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# Positive and negative interactions jointly determine the structure of Müllerian mimetic communities

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## ABSTRACT

Negative and positive ecological interactions have opposite effects on the structure of ecological communities, in particular in terms of ecological similarity among interacting species. In nature, species belonging to the same guild often interact in both negative and positive ways, yet the interplay between interactions of different kinds in intraguild community dynamics remains poorly understood. Müllerian mimetic communities are particularly suited for investigating this interplay because positive (mutualistic mimicry) and negative (competition for trophic resource and micro-habitat) interactions are relatively easy to identify. Empirical research has shown that the combination of mutualistic mimicry and competition does not necessarily drive convergence along all dimensions of the ecological niche, but the determinants of such mixed result are unknown. Here, we analyze the structure of Müllerian mimetic communities simulated with an agent-based model. We show that mutualistic mimicry favours ecological similarity on dimensions along which similarity favours fine-scale co-occurrence. Co-mimetic species use similar micro-habitats, but do not necessarily use similar resources. Heterogeneity of resources among micro-habitats is necessary for ecological similarity on resource use among co-mimetic species to occur. We therefore highlight the importance of fine-scale co-occurrence if we are to understand how positive and negative interactions structure ecological communities.

## INTRODUCTION

Unraveling patterns of species coexistence is a fundamental question in community ecology. The occurrence of species is constrained by their ecological niche, which is defined as the environmental conditions (e.g., temperature, micro-habitat, resources available) required for species persistence (Hutchinson 1957). In addition to those abiotic requirements, interactions among species play a major role in determining the persistence of species in communities. In particular, negative interactions (typically, competition) among ecologically similar species have been seen as the major force shaping local species assemblages, biasing community assembly towards more ecologically divergent species via character displacement or environmental filtering (Gause 1934, MacArthur and Levins 1967).

For the past decades, the role of positive interactions among species belonging to different guilds (e.g., plants and their pollinators) or to the same guild (e.g., plants engaging in facilitative interactions) in structuring biological communities has been acknowledged (Bascompte et al. 2003, Bruno et al. 2003, Thébault and Fontaine 2010). In particular, positive interactions can lead to ecological convergence. For instance, positive interactions among plant species may emerge from the presence of common pollinators (because different plant species attract each other's pollinators), which may in turn drive convergence in chemical and visual floral phenotypes acting as cues for pollinators (Thomson and Wilson 2008, Kantsa et al. 2017). Likewise, because species that benefit from co-occurrence often have similar habitat requirements, it has been suggested that positive interactions can lead to habitat convergence among plants (Moeller 2004), animals (Stensland et al. 2003, Elias et al. 2008) and micro-organisms (Anderson et al. 2004).

The effects of negative and positive interactions on community structure have been studied independently for methodological convenience. In general, species belonging to different guilds interact either negatively (e.g., predation or parasitism) or positively (e.g., service-resource relationships such as pollination or zoochory, or service-service relationships such as ant nesting in special plant cavities and defending the plant against natural enemies). On the contrary, species that belong to the same guild are generally involved in both negative and positive interactions (Crowley and Cox 2011, Jones et al. 2012). Species from the same guild are often ecologically similar and compete for resources or habitat, but they may also interact positively, as for example in some communities of birds (via increased foraging efficiency or reduced predation; Wiley 1971), mammals (via beneficial joint hunting or shared vigilance; Stensland et al. 2003), plants (e.g., via shared pollinators, Moeller 2004) and yeasts (Anderson et al. 2004). Accounting for the combined effects of both negative and positive interactions is therefore necessary if we are to understand how ecological communities are structured (Fontaine et al. 2011). In a standard resource-competition model, positive interactions among ecologically similar species have been shown to counterbalance the negative effects of competition for niche

space on long-term species coexistence, thereby fostering higher diversity (Gross 2008). This model suggests that positive interactions may drive stable multi-species coexistence with a single resource, even when the net interspecific interaction remains negative. Yet, only few empirical and theoretical studies have investigated how often and why positive interactions overcome competition in shaping ecological communities (Jones et al. 2012). Additionally, empirical evidences for such phenomena are biased towards plants ('facilitative interactions', whereby a 'nurse' plant species provides shade and attracts water and nutrients, which are beneficial to other plant species in the close vicinity) (Valiente-Banuet and Verdú 2007, Brooker et al. 2008). However, because facilitative interactions in plants acts through changes in the abiotic environment or through other organisms, the nature of interactions among plants is difficult to identify.

