more rapid declines across all models. Even at very high levels of trait lag, species still had a non-zero chance of evolutionary rescue, provided both mean and genetic variance were evolving. (D) Species with higher degrees were less likely to decline and more likely to exhibit evolutionary rescue when the mean trait evolved and when both mean trait and genetic variance evolved. (E) Species that are least connected to a super-generalist had higher chances to decline and low chances of exhibiting evolutionary rescue. Parameters as in Table 1.

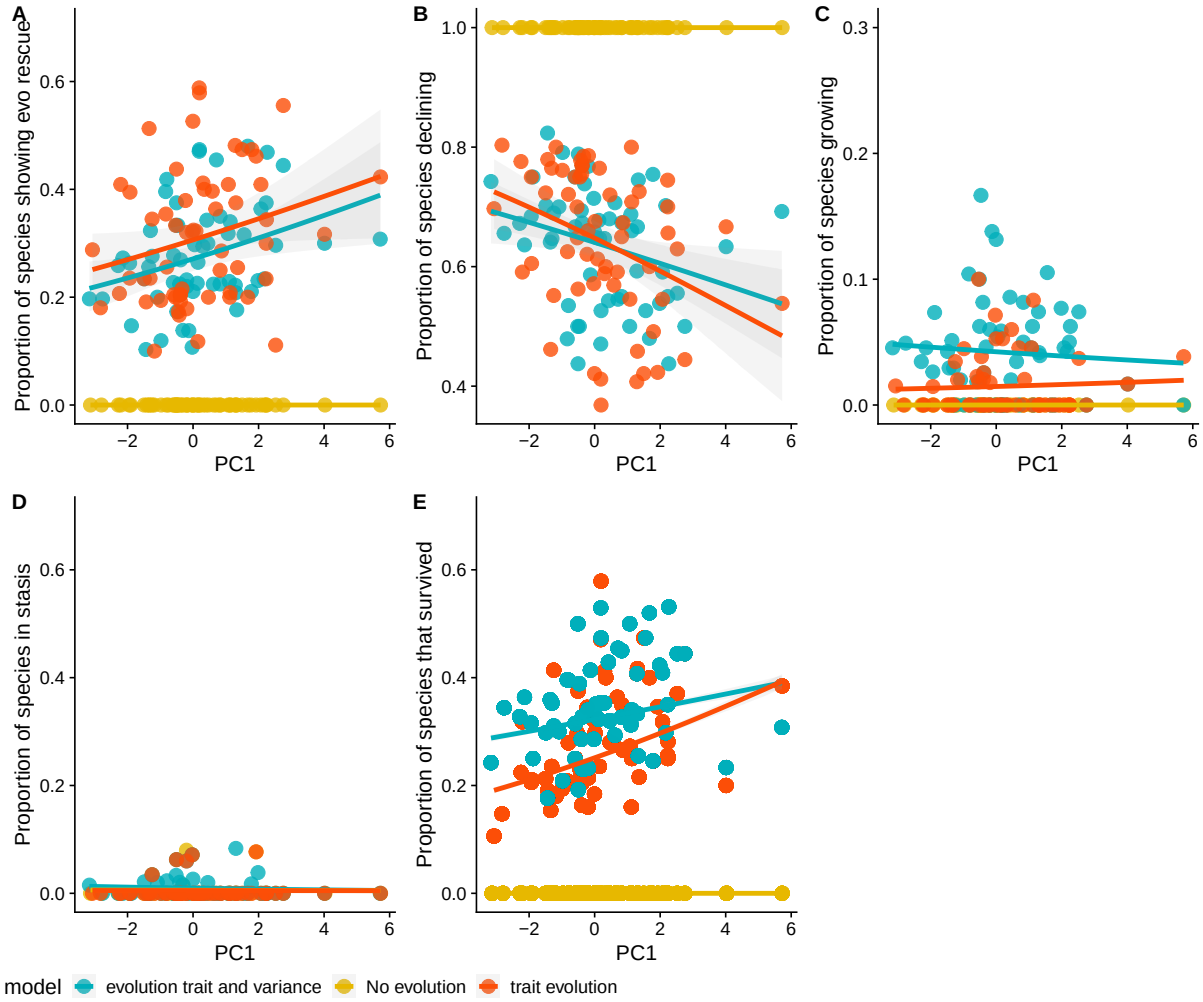

Figure 5: Relationship between proportion of species showing (A) evolutionary rescue, (B) decline, (C) growth, (D) stasis and (E) survival in relation to PC1 which correlates with high nestedness and connectance and low modularity of plant-pollinator networks. Overall, larger PC1 values lead to more species surviving and exhibiting evolutionary rescue and slightly fewer species exhibiting growth for models which had evolution of mean trait and evolution of mean and genetic variance. Parameters as in table 1.

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