
Dinâmica evolutiva de anéis miméticos em comunidades ecológicas heterogêneas



IRINA BIRSKIS BARROS

São Paulo

Maio, 2017

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Evolutionary dynamics of mimetic
rings in heterogeneous ecological
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A poesia está guardada nas palavras — é tudo que eu sei.
Meu fado é o de não saber quase tudo.
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Não tenho conexões com a realidade.
Poderoso para mim não é aquele que descobre ouro.
Para mim poderoso é aquele que descobre as insignificâncias

[(do mundo e as nossas).

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Fiquei emocionado.
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Resumo



No mimetismo Müllleriano, indivíduos de diferentes espécies, ao compartilharem um mesmo sinal de advertência, beneficiam-se mutuamente devido ao menor risco de predação. Em comunidades ricas em mímicos há a formação de grupos simpátricos de espécies denominados anéis miméticos, que compartilham os mesmos sinais de advertência, como por exemplo padrões de coloração. A coexistência de anéis miméticos parece paradoxal, uma vez que, em teoria, a seleção favoreceria a convergência das espécies impalatáveis e, portanto, geraria um único padrão de cor. A evolução de diferentes anéis miméticos em habitats distintos poderia explicar a coexistência desses anéis em uma comunidade. No entanto, a maneira como as espécies utilizam esses habitats talvez influencie também a emergência dos múltiplos anéis miméticos. Utilizamos modelos matemáticos e simulações computacionais para melhor compreender como a heterogeneidade de habitats, a seleção ambiental e espécies generalistas de habitat influenciam a formação de anéis miméticos em uma comunidade. Demonstramos que diferentes pressões seletivas, derivadas de uma heterogeneidade de habitats, podem favorecer a formação de anéis miméticos. Porém, a simples coexistência das espécies é suficiente para a emergência de anéis. Em simulações nas quais só havia seleção imposta por espécies impalatáveis ou pelo ambiente, o tempo de convergência foi mais rápido do que quando as duas forças seletivas atuavam juntas. Isto demonstra que provavelmente há conflito entre a seleção biótica e abiótica, não favorecendo o mesmo ótimo

fenotípico. A presença de uma espécie generalista de habitat favoreceu a convergência de espécies para um valor fenotípico similar, diminuindo a distinção entre os anéis. Um único anel foi formado quando os diferentes fenótipos favorecidos pela seleção imposta pelo ambiente eram muito similares entre habitats, ou quando muitas espécies eram generalistas de habitat. Nosso trabalho sugere que múltiplos anéis miméticos simpátricos são formados por uma complexa interação entre seleção biótica e abiótica e que só são possíveis em grupos no qual a diversidade é estruturada em pequenas escalas espaciais, como borboletas.

Abstract



Müllerian mimicry theory postulate that individuals of different species benefit from decreased per-capita attack risks by sharing similar warning signals. In species-rich mimetic assemblages, there is the formation of several distinct sympatric groups of species sharing the same warning signals, often color pattern, called mimetic rings. The coexistence of multiple rings seems paradoxical considering that selection among unpalatable species should favor convergence and thus reinforce a single color pattern. Different rings evolving in distinct habitats could explain the coexistence of multiple mimicry rings. However, the way species use the habitats might influence the emergence of multiple mimicry rings. We combined mathematical modeling and numerical simulations to explore how habitat heterogeneity, abiotic selection and habitat generalist species influence the formation of mimicry rings in a community. We showed that distinct selection pressures, derived from habitat heterogeneity, favored the formation of distinctive mimicry rings. Nevertheless, just the co-existence of species was enough to drive the emergence of the rings. Simulations in which there was just biotic or abiotic selection, time for convergence was faster than when both sources of selection acted together, suggesting conflicting selective pressures exerted by environment and co-existing species. In the presence of species that was habitat generalist, species converged to similar trait values, decreasing the distinctiveness of mimicry rings. A unique mimicry ring was formed if the different habitats optima in the community were

very similar or when most species were habitat generalists. Our results suggest that multiple sympatric mimicry rings are formed by a complex interplay between abiotic and biotic selection and is only possible in groups of animals in which local species composition is strongly affected by habitat heterogeneity such as butterflies.

Introduction



Species interactions have a fundamental effect on evolution and diversification of life (Thompson, 2006; Barraclough, 2015). Adaptive evolution due to species interaction can result in trait patterns at community level, shaping the organization of interacting assemblages (Elias et al., 2008; Newman et al., 2015). One striking example of community level patterns shaped by species interactions is the phenotypic convergence of mutualistic partners. Phenotypic convergence emerges in different mutualistic interactions such as plant-pollinator interactions (Anderson et al., 2014), plant-seed disperser interactions (Jordano, 1995), cleaning symbiosis in marine ecosystems (Stummer et al., 2004) and Müllerian mimicry, in which the per-capita predation risks of unpalatable individuals from different species with similar warning signals decay because they share costs of predators learning warning signals (Müller, 1879; Kapan, 2001; Ruxton et al., 2004; Meyer, 2006; Rowland et al., 2007; Elias et al., 2008). There are theoretical and empirical evidences that reciprocal selection imposed by mutualism can result in convergence between species (Guimaraes Jr et al., 2011; Thompson, 2006; Marek & Bond, 2009; Nuismer et al., 2013; Pinheiro et al., 2016). A central problem to address is in which scenarios selection imposed by mutualistic interactions lead to convergence in traits across interacting species. In this context, Müllerian mimicry represents a useful study system in which evidence for similar patterns of warning signals associated with defensive traits was recorded for different taxa, in-

cluding birds (Dumbacher & Fleischer, 2001), bumble bees (Plowright & Owen, 1980; Williams, 2007), butterflies (Langham, 2004), fishes (Randall, 2005), frogs (Symula et al., 2001; Stuckert et al., 2014), velvet ants (Wilson et al., 2012), and even plants (Lev-Yadun, 2009).

The great naturalist Fritz Müller described the mimicry among unpalatable species and used the first mathematical model in evolutionary biology to show that selection should favor convergence of warning signals among unpalatable species (Müller, 1879). In fact, similar phenotypic patterns in Müllerian mimicry is mainly due to selection favoring convergence in color patterns (Joron & Mallet, 1998; Mallet, 1999), although trait similarity in some mimetic species may be due to multiple evolutionary processes (Merrill et al., 2015), including shared evolutionary history (Kozak et al., 2015; Joshi et al., 2017) and introgression of genes associated with the color patterns in closed-related species (Pardo-Diaz et al., 2012). Empirical and theoretical studies corroborate the notion that convergence among unpalatable species in a community should emerge because of selection, forming mimetic rings, in which multiple unpalatable species show the same color pattern (Benson, 1972; Kapan, 2001; Pinheiro, 2003; Beatty et al., 2004; Elias et al., 2008). In some species-rich mimetic assemblages, multiple mimetic rings coexist (Papageorgis, 1975; Plowright & Owen, 1980; Papageorgis, 1975; Beccaloni, 1997; Marek & Bond, 2009). The coexistence of multiple mimetic rings in a community seems paradoxical, once species would have a maximum defensive benefit against predator if they all converged into a unique mimetic ring (Mallet & Gilbert, 1995; Joron & Iwasa, 2005).