Müllerian mimetic communities are particularly suited for investigating the interplay between positive and negative interactions in animal community dynamics. Müllerian mimics are unprofitable prey species that share the same warning signal, such as a conspicuous colour pattern, sound or odour. In short, Müllerian mimicry corresponds to the convergence in warning signal among co-occurring defended prey species. Indeed, species with defenses (e.g., chemical defenses) benefit from harbouring a warning signal avoided by predators (aposematism). The more abundant a warning signal, the higher the probability that a prey harbouring this signal encounters a predator that has already learned to avoid it (positive frequency-dependent selection). Therefore, selection favours convergence on warning signals among prey species that face the same suite of predators and that effectively share the cost of 'educating' those predators, thereby leading to Müllerian mimicry (Müller 1879). Müllerian mimicry is observed in a variety of organisms. Phylogenetic studies have revealed convergent evolution of warning colour patterns between both closely and distantly related aposematic species, such as butterfly (Müller 1879, Jiggins et al. 2006), frog (Symula et al. 2001), bird (Dumbacher and Fleischer 2001), bumblebee (Williams 2007), catfish (Alexandrou et al. 2011), ground beetle (Munoz-Ramirez et al. 2016) and velvet ant species (Wilson et al. 2012).

Müllerian mimicry is a mutualistic interaction that occurs among co-mimetic species (i.e., belonging to the same 'mimicry ring'), which share a common warning signal and face the same predators. Because similarity in warning signal (typically, colour pattern) can easily be assessed, identifying which species are likely to interact positively in a mimetic community seems straightforward. Additionally, Müllerian mimetic species are typically members of the same guild and are ecologically similar in a broad sense. Because of competition for niche space (e.g., micro-habitat or trophic resources), pairs of species can simultaneously interact in positive and negative ways, allowing empiricists to assess the relative importance of each kind of interaction in structuring Müllerian mimetic communities. Yet, empirical research is mixed in this regard. While Müllerian mimicry drives ecological convergence along multiple ecological axes despite competition in the Neotropical butterfly tribe Ithomiini (Nymphalidae) (Elias et al. 2008), it does not outweigh ecological differentiation in trophic resource use in neotropical catfishes (Alexandrou et al. 2011). Similarly, in ithomiine butterflies, co-

mimetic species sometimes use similar larval host plant species, but sometimes do not (Willmott and Mallet 2004). In other words, mimicry may not necessarily drive ecological convergence in resource use.

In this paper, we investigate theoretically the interplay between positive (mimicry) and negative (competition for resource and micro-habitat) interactions in structuring Müllerian mimetic communities. The ecological niche space is multidimensional and Müllerian mimicry may affect species niche use differently among niche axes. In mimetic communities, competition occurs along two niche components that may function differently, namely trophic resources (hereafter, resources) and micro-habitats (e.g., forest structure, topography, flight height in ithomiine butterflies; Beccaloni 1997, DeVries et al. 1999, Elias et al. 2008, Hill 2010, Willmott et al. 2017). For instance, mimetic butterflies may compete for host-plants where caterpillars can feed on and adult butterflies may compete for space within micro-habitat (e.g., ‘perching sites’ where males can court females, or sunny opening area facilitating body warming). Eventually, competition might drive ecological divergence along those niche axes. By contrast, Müllerian mimicry is expected to drive ecological convergence along those same niche axes. However, we hypothesize this may occur only if ecological convergence promotes co-occurrence in the eyes of predators, thereby strengthening mutualistic mimicry. This is the case for micro-habitat, but not necessarily for resources, unless resources are segregated by micro-habitat.

To link local processes and community structure within an explicit ecological niche space, we extend a stochastic individual-based model that showed that the heterogeneity of predator micro-habitat use can maintain mimicry diversity (Gompert et al. 2011). Here, we implement competition for resources, and we investigate how the extent of resource heterogeneity among micro-habitats changes the outcome of the interplay between positive and negative interactions in Müllerian mimetic communities. Moreover, we explicitly model assortative mating based on micro-habitat or colour pattern, as observed in many mimetic organisms (Jiggins et al. 2001, Reynolds and Fitzpatrick 2007, Fitzpatrick et al. 2008). Finally, we take the opportunity to highlight possible biases caused by the arbitrary criterion used by empiricists to identify species interacting positively. In the field, similarity in warning signal can easily be assessed, and this criterion has therefore been widely used to identify which species interact positively in a mimetic community (including in Elias et al. 2008 and Alexandrou et al. 2011). In this paper, we specifically evaluate the accuracy of this simple criterion when it comes to assess the interplay between positive and negative interactions in structuring Müllerian mimetic communities.