One possible explanation for the coexistence of multiple mimetic rings in a community is that species in different habitats are facing distinct predators and different environmental selective pressures, favoring the emergence of distinct mimetic rings within a community (Mallet & Gilbert, 1995; Joron et al., 1999; Gompert et al., 2011). In fact, Müllerian rings of butterfly species are often associated with distinct habitats (Beccaloni, 1997; DeVries et al., 1999; Hill, 2010). However, in other groups in which Müllerian mimicry occurs, a single mimetic ring is formed across large spatial areas, as observed in catfishes (Alexandrou et al., 2011), frogs (Symula et al., 2001), and velvet ants (Wilson et al., 2012). Therefore, a problem to solve is how evolution and coevolution shape assemblages of interacting species and in which conditions habitat heterogeneity leads to the formation of multiple Müllerian rings within ecological communities. The answer to this question may, at least in part, rely in the habitat specialization and generalization of unpalatable species. Coevolutionary models for species-rich mutualisms suggested that just a few highly connected species (generalists) are enough to lead the emergence of phenotypic convergence in mutualistic interactions at community level by linking otherwise isolated groups of interacting species (Guimaraes Jr et al., 2011). Accordingly, habitat generalists, by linking otherwise isolated groups of unpalatable species, may prevent the emergence of multiple mimetic rings even if the community is structured in many heterogeneous habitats (Figure 1).

We combined mathematical model and numerical simulations to investigate how evolutionary and coevolutionary processes generate the multiple mimetic rings in a community. We address three main questions: 1) How

does the habitat heterogeneity influence the formation of mimetic rings in a community? 2) How important is environmental selection in shaping mimetic rings patterns in a community? 3) How does the presence of habitat generalist species influence the formation of mimetic rings in a heterogeneous community? We expect that heterogeneity will directly affect the coexistence of multiple mimetic rings (Figure 1 a-c). However, we hypothesize that species need to be habitat specialists, because only a few habitat generalist species may drive convergence to a single mimetic ring (Figure 1 d-f).

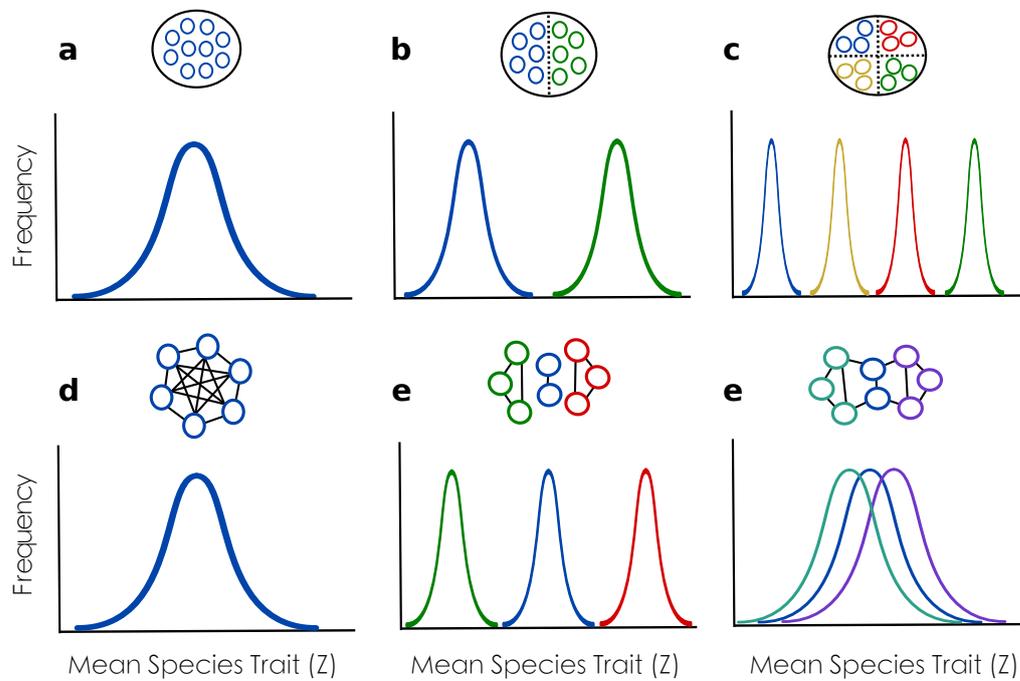


Figure 1: A theoretical example of the expected frequencies of traits values (Z) for distinct scenarios of habitat heterogeneity and species specialization in habitats. In a-c black circles represent communities, small circles represent species, and colors represent mean trait value of species. Species that have the same color compose a mimicry ring. a) Homogenous communities with only one habitat. In this case only one ring is formed. b) Community with just two habitats (separated by dashed lines). In this case, two rings are formed. c) Community with multiple habitats. In this case many rings are formed. In d-f species that co-occur are represented by a continuous line link. d) All species occur in all habitats. In this case only one ring is formed. e) Distinct species occurs in different habits. In this case each habitat formed a different mimicry ring. f) Two species are habitat generalist occurring in more than one habitat. In this case each habitat formed a mimicry ring, however their trait values are very similar.

Methods



Model

We used a coevolutionary model to explore how spatial heterogeneity and habitat specialization drive the emergence of multiple Müllerian mimetic rings in species-rich assemblages of aposematic species, i.e., unpalatable species that show warning signals. Our model was built upon a coevolutionary model for ecological networks (Guimaraes Jr et al., 2011; Andreazzi et al., 2017). We modeled the evolution of an aposematic species single trait, which describes the warning signal of the unpalatable species, such as warning color patterns. We assumed that this trait is a continuous trait with multiple genes contributing to its phenotypic expression and, consequently, the warning signal can be described as a real number associated to each individual of each population. We used a mean-field approach, modeling directly the evolution of the mean trait values for a given species i , (Z_i). In our model, trait values evolve as a consequence of selection imposed by different factors and species with similar trait values within a given ecological community form mimetic rings. All variables and parameters used in this model are listed in *Table 1*.

Initially the mean trait value of a given species i , Z_i^t , was randomly sampled from a uniform distribution between 0 and 1. Trait evolution was modeled as discrete events and at each time step t , Z_i^t changes due to both selective pressures imposed by the habitats in which the species occurs and selective pressures imposed by the coexistence with other aposematic spe-

cies j . We assumed selection imposed by the habitat favor particular traits, e.g., conspicuous colors when facing a particular habitat background (Ruxton et al., 2004; Cazetta et al., 2009). We assumed that aposematic species that co-occur in the same habitat share the same potential predator. As a consequence, selection mediated by the coexistence with other aposematic species and due to the presence of a common predator favored convergence in the trait values (Müller, 1879; Sherratt, 2006; Gompert et al., 2011).

We assumed that the same predator may attack species within a habitat but not species in different habitats. Predator-prey interactions may lead to complex eco-evolutionary feedbacks between traits and abundances (Abrams, 2000). As a first approximation, we focus in this study on the evolutionary dynamics, by assuming the predator has a generalist diet and does not rely on the aposematic species in the model for survival. In fact, generalist predators are likely to impose stronger selection favoring Müllerian mimicry (Beatty et al., 2004). Under the assumption of a generalist predator, we could avoid the eco-evolutionary feedbacks, because predator ecological dynamics was not affected by the consumption of aposematic species. Therefore, predators were not explicitly modeled in our approach.

The two components of selection, namely abiotic selection imposed by habitats and biotic selection imposed by co-occurring aposematic species through shared predators, determine the selection gradient, shaping mean trait value of species i in the next time step, Z_i^{t+1} . We assumed that for any given species at any time step, the selection gradient was defined as for the classical equation from quantitative genetics (Lande, 1976):

$$Z_i^{t+1} = Z_i^t + h_i^2 \sigma_{F_i}^2 \left(\frac{\partial W_i}{\partial Z_i} \right) \quad (1)$$

in which h_i^2 is the heritability of trait Z_i and assumed to be fixed, $\sigma_{F_i}^2$ is the phenotypic variance of Z_i^t and also assumed to be fixed, and $\frac{\partial W_i}{\partial Z_i}$ is the selection gradient, describing how changes in the mean trait value, Z_i , affect the mean fitness of the population of species i , W_i .

We assumed a linear selection gradient:

$$\frac{\partial W_i}{\partial Z_i} = \xi_i (Z_{i,m}^t - Z_i^t) \quad (2)$$

in which ξ_i is the sensitivity of the adaptive landscape to changes in trait matching. Using equation (2) and the fact that $h_i^2 = \sigma_{G_i}^2 / \sigma_{F_i}^2$, in which $\sigma_{G_i}^2$ is the additive variance, the equation (1) simplifies to:

$$Z_i^{t+1} = Z_i^t + \varphi (Z_{i,m}^t - Z_i^t) \quad (3)$$

in which $Z_{i,m}^t$ is the mean trait that defines the adaptive peak for the species at time step t and $\varphi = \sigma_{G_i}^2 \xi_i$, is a scaling parameter controlling the rate of directional change in Z_i due to selection. We defined the adaptive peak, $Z_{i,m}^t$, as the outcome of the multiple and possibly conflicting selective pressures imposed by the environment and the presence of other aposematic species:

$$Z_{i,m}^t = p_i \theta_i + \sum_j^S q_{ij} Z_j^t \quad (4)$$

in which p_i is the strength of abiotic selections on species i , and $0 < p_i <$

$1 - \sum_j^S q_{ij}$ and we set p_i to any species i , θ_i is the trait value favored by selection imposed by distinct environments in which species i occurs, q_{ij} is the contribution of selection on species i imposed by species j to the selection gradient, which favor trait similarity between aposematic species, $Z_i^t = Z_j^t$. We defined $\sum_j^S q_{ij} Z_j^t = q = 1 - p$ and the evolutionary effect q_{ij} is defined as:

$$q_{ij} = \frac{a_{ij} m_{ij}^t}{\sum_{n=1}^S a_{in} m_{in}^t} \quad (5)$$

in which a_{ij} is the abundance of species i relative to j , and m_{ij}^t is the trait matching of species i in relation to j at each time step t . We described a_{ij} as:

$$a_{ij} = \frac{\sum_{k=1}^N a_i^{(k)} a_j^{(k)} A^{(k)-2}}{\sum_{n=1}^S \sum_{m=1}^N a_i^{(m)} a_n^{(m)} A^{(m)-2}} \quad (6)$$

in which $a_i^{(k)}$ is the abundance of species i at habitat k , $a_j^{(k)}$ is the abundance of species j at habitat k , $A^{(k)}$ is the abundance of all S aposematic species at habitat k , and N is the number of habitats. The species abundances in the habitat, k , is an integer number randomly sampled from 1 to 10. Using a sensitivity analysis we explored the effects of species abundance in the evolutionary dynamics (see Figure S. 3). Trait matching was described as:

$$m_{ij}^t = \frac{e^{-\alpha(Z_j^t - Z_i^t)^2}}{\sum_{l=1}^S b_{il} e^{-\alpha(Z_l^t - Z_i^t)^2}} \quad (7)$$

in which α is weighting the evolutionary effect of color matching between species and $b_{il} = 1$ if both species co-occur at least in one habitat ($\sum_k a_i^{(K)} a_j^{(K)} >$

0), and $b_{il} = 0$ otherwise.

Because speciation events are unlikely to occur in a short period of time, we assumed that our species richness, S , is fixed. Also, because Müllerian mimicry is more likely to evolve in species-rich communities (Beatty et al., 2004), we simulated our model in a rich-community, with $S = 50$. We also assumed that our population is large enough and therefore, genetic drift has a negligible effect and also that the effects of migration are negligible. We explored the effects imposed by abiotic selective pressure and species habitat generalist using distinctive parameterizations (scenarios) of the model. For all scenarios we simulated the model over 100 times step and fixed $S = 50$, $N = 10$, $h^2 = 0.25$, and $\alpha = 2$. All simulations were run in R 3.1.3 (R Core Team, 2016).

How does the habitat heterogeneity influence the formation of mimetic rings in a community?

We used a set of simulations to explore the effects imposed by abiotic selective pressure. In this set of simulations, the community is structured in 10 different habitats and five habitat specialists occur in each habitat (*perfect modular scenario*). For example if 1, 2, 3, 4, and 5 are five species occurring only at the same habitat k , then $\theta_k = \theta_1 = \theta_2 = \theta_3 = \theta_4 = \theta_5$. For a better understanding of the abiotic and the biotic selection in the formation of mimetic rings, we used three different scenarios. In the first scenario both abiotic and biotic selections affect trait evolution (baseline scenario, $p = 0.3$). In the second scenario, we analyzed the sole effect of

Tabela 1: Variables and parameters of the model and their descriptions

Parameter	Description
Z_i	Mean trait value of species i
h_i^2	Heritability of trait Z_i
$\sigma_{F_i}^2$	Phenotypic variance of trait Z_i
$\frac{\partial W_i}{\partial Z_i}$	Selection gradient
ξ_i	Fitness sensitivity to change
$\sigma_{G_i}^2$	Additive genetic variance
p_i	Strength of abiotic selections
a_i	Abundance of a species i
A	Abundance of all species
α	Weight of evolutionary effect between species
S	Species richness
N	Number of habitats

abiotic selection on trait evolution by removing the effect of biotic pressure ($p = 1$ and $q = 0$). Finally, in the third scenario we analyzed the effect of just the biotic pressure in trait evolution, assuming that there was no abiotic selection ($p = 0$ and $q = 1$). Each simulation had 100 times steps and because we were interested on the role of the two sources of selection, we then compared how environmental and biotic selection varied across scenarios.