## THE MODEL

### Purpose

We investigate how positive and negative interactions jointly determine the structure of Müllerian mimetic communities, and specifically whether co-mimetic species tend to converge, or instead diverge, on resource

and micro-habitat use. A flowchart of the model is represented on Figure 1, and parameter notations and default values are summarized in Table 1.

We consider a community of toxic prey species, which exhibit colour patterns (hereafter, morphs) used as warning signals by predators. Two components of the ecological niche space are modelled independently: micro-habitat use and resource use. Each prey individual occupies a specific micro-habitat and uses a specific resource. Prey individuals undergo predation, reproduction and competition (Fig. 1e).

During predation, we consider that predator micro-habitat use is either homogeneous or heterogeneous (Fig. 1c). A high heterogeneity of predator micro-habitat use can maintain diversity in warning signals despite positive frequency-dependent selection, and leads to the segregation of mimicry rings by micro-habitat (Gompert et al. 2011, Willmott et al. 2017). Species converging to the same warning signals are mutualist if they are facing the same community of predators.

During the reproduction phase, we implement assortative mating based on micro-habitat or morph. Indeed, mating is rarely random in Müllerian mimetic communities. First, mating probability may be higher among individuals using similar micro-habitats, because the encounter probability is expected to be high within micro-habitat (as suggested by Fitzpatrick et al. 2008). Second, because offspring between individuals harbouring different morphs typically display distinct non-mimetic morphs and therefore suffer a high predation rate, preference for mates with the same morph has often evolved by indirect selection in Müllerian mimetic communities (Jiggins et al. 2001, Reynolds and Fitzpatrick 2007), likely as a result of reinforcement (Kronforst et al. 2007). We implement mutations on morph and micro-habitat use in offspring, and the entire population is reconstituted from offspring after the reproduction phase.

Competition for micro-habitat and resource occurs among offspring individuals, and favours ecological dissimilarity among species. We consider a full range of resource heterogeneity, from homogeneous to highly segregated across micro-habitats (Fig. 1d). In the former case, prey are faced with a diverse set of rare resources and, in the latter case, prey using similar micro-habitats are faced with a limited set of abundant resources.

Starting from random communities of monomorphic prey species occupying the entire micro-habitat space (schematized in Fig. 1a), evolution of morph and micro-habitat use occurs. We then assess the level of ecological similarity among co-mimetic species (on micro-habitat use and on resource use) as compared to all species pairs in the resulting Müllerian mimetic communities (schematized in Fig. 1b). Due to technical limits (see below), shift in resource use is not implemented, and the patterns of increased similarity or dissimilarity of resource use among species is exclusively caused by species filtering by mimicry and/or competition. In nature, however, character displacement (convergence *sensu stricto*) may occur, and we anticipate resulting shifts in resource use lead to the same pattern as species filtering by mimicry and/or competition.

To highlight an important bias that empiricists may face when analyzing data on mimetic species, statistics measuring ecological similarity in resource use is calculated either from truly *co-mimetic* species (with the same morph and co-occurring in the eyes of predators, i.e., always mutualist) or from *homomorphic* species (with the same morph but not necessarily co-occurring in the eyes of predators, i.e., not necessarily mutualist).

## State variables and scale

The Müllerian mimetic community is composed of populations of conspicuous and toxic individuals belonging to different species. Individuals are characterized by the following state variables: species, morph, position in the micro-habitat space, and resource use (Fig. 1e). Each individual  $i$  belongs to one species  $s_i$  among the  $N_{\text{species}}$  species implemented initially. Intraspecific competition is assumed to be stronger than interspecific competition.

The morph  $m_i$  of individual  $i$  is a discrete number with  $m_i \in \{1, 2, \dots, N_{\text{morph}}\}$  assuming  $N_{\text{morph}}$  as the number of possible morphs. Morphs are used as warning cues by predators during associative learning. They can also be used as mating cues (assortative mating based on morph).

The micro-habitat occupied by individual  $i$  is described by its position  $z_i$  in a two-dimensional space. The micro-habitat occupied by an individual is thus a point with coordinates  $z_i = (x_i, y_i)$  in the micro-habitat space with  $(x_i, y_i) \in \mathbb{R}^2$  and  $(x_i, y_i) \in [0, 1]^2$ . Competition is assumed to be stronger between individuals using similar micro-habitats (niche overlap) than between individuals using different micro-habitats. Mating can also be more frequent between individuals using similar micro-habitats than between individuals using different micro-habitats (assortative mating based on micro-habitat).