How important is abiotic selection in shaping mimetic rings patterns?

We also explored how different abiotic selection strength affects the co-evolutionary dynamics. For this we used a set of simulations considering different strength of abiotic selection values, p . We varied p from 0 to 1 by 0.1 and for each value we ran 20 simulations. In this set of simulations, we also considered the *perfect modular scenario*, in which our assemblage is structured in 10 different habitats and five habitat specialists species occur in one habitat. For explore the distinctness of mimetic rings we analyzed the variability of species trait value (Z_i) after 100 times steps in our simulation, which was enough time for species traits in all simulations to converge.

How does the presence of habitat generalist species influence the formation of mimetic rings?

We used a set of simulations to explore the effects of habitat generalist species, starting with a *perfect modular scenario*, in which all species were

habitat specialists occurring in just one habitat. In this set of simulations, we randomly sampled one species of our community to occur in all habitats, thus simulating a “supergeneralist” (SG) species. In each habitat k there is a trait value favored by selection imposed by the environments (θ_k), and θ_i is the trait value favored by selection when considering all the distinct environments in which species i occurs:

$$\theta_i = \frac{\sum_{k=1}^{H_i} h_{ik}\theta_k}{H_i} \quad (8)$$

in which $h_{ik} = 1$ if the species i occurs at habitat k and it is zero otherwise, and H_i is the total number of habitat species i occurs.

Furthermore, we varied the percentage of supergeneralists in our community from 10% up to 70%, by 10% increments, running 20 simulations for each percentage. We also analyzed the species trait value variability after 100 times steps. Then, to explore if the effects of supergeneralists were a consequence of the increased overall level of habitat generalization in the species assemblage, we contrasted 1) simulations in which supergeneralists were added to the community with 2) simulations in which the levels of habitat generalization of component species were randomly increased. We increased the level of generalization by randomly adding occurrences of habitats to species in the community. One occurrence is the same as the presence of a species in a new habitat. This means that, when we had 10% of supergeneralists in our community, for instance, we have added 45 occurrences in total in our community. However, this was structured, once a supergeneralist occurs in all habitats, which means that this species has 10

occurrences. We wanted to understand if there was any difference for the formation of mimetic rings if, for instance, the same 45 occurrences were randomly distributed in our community. For this, we started from a *perfect modular scenario*, which has 55 occurrences, and added from 10% up to 70% occurrences in the community and for each value, we ran 20 simulations. For a better comprehension of species distinctness, we analyzed the species trait value variability after 100 times steps and also the path length belong species in our community.

Results



In our model, we found distinct outcomes of the evolutionary dynamics of mimetic assemblages. Our results show that the formation of distinct mimetic rings in a community can be explained by habitat heterogeneity and abiotic selection. However, the distribution of species has great influence on this. Indeed, distinct mimetic rings are formed just by the coexistence of species. In contrast, the presence of just a few generalist species is enough to make all species converge to a single mimetic ring in a community. Below we will explain how each of these factors influences the formation of mimetic rings:

How does the habitat heterogeneity influence the formation of mimetic rings in a community?

We first explored the scenario in which each habitat has its own assemblage of species and there is no overlap between habitats in species composition (*perfect modular scenario*). In a *perfect modular scenario* and $p = 0.3$, species form mimetic rings, in which co-occurring species show the same trait value favored by abiotic selection (habitat optima, Figure 2a). We then used two sets of simulations to explore the role of the two sources of selection, namely abiotic selection and biotic selection. When there was just abiotic selection and no biotic selection, species also converged to habitat optima where they occurred (Figure 2b), indicating that selection imposed by co-occurring aposematic species is not needed to generate

habitat-based mimetic rings. Accordingly, there was formation of distinct mimetic rings even when the abiotic selection pressure was absent (Figure 2c), indicating that abiotic selection was not fundamental for mimetic rings formation. The complex interplay between abiotic and biotic selection also affected evolutionary dynamics. For example, if abiotic and biotic selective pressures were both affecting trait evolution the time to equilibrium was twice as longer than in scenarios in which just one selective pressure (abiotic or biotic) was driving trait evolution (Figure 2a-c).

How important is abiotic selection in shaping mimetic rings patterns?

Sensitivity analysis and an analytical approximation of our model showed that the trait values defining mimetic rings were not affected by the strength of abiotic selection (Figure 2d). Trait evolution led traits to the habitat optima if there was strength of abiotic selection ($p > 0$, Figure 2d). If there was no abiotic selection ($p = 0$), trait values of species from distinct habitats approached each other, converging species trait to a more similar value, decreasing the variability between species and, consequently, decreasing the distinctiveness between the rings (Figure 2c).

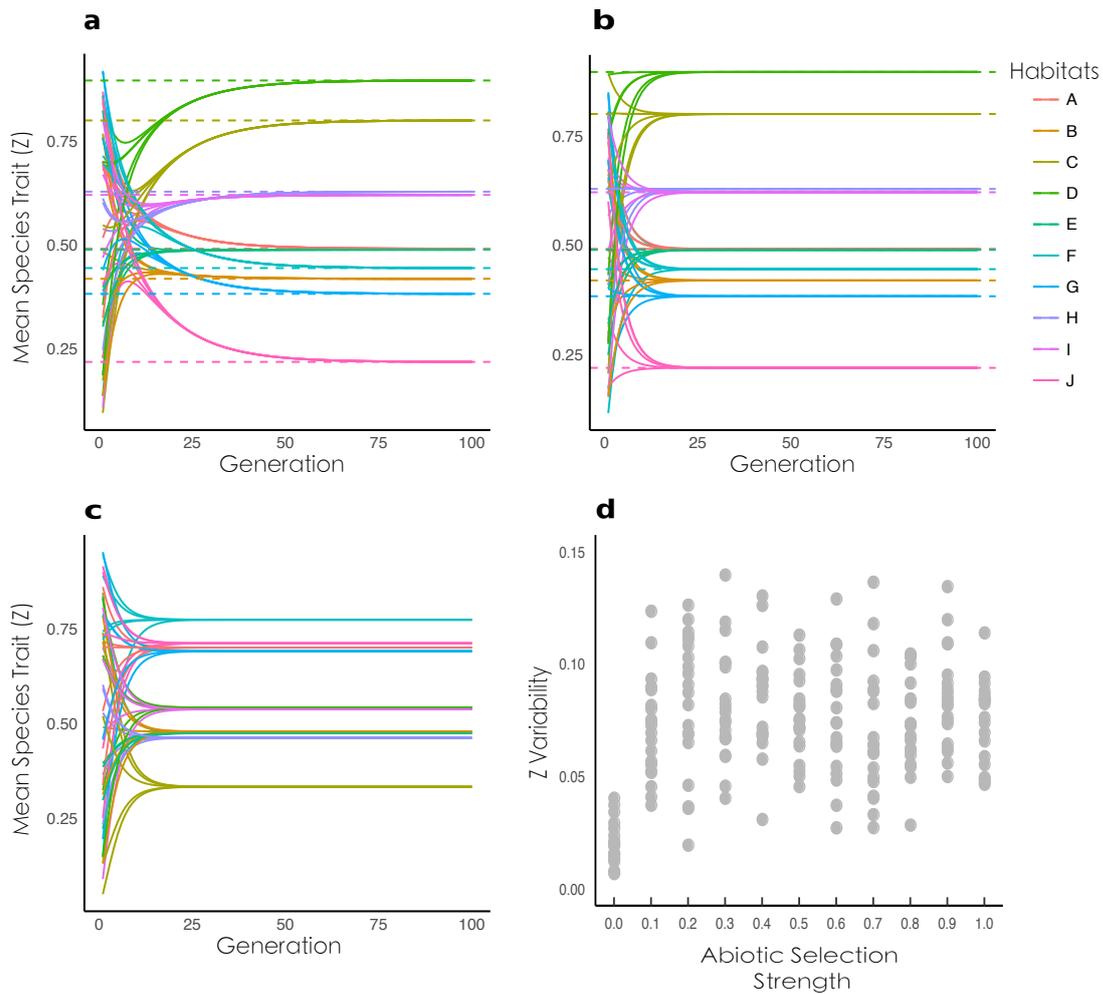


Figure 2: Exploring biotic and abiotic selection, how the trait value change in 100 generation. In these cases, species are loyal to their habitat, occurring in only one habitat, in a *perfect modular scenario*. In a-c each habitat is represented by one color, dashed line is the habitat optima, each continuous line is one species and their color is the same as their habitat optima they occur a) The change of trait value in 100 generations when the strength abiotic selection p is 0.3 b) The change of trait value in 100 generations when there is only abiotic selection ($p = 1$) and no biotic selection ($q = 0$) c) The change of trait value in 100 generations when there is only biotic selection ($q = 1$) and no abiotic selection ($p = 0$) d) Variability of trait values after 100 generations in different strengths of abiotic selection. Each point corresponds to one simulation.

How does the presence of habitat generalist species influence the

formation of mimetic rings?

Habitat supergeneralists, i.e. species that occur in all habitats in the community, had a major impact in the evolutionary dynamics of mimicry rings. Even the addition of a single supergeneralist in the *perfect modular scenario* (scenario where each species occurred in a single habitat) changed the evolutionary dynamics in two distinct ways. First, the presence of a supergeneralist drove other species to converge, reaching trait values that were not the ones favored by habitat-based abiotic selection (Figure 3a). Second, the presence of supergeneralists decreased the distinctiveness among mimicry rings in the community (Figure 3a). If 10% of species were supergeneralists, the overall trait similarity increased, flattening the differences among mimicry rings (Figure 3b). By adding more supergeneralists, trait variability between species decrease, with a consequently decrease in mimicry ring distinctiveness (Figure 3c). For example, in communities in which 10% of species were supergeneralists the trait variability among species were five times bigger than in community in which more than 60% of species were supergeneralists. Ancillary simulations revealed that effects of supergeneralists in driving convergence in traits of unpalatable species at community level is faster in the absent of abiotic selection (Figure S.4).

The effects of habitat supergeneralists in the evolutionary dynamics of aposematic species have two components: (1) it generates a single species that co-occurs with all other species and (2) it increases the mean level of habitat generalization of unpalatable species. To investigate the effects

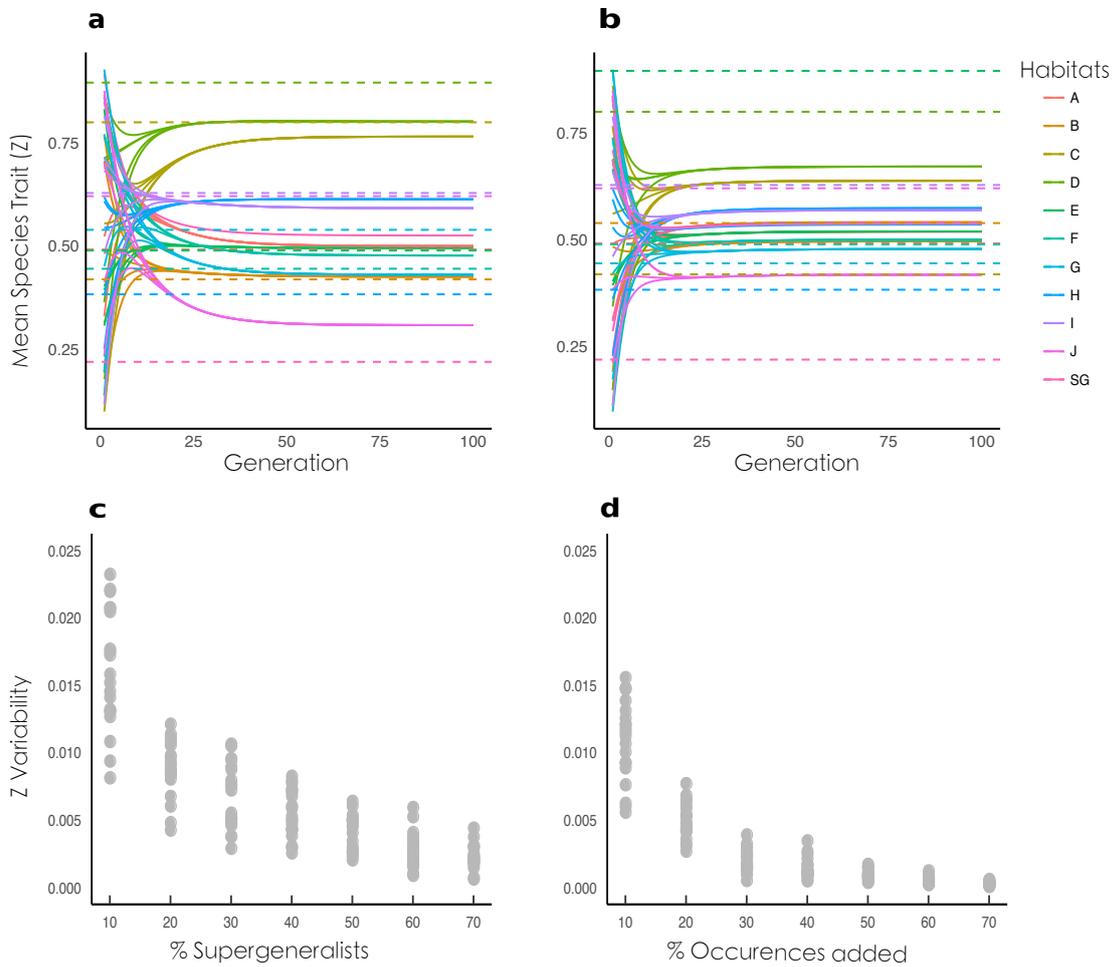


Figure 3: Including supergeneralists, a species that occur in all habitats, or occurrences, starting from a *perfect modular scenario*. In a and b each habitat is represented by one color, dashed line is the habitat optima, each continuous line is one species and their color is the same as their habitat optima a) The change of trait value in 100 generations when there is only one supergeneralist (SG) in a community b) The change of trait value in 100 generations when 10% of the species in a community are supergeneralist (SG) c) Variability of trait values after 100 generations with different percentages of supergeneralists in a community. Each point corresponds to one simulation d) Variability of trait value after 100 generations with different percentages of occurrence in a community. Each point corresponds to one simulation.