The resource  $r_i$  used by individual  $i$  is a discrete number with  $r_i \in \{1, 2, \dots, N_{\text{resource}}\}$  assuming  $N_{\text{resource}}$  as the number of possible resources. Competition is assumed to be stronger between individuals exploiting the same resource than between individuals exploiting different resources.

Individuals from the same species can exhibit different morphs and use different micro-habitats, but they all exploit the same resource. Implementing the possibility of shifting resource use always leads to generalist species because reducing intraspecific competition for resources is highly advantageous. Given that species are rarely generalist in nature, we decide not to implement shift in resource use.

We use discrete time steps, corresponding to non-overlapping generations.



## Process overview and scheduling

Within each time step, several phases are processed in the following order: predation, reproduction (with mutations affecting offsprings' morph and micro-habitat use) and competition. After reproduction, parents are completely replaced by their offspring. These processes are represented in Figure 1e, and are described in the subsection "Submodels" below.

## Design concepts

**Stochasticity.** – All processes are probabilistic. Predation, reproduction and survival rates are computed from the composition of the prey community.

**Interactions.** – Individuals compete for resources. The intensity of competition between two individuals depends on their species, their micro-habitat (i.e., the distance separating them in the micro-habitat space) and their resource use. In addition to this negative interaction, predation and predators' learning process – characterized by the avoidance of prey with a morph known to be associated with toxicity – lead to mutualism between species sharing the same morph and facing the same community of predators. Co-mimetic species share the cost of educating those predators and therefore benefit from a reduced *per capita* attack rate.

**Adaptation.** – Individuals' morph and micro-habitat use are adaptive traits, which determine the fitness of individuals. Individuals experience a low predation rate if they harbor a morph frequently encountered by the local predator community. If predator micro-habitat use is heterogeneous, co-mimetic species using similar micro-habitats experience the same predator community and benefit from a low predation rate. Individuals also experience a low death rate if their micro-habitat use reduces competition and provides them resources (if resource distribution among micro-habitats is heterogeneous).

**Emergence.** – Several features emerge from the model. Different mimicry rings (i.e., sets of species sharing the same morph) can emerge depending on the micro-habitat use of the predator communities. Indeed, prey facing the same predator community – i.e., all prey if predation is homogeneous or prey within similar micro-habitats if predation is heterogeneous – rapidly converge on a common morph. Polymorphic species are rare (Fig. A1; in [Appendix 1](#)). However, some species shift to a morph that provides better protection, thereby joining another mimicry ring. Additionally, the level of ecological similarity among mimetic species hinges on the relative strengths of positive and negative interactions (leading to ecological similarity and dissimilarity, respectively), which depends on the morph composition, the micro-habitat use and the resource use of the prey community.

**Observation.** – We record the state variables of all individuals at the end of each simulation. Ultimately, co-mimetic species can either use the same resource or different resources. Likewise, co-mimetic species can

either use similar micro-habitats or different ones. We are interested in the extent of ecological similarity/dissimilarity among co-mimetic species interacting positively.

## Initialization

At initial state, we introduce  $N_{\text{species}} = 20$  at their carrying capacities. Within a species, individuals display the same morph and use the same resource. To ensure all species are equally protected and suffer from the same competition intensity at initial state, we assume that all morphs and resources initially present are equally represented and exploited, respectively. The parameters  $N_{\text{species}}$ ,  $N_{\text{morph}}$  and  $N_{\text{resource}}$  implemented are chosen accordingly (Table 1).

All possible morphs are initially present, and species sharing the same morph do not necessarily use the same resource – i.e., each species is assigned randomly one of the morphs and one of the resources, thereby avoiding any initial association between morph and resource use. Additionally, a micro-habitat position defined by coordinates  $z_i = (x_i, y_i)$  in a two-dimensional space is assigned to each individual  $i$  by drawing  $x_i$  and  $y_i$  from a uniform distribution bounded between 0 and 1 – i.e., all species use the whole micro-habitat space. This initial state is schematized in Figure 1a.

## Submodels

**Predation.** – Following Gompert et al. (2011), predators are not modelled individually but as fixed communities that may show variable micro-habitat segregation. We implement  $N_{\text{predator}}$  distinct predator communities. At each time step, each predator community encounters  $N_s$  individual prey. Prey are encountered by predators following a beta probability density function that is dependent on their micro-habitat. The relative probability of predators from predator community  $p$  encountering a prey individual with micro-habitat use  $z_i = (x_i, y_i)$  is:

$$P(\text{encounter} | z_i) \propto \frac{x_i^{\alpha_1^p - 1} (1 - x_i)^{\beta_1^p - 1}}{B(\alpha_1^p, \beta_1^p)} \cdot \frac{y_i^{\alpha_2^p - 1} (1 - y_i)^{\beta_2^p - 1}}{B(\alpha_2^p, \beta_2^p)} \quad (1)$$

where  $(\alpha_1^p, \beta_1^p, \alpha_2^p, \beta_2^p)$  are the parameters of the beta predation function  $B$  for predator community  $p$  within a two-dimensional micro-habitat space. They are chosen to adjust the heterogeneity of predator micro-habitat use such that the sum of encounter probabilities across all predator communities are nearly uniform across micro-habitat space (Fig. 1c).