of both factors on the evolutionary dynamics, we contrasted simulations in which supergeneralists were added to the community with simulations in which we randomly included the same number of species occurrences on habitats. In fact, randomly increasing the mean level of habitat generalization led to smaller trait variability among species than adding more supergeneralists. For example, starting with the scenario where each species occur in a single habitat (*perfect modular scenario*) and randomly adding 10% more occurrences in the community, variability was about one and half smaller than adding 10% of supergeneralists (Figure 3c e 3d). Thus, the comparison of both sets of simulations suggests that increasing the mean level of habitat generalization has a greater influence in trait values evolution than increasing the number of supergeneralists.

We performed additional analyses to explore the drivers of different levels of trait variation in simulations adding habitat supergeneralists and randomly adding occurrences in the community. We tested if final trait variation was correlated with variation in environmental optima and, because patterns of co-occurrence can create pathways favoring convergence (Guimaraes Jr et al., 2011), we tested if final trait variation was also associated with the path length connecting species. We measured path length as direct and indirect links in a spatial network, in which nodes represent species and links represent that species co-occur in at least one habitat (Figure 1d-f). These analyses revealed the underlying mechanism shaping convergence in simulations with abiotic selection and biotic selection. Final trait variation is a function of variation in mean species habitat optima (see Equation 8). In simulations in which we randomly added co-occurrences,

variations in mean species habitat optima (θ_i) and path length were smaller than in simulations in which supergeneralists were added to the community (Figure S. 1 and 2).

Discussion



Warning display and mimicry are unique and interesting phenomena that have been under the spotlight since Darwin (1881) and Wallace (1889). Müller (1879) used the first mathematical model in biology to support an evolutionary hypothesis and explained that species benefits for decreasing the costs in teaching naïve predators to avoid them. Until nowadays, many efforts have been made trying to understand the underlying processes shaping Müllerian mimicry (Turner, 1987; Mallet, 1999; Balogh et al., 2010; Ruxton et al., 2004; Sherratt, 2008; Ferreira & Marcon, 2014). In this study, we investigated a central problem to the evolution of Müllerian mimetism: why are there so many mimetic rings in a community? The answer to this question may have consequences to our understanding of how ecological interactions shape trait evolution and, especially, convergence in traits of non-related species. Previous work had suggested how habitat heterogeneity due to stratification or across microenvironments might affect the evolution of mimicry rings (Papageorgis, 1975; Mallet & Gilbert, 1995; Turner & Mallet, 1996; Beatty et al., 2004; Elias et al., 2008; Gompert et al., 2011; Ferreira & Marcon, 2014). Here, by introducing a novel approach, our work contributes to a step towards in the comprehension of what are the main factors driving the emergence of distinct sympatric mimetic rings in a community.

First, we showed that if all species are habitat specialists they evolve towards the habitat optima where they occur. In a community with habitat

heterogeneity, which has distinct selective pressures, specialists in different habitats diverge in their traits, leading to the formation of distinct mimetic rings. On the other hand, if habitats are more homogeneous, selection imposed by habitat may favor similar warning signals, leading to similar color patterns. In fact, the formation of multiple mimetic rings is more common in heterogeneous tropical than in homogeneous temperate zones (Sheppard et al., 1985; Beccaloni, 1997; Joshi et al., 2017). If mimetic rings are, at least in part, a consequence of abiotic selections, we should expect that changes in habitat's features would lead to changes in phenotypes favored by habitats, what would favored species to converge to a different phenotypic patterns. In fact, there is evidence that the composition of mimetic rings change with habitat disturbance (Uehara-Prado & Freitas, 2009). Although the main mechanism for these changes in composition of mimetic rings is species sorting, evolutionary dynamics driven by habitat-based selection may also fuel new types of mimetic rings, which in turn may explain why the same species may be part of distinct mimetic rings across large geographical areas.

Second, our analyses showed that selective pressure exerted by the co-occurrence of other unpalatable species is enough for the emergence of distinct mimetic rings in a community, if the unpalatable species are specialized in the same habitat. Mutualistic interactions between co-occurring species are known to shape community structure, leading to convergence along multiple ecological features (Elias et al., 2008; Gompert et al., 2011). Thus, in this scenario, coevolution is the evolutionary process behind the formation of mimetic rings, supporting the notion that mutualistic interac-

tions has the potential to affect the evolutionary dynamics in diverse communities (Thompson, 1994; Bronstein, 2015). Our results indicate that the presence of mimetic rings is not an indicative of either abiotic or biotic selective pressures shaping warning signal in unpalatable species because both abiotic selection alone and biotic selection alone can lead to the formation of mimetic rings. In this sense, studies that focus on the structure of selection in mimetic rings (Gompert et al., 2011), the natural history of the interactions (DeVries et al., 1999; Willmott & Mallet, 2004), and on the functional biology of warning signals (Kingsolver, 1988) are needed to disentangle the contribution of both abiotic and biotic components of selection. In most cases, however, it is probable that both abiotic and biotic selection are affecting the evolution of Müllerian mimetism (Brown Jr, 1988; Chazot et al., 2013).

For example, color patterns, which are one of the most conspicuously traits involved in Müllerian mimicry, performs other functions related to both biotic and abiotic selection, such as sexual selection or thermoregulation (Kingsolver, 1988; Finkbeiner et al., 2014). Moreover, color patterns vary in their conspicuousness depending of the habitat background, as demonstrated to a variety of organisms, including prey (Endler, 1978), and even plant structures (Cazetta et al., 2009), thus indicating that selection imposed by Müllerian mimetism is often habitat-dependent. Therefore, the scenario where multiple selective pressures are acting in the same traits responsible for the mimicry seems like a more plausible explanation in natural systems (Williams, 2007; Chazot et al., 2013), which makes both divergence (due to abiotic selection) and coevolution (due to biotic selection)

as the responsible processes in the formation of mimicry rings (Sheppard et al., 1985). In this way, our results shed light on the consequences of the complex interplay between abiotic and biotic selective pressures.