Among the  $N_s$  prey that each predator community encounters,  $n_k$  prey individuals of each morph are consumed (Müller 1879). When  $n_k$  individuals of a morph have been eaten by a predator community, predation on this morph ceases (i.e., the local predator community has learned to avoid this morph). Each morph is treated independently by each predator community, and the learning process is reset at each time step. Individuals carrying an abundant morph therefore benefit from a reduced predation risk.

**Reproduction.** – For simplicity, we assume that all individuals are hermaphroditic. Each individual gives birth to  $b$  offsprings (mother role) with a mate from the same species (father role). Mates are encountered following a probability density function that is dependent on their micro-habitat and morph. The relative probability of an individual  $i$  (using micro-habitat  $z_i$  and with morph  $m_i$ ) encountering a mate  $j$  (using micro-habitat  $z_j$  and with morph  $m_j$ ) is:

$$P(\text{mating} | z_i, z_j) \propto \left[ 1 - \frac{1}{1 + \frac{1}{a_m}} \cdot \mathbb{1}_{m_i \neq m_j} \right] \times \exp\left(-a_h^2 \cdot \|z_i - z_j\|^2\right) \quad (2)$$

In the first term of this equation,  $\mathbb{1}_{m_i \neq m_j} = 0$  if  $m_i = m_j$  and  $\mathbb{1}_{m_i \neq m_j} = 1$  if  $m_i \neq m_j$ . Therefore, the probability of mating can be reduced if individuals display different morphs. Parameter  $a_m$  reflects the strength of such assortative mating based on morph. In the second term,  $\|z_i - z_j\|$  is the Euclidean distance between the individuals' micro-habitat and  $a_h$  reflect the strength of assortative mating based on micro-habitat (following the equation of Carvajal-Rodriguez and Rolán-Alvarez 2014). If  $a_m = 0$  and  $a_h = 0$ , mating is random. If  $a_m > 0$ , mating mostly occurs among individuals with the same morph. If  $a_h > 0$ , mating mostly occurs among individuals using similar micro-habitats.

We determine offspring micro-habitat use by sampling each micro-habitat variable  $(x_i, y_i)$  from a normal distribution with a mean equal to the mean of the parents' variables and a specified variance  $\sigma_z$ . Offspring also randomly inherit one of their parents' morph, except when mutation occur with probability  $m_{\text{morph}}$ . In this case, offspring exhibit a different morph that is randomly sampled. After the reproduction phase, the entire population is reconstituted from offspring.

**Competition.** – Offspring survival depends on its resource use and on competition with all other individuals. Survival probability is calculated using an analog of the Beverton-Holt stock-recruitment model (Kot 2001):

population growth is logistic as a consequence of density-dependent resource competition. Offspring individual  $i$  thus survive to the reproduction stage with probability  $v_i$  :

$$v_i = \frac{1}{1 + (b-1) \frac{\sum_j \alpha_{ij}}{K_i}} \quad (3)$$

with :

$$K_i = K_{\max} \exp\left(-\frac{\|z_i - z_{r_i}^*\|^2}{2 \cdot \sigma_K^2}\right) \quad (4)$$

$$\alpha_{ij} = A_{ij} \exp\left(-\frac{\|z_i - z_j\|^2}{2 \cdot \sigma_c^2}\right) \quad (5)$$

where  $K_i$  is the carrying capacity associated with the phenotype of offspring individual  $i$  (using resource  $r_i$  and using micro-habitat  $z_i$ ) (Fig. 1d). The carrying capacity function models a continuous distribution of resources. It is a Gaussian function with maximum  $K_{\max}$  at phenotype  $z_{r_i}^*$ , which is the ecological optimum to exploit resource  $r_i$ , and standard deviation  $\sigma_K$ . Ecological optima  $z_{r_i}^*$  differ among resources, and  $\sigma_K$  is inversely proportional to the strength of resource heterogeneity.