Our results showed that the time for species to reach stable trait values slows down when both abiotic and biotic selective pressures are shaping traits in sets of unpalatable species. In our model, this pattern is a consequence of the conflicting selective pressures. Conflicting selection, in turn, in addition of stabilizing selection and “the Red King effect” (Bergstrom & Lachmann, 2003), is one of the multiple processes that slow the pace of evolution in mutualisms (Herrera, 1986; Adler & Bronstein, 2004; Siepielski & Benkman, 2010; Raimundo et al., 2014). Moreover, our analysis showed that the abundance of species does not influence species trait convergence when there is abiotic selection (Figure S. 3). Indeed the notion that the most abundant species is a model for Müllerian mimetism has two underlying assumptions: (1) the strength of selection is positively associated with the frequency of interactions – which is an assumption that does not necessarily hold for ecological interactions (Benkman, 2013) and, as showed in our results, (2) traits are not under abiotic pressure.

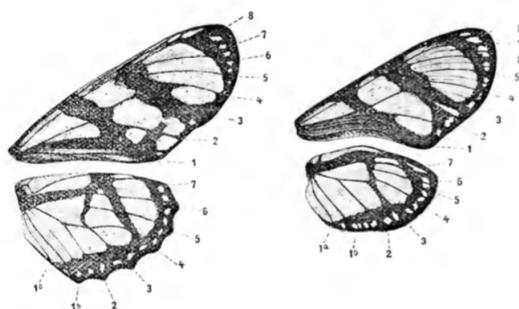
Third, our results showed that just a few habitat supergeneralists are enough for making all potentially distinct mimicry rings converge to a single mimicry ring. Our analysis revealed that adding random occurrences between species led to faster trait convergence than adding supergeneralists, suggesting that effects of habitat generalists in collapsing mimetic rings is a consequence of increasing the mean level of generalization in the community. Patterns of convergence in species-rich mutualisms were as-

sociated with a type of network-based pattern called “small-world effect” (Guimaraes Jr et al., 2011). The small-world effect occurs when there is a short pathway connecting species (nodes) in a community (network) (Watts & Strogatz, 1998). In species-rich sets of unpalatable species, species can be viewed as nodes and co-occurrences at the same habitat as links. In fact, by adding habitat supergeneralists or increasing the mean level of habitat generalization in the community, we reduced the length of pathways connecting species through patterns of co-occurrence (Figure S.1 e 2), leading to a rapidly convergence in color traits.

Because even a few supergeneralists or moderate levels of mean habitat generalization would collapse several mimicry rings to a single one, our simulations provide us insights on the role of what are the mechanisms that allow the coexistence of mimicry rings. For instance, *Heliconius* butterflies are known to be very loyal to their home-range, roosting and reproductive sites and *Ithominae* butterflies to habitat type and flight height (vertical stratification) (Papageorgis, 1975; Brown Jr, 1981; Beccaloni, 1997; DeVries et al., 1999; Willmott & Mallet, 2004; Bonebrake et al., 2010). Moreover, mimicry rings in butterflies are often associated with particular habitats, indicating that the co-occurrence of habitat specialists is congruent with the patterns of mimicry rings. However, in other mimetic groups with broad habitat use, *e.g.*, frogs (Twomey et al., 2016), snakes (Greene & McDiarmid, 1981), velvet ants (Wilson et al., 2012), the formation of mimicry rings seems indeed to have a spatial structure, and different mimicry rings are often allopatric.

In conclusion, this study is a step towards the understanding of Mül-

lerian mimicry and the processes generating multiple mimicry rings. We argue here that the habitat heterogeneity can explain the formation of sympatric mimicry rings. However, only the biotic pressure exerted by species co-existence can also explain the same pattern of sympatric mimicry rings in a community. In this case, both abiotic and biotic selection alone can lead to the formation of mimicry rings, and the formation of these must be due to a complex interplay between these selective pressures. Also, the inclusion of just a few generalist species in the system would collapse all rings in one, showing that the formation of distinct mimicry rings in a community are more likely to happen if species are habitat specialists. We already know that palatable mimics, i.e. Batesian mimics, rapidly converge towards the color trait pattern of species they co-occur (Joshi et al., 2017) and also influence the evolution of the mimetic rings (Franks & Noble, 2004). Therefore, we suggest that future works should investigate what are the effects of including Batesian mimics in a heterogeneous community for the formation of mimicry rings.



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Supplementary Materials

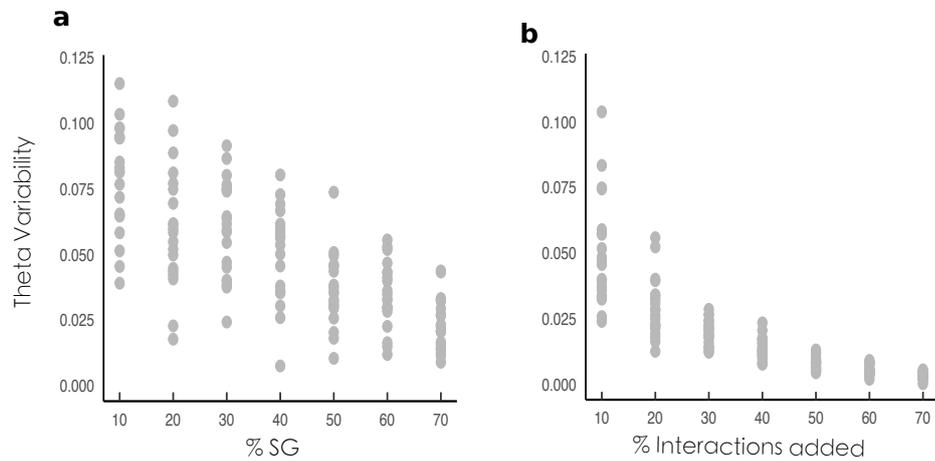


Figure S. 1: a) Variability of theta values among species in a community with different percentages of supergeneralists (SG). b) Variability of theta values among species with different percentages of occurrence in a community. Each point corresponds to one simulation.

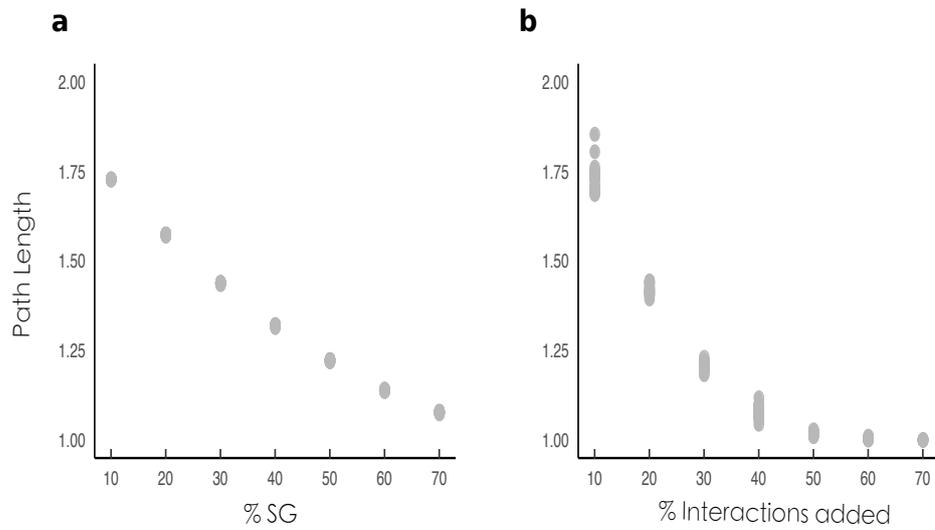


Figure S. 2: a) Path length between species in a community with different percentages of supergeneralists (SG). b) Path length between species with different percentages of occurrences in a community.

In order to evaluate the impact of different abundances between species, we did a sensitivity analysis considering that all species have the same abundance (Figure 2a and Figure 3a-b).

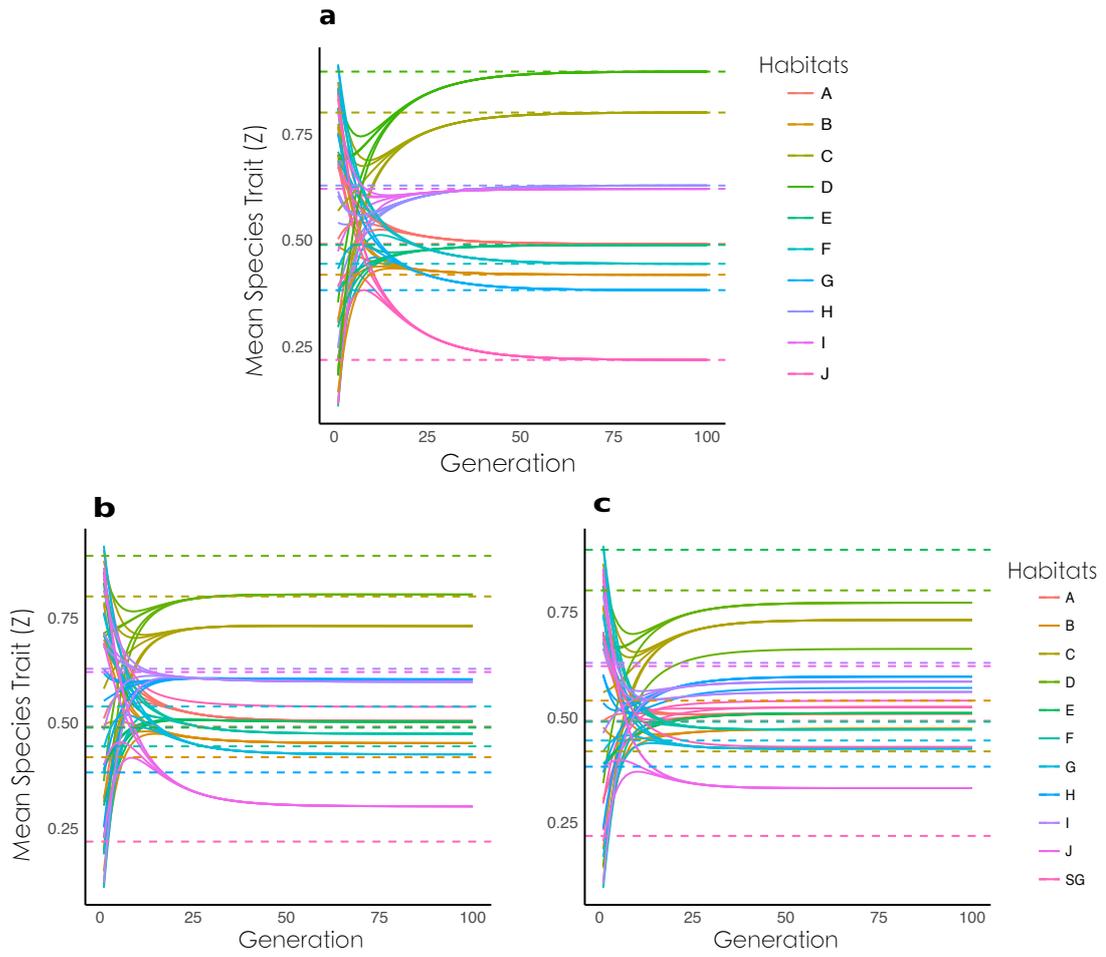


Figure S. 3: Exploring biotic and abiotic selection when all species have the same abundance. Each habitat is represented by one color, dashed line is the habitat optima, each continuous line is one species and their color is the same as their habitat optima they occur. a) the change of trait value in 100 generations when all species are loyal to their habitat, occurring in only one habitat, in a *perfect modular distribution* b) the change of trait value in 100 generations when there is only one supergeneralist (SG) in a community c) the change of trait value in 100 generations when 10% of the species in a community are supergeneralist (SG)

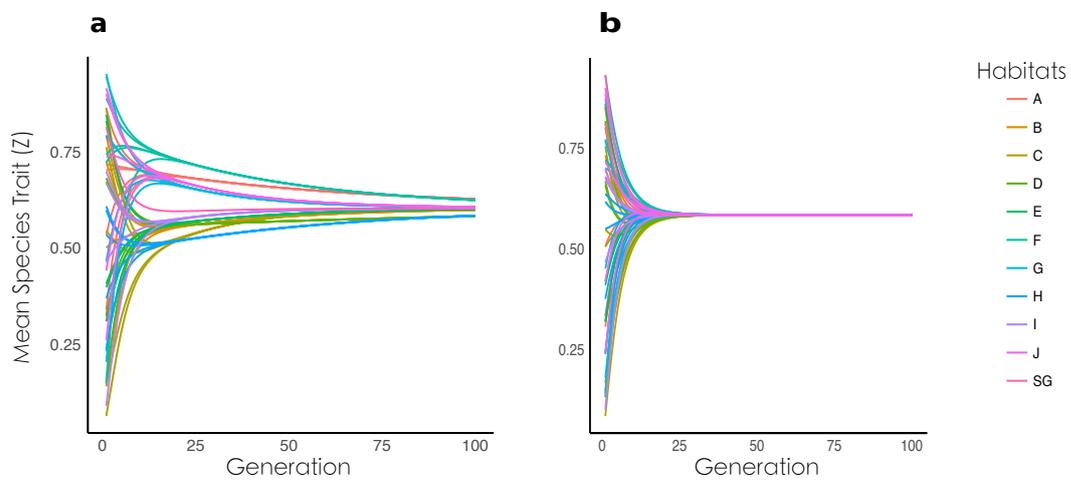


Figure S. 4: Exploring abiotic selection and including supergeneralists, how the trait value change in 100 generation. Each habitat is represented by one color and continuous line is one species and their color is the same as their habitat optima. Starting from a *perfect modular scenario* and including a) only one supergeneralist in the community; c) 10% of supergeneralist in all species' community