Contrary to the original Beverton-Holt stock-recruitment model, all pairs of offspring individuals do not compete with the same intensity. Competition strength  $\alpha_{ij}$  between each pair of offspring individuals  $(i, j)$  is modelled as a Gaussian function of the Euclidean distance between their micro-habitat  $(z_i, z_j)$  with maximum value  $A_{ij}$  and standard deviation  $\sigma_c$ .  $A_{ij}$  depends on whether individuals  $i$  and  $j$  belong to the same species and whether they use the same resource, such that  $A_{ij} = A_{\text{sp}} \times A_{\text{res}}$ . Interspecific competition is assumed to be weaker than intraspecific competition:  $A_{\text{sp}} = A_{\text{diffsp}} < 1$  if  $i$  and  $j$  are from different species,  $A_{\text{sp}} = 1$  otherwise. Competition is also assumed to be weaker between individuals exploiting different resources than between individuals exploiting the same resource;  $A_{\text{res}} = A_{\text{diffres}} < 1$  if  $i$  and  $j$  are using different resources,  $A_{\text{res}} = 1$  otherwise. Therefore,

competition is lower between individuals from different species and between individuals using different resources. Notably,  $A_{\text{diffres}}$  reflects the strength of competition among individuals using different resources.

Overall, in Equation 3,  $\sum_j \alpha_{ij}$  can be seen as the expected number of individuals with which the offspring individual  $i$  compete.

## SIMULATION EXPERIMENTS AND STATISTICS

### Parameterization

We implement  $N_{\text{species}}=20$  ,  $K_{\text{max}}<600$  ,  $A_{\text{diffsp}}=0.05$  and  $A_{\text{diffres}}=0.5$  to limit the total number of individuals (  $\approx 3,500$  ). As supplementary analyses, we show that our results are robust to changes in the strength of competition between individuals using different resources (  $A_{\text{diffres}}$  , Fig. A2 and A3).

We choose the same parameters for the beta predation function as in Gompert et al. (2011) (Table A1). Predator micro-habitat use is either homogeneous or heterogeneous in our simulations (Fig. 1c). Homogeneous predator micro-habitat use is used as a control; without assortative mating based on morph, mimicry diversity is not expected to be maintained under this condition (Gompert et al. 2011). For simplicity, in the main analysis, we consider successively cases where assortative mating is based on micro-habitat (  $a_h>0$  ,  $a_m=0$  ) and morph (  $a_h=0$  ,  $a_m>0$  ). As a supplementary analysis, we consider the case where assortative mating is based on both micro-habitat and morph (  $a_h>0$  ,  $a_m>0$  , Fig. A4).

Resource distribution among micro-habitats is either homogeneous, moderately heterogeneous or highly heterogeneous with parameters  $(\sigma_K, K_{\text{max}})=(\infty, 500)$  ,  $(1.5, 550)$  and  $(1.0, 575)$  , respectively (Fig. 1d).  $K_{\text{max}}$  is adjusted upward if resources are heterogeneously distributed (from 500 to 575). Heterogeneously distributed resources are more abundant locally than homogeneously distributed resources. This ensures equal prey population densities among simulations, i.e., differences among simulations are not caused by differences in population densities (which affect predation rate and therefore the maintenance of mimicry diversity). Note that all resources are present in all micro-habitats even if they are heterogeneously distributed (  $K \geq 200$  , Fig. 1d). Dissimilarities in resource use cannot be explained by the absence of resources within micro-habitat.

Micro-habitat space is continuous. When there is heterogeneity in resource distribution and/or predator micro-habitat use, this space amounts to four types of micro-habitat with distinct resources and/or predator communities (  $N_{\text{resource}}=4$  ,  $N_{\text{predator}}=4$  ) (Fig. 1c-d).

Our aim is not to understand the conditions under which mimicry diversity is maintained (this has been addressed in Gompert et al. 2011). Given that mimicry diversity is pervasive within natural communities (Briolat et al. 2019), we implement parameters favouring the maintenance of mimicry diversity (heterogeneous predator micro-habitat use,  $N_s=500$  ,  $n_k=15$  ). As supplementary analyses, we show that mimetic community structures are similar to those observed in the main analyses, as long as mimicry diversity is maintained (variations in parameters  $N_s$  and  $n_k$  ; Fig. A5 and A6). We also show that the results are qualitatively the same with a three-dimensional niche space (with 8 types of available resources and 8 predator communities; Fig. A7). Likewise, initial conditions are necessarily unrealistic (with high mimicry diversity) because *de novo* generation of diversity is not possible with such model (Gompert et al. 2011). Therefore, we are not interested in the evolutionary dynamics leading to the equilibrium state; we instead analyze the resulting communities at equilibrium after environmental filtering (i.e., after species evolution and extinction driven by the environment). The mutation rate on morph in offspring (  $m_{\text{morph}}=0.01$  ) and the variance between parent and offspring micro-habitat use (  $\sigma_z=0.05$  ) are deliberately high to reduce simulation runtime.

## Simulations conducted

Simulations end after 1,000 generations, allowing sufficient time for equilibrium to be reached. For each combination of parameters tested, we performed 100 simulations.

The model is implemented in Julia (version 1.1.0) and the code is available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.cnp5hqc24>.

## Statistics

In the field, distinguishing *homomorphic* species (with the same morph but not necessarily co-occurring in the eyes of predators, i.e., not necessarily mutualist) from truly *co-mimetic* species (with the same morph and co-occurring in the eyes of predators, i.e., always mutualist) is difficult, and homomorphic species are therefore assumed to be co-mimetic. To assess whether patterns of ecological similarity among homomorphic species accurately reflect those among co-mimetic species, we compute statistics measuring ecological similarity both among homomorphic species (  $S_{\text{micro-habitat}}$  and  $S_{\text{resource}}$  ) and among co-mimetic species (  $\hat{S}_{\text{resource}}$  ) (see schematized examples of final states in Fig. 1b). We do not measure similarity in micro-habitat use

among co-mimetic species because we define co-mimetic species according to their micro-habitat use. Under homogeneous predation, homomorphic species (independently of their micro-habitat use) face the same predator community and are necessarily co-mimetic. Under heterogeneous predation, however, only homomorphic species using similar micro-habitats face the same predator community and are therefore co-mimetic.

**Mimicry diversity.** – We calculate the effective number of mimicry rings for each community as

$$\exp\left(-\sum_m p_m \ln p_m\right) \text{ where } p_m \text{ is the relative frequency of prey individuals with morph } m \text{ (we use}$$

the criterion of homomorphy). We refer to this statistics as mimicry diversity. This is the exponential of the Shannon diversity index (a measure of entropy) and follows the formulation for effective diversity given by Jost (2006).

**Similarity in micro-habitat use among homomorphic species.** – We assess the level of similarity in micro-habitat use among pairs of homomorphic species (i.e., species sharing the same morph) compared to all species pairs. In each simulation, we calculate the mean micro-habitat distance among pairs of homomorphic species (i.e., the mean Euclidean distance between individuals' positions in the two-dimensional micro-habitat space). We assess the extent of similarity in micro-habitat use among homomorphic species ( $S_{\text{micro-habitat}}$ ) by subtracting this micro-habitat distance from the mean micro-habitat Euclidean distance among all pairs of species. If  $S_{\text{micro-habitat}}=0$ , homomorphic species use similar micro-habitats as often as random species. On the contrary,  $S_{\text{micro-habitat}}>0$  (resp.  $S_{\text{micro-habitat}}<0$ ) reflects high similarity (resp. dissimilarity) in micro-habitat use between homomorphic species compared to random pairs of species.

**Similarity in resource use among homomorphic species.** – We assess the level of similarity in resource use among pairs of homomorphic species compared to all species pairs. In each simulation, we determine the proportion of pairs of homomorphic species that use different resources (which is analogous to the "mean distance in resource use" among pairs of homomorphic species). We assess the extent of similarity in resource use among homomorphic species ( $S_{\text{resource}}$ ) by subtracting this proportion from the overall proportion of pairs of species using different resources. If  $S_{\text{resource}}=0$ , homomorphic species share resources as often as random species. On the contrary,  $S_{\text{resource}}>0$  (resp.  $S_{\text{resource}}<0$ ) reflects high similarity (resp. dissimilarity) in resource use between homomorphic species compared to random pairs of species.

**Similarity in resource use among co-mimetic species.** – We assess the level of similarity in resource use among pairs of co-mimetic species compared to all species pairs ( $\hat{S}_{\text{resource}}$ ). Under homogeneous predator

micro-habitat, all homomorphic species are faced with the same predator community and are therefore co-mimetic. Under heterogeneous predator micro-habitat, however, we define co-mimetic species as species with the same morph and using similar micro-habitats (Euclidean distance between their micro-habitat  $< 0.3$ ), i.e, facing the same predator community. The calculation of  $\hat{S}_{\text{resource}}$  is similar to that of  $S_{\text{resource}}$ .

Those statistics measuring similarity do not account for the variance in micro-habitat use and resource use within population. In supplementary analyses, we show that comparing the strengths of the statistical association between mimicry groups (defined with the criterion of homomorphy or of co-mimicry) and micro-habitat use (using the Pillai's trace statistic from a MANOVA, as in Gompert et al. 2011) or resource use (using the  $\chi^2$  statistic) lead to qualitatively similar results (Fig. A8).

Mimicry diversity affects statistics measuring similarity among homomorphic (or co-mimetic) species. Therefore, for each combination of parameters tested, simulations are classified according to the number of morphs that remain in the mimetic community at the end, such that simulations within the same category can be compared.

## RESULTS

We aim at evaluating the relative effects of positive (mutualistic mimicry) and negative interactions (competition) on the level of ecological similarity among interacting species. Given that mimicry and competition have opposite effects, we can infer the relative importance of those interactions from their joint effect. If mutualistic mimicry is the driving force, then co-mimetic species should be more ecologically similar than random pairs of species. On the contrary, if competition is the driving force, then co-mimetic species should be as ecologically similar as random pairs of species.

### When assortative mating is based on micro-habitat

Assortative mating based on micro-habitat enables community-level mimicry diversity to persist only under heterogeneous predation (especially if resource distribution is heterogeneous, Fig. 2b). In that case, species converge on different morphs and the prey community is composed of multiple mimicry rings. If predator micro-habitat use is homogeneous, however, mimicry diversity is not maintained because of positive frequency-dependent predation (Fig. 2b) (just like without assortative mating, Fig. 2a). In that case, all species converge on the commonest morph. All species eventually share the same morph and it is not possible to compare the level of ecological similarity among homomorphic (or co-mimetic) species to that of randomly selected species.



When mimicry diversity is maintained under heterogeneous predation, homomorphic species (with the same morph) tend to use more similar micro-habitats than random pairs of species (statistics measuring similarity  $S_{\text{micro-habitat}} > 0$ , Fig. 3a; see also examples of simulations in Fig. A9, A10 and A11). Under heterogeneous predation, co-mimetic species using similar micro-habitats co-occur in the eyes of predators. Similarity in micro-habitat use therefore strengthens the mutualistic benefit of mimicry and this effect outweighs the competitive cost caused by micro-habitat overlap. Note that using the pragmatic criterion of homomorphy does not allow a perfect identification of co-mimetic species interacting positively (Fig. 4a and see one example in Fig. A11). If the identification of co-mimetic species is not accurate, the statistics measuring similarity in micro-habitat use among homomorphic species ( $S_{\text{micro-habitat}}$ ) is not fully reliable. For instance, if resource distribution is heterogeneous, identifying co-mimetic species from homomorphic species is particularly inaccurate (Fig. 4a) and this associates with a slight decrease of  $S_{\text{micro-habitat}}$  (Fig. 3a). However, even in this case, using homomorphy as a pragmatic criterion enables the detection of increased micro-habitat similarity compared to random species.

Contrary to micro-habitat use, homomorphic and co-mimetic species do not necessarily use more similar resources than random pairs of species (Fig. 3b-c; see also Fig. A9, A10 and A11). If resource distribution is homogeneous, competition favours dissimilarity in resource use among co-mimetic (and homomorphic) species to the same extent as randomly selected species (statistics measuring similarity  $S_{\text{resource}}$  and  $\hat{S}_{\text{resource}} \approx 0$ , Fig. 3b-c). If resource distribution is heterogeneous, however, co-mimetic (and, to a lesser extent, homomorphic) species use more similar resources than random pairs of species ( $S_{\text{resource}}$  and  $\hat{S}_{\text{resource}} > 0$ , Fig. 3b-c). In that case, similarity in resource use is linked to shared micro-habitat and therefore patterns of co-occurrence in the eyes of predators. This strengthens the mutualistic benefit of mimicry, which outweighs the competitive cost caused by micro-habitat and resource overlap. The extent of competition for resources has no effect on this outcome; if resource distribution is heterogeneous, co-mimetic species use similar resources even under strong competition for resources (for  $A_{\text{diffres}} = 0$ ; Fig. A2). Here, statistics measured from pairs of homomorphic species are reliable to dissect the interplay of positive and negative interactions in structuring Müllerian mimetic communities (results are qualitatively similar in Fig. 3b and 3c, as long as mimicry diversity is maintained).

## When assortative mating is based on morph

Assortative mating based on morph enables community-level mimicry diversity to persist even under homogeneous predation. Positive frequency-dependent sexual selection caused by assortative mating prevents shift to other, more abundant morphs found in other species (like in Gompert et al. 2011) (Fig. 2c). If

predator micro-habitat use is homogeneous, all species are facing the same predator community (using all micro-habitats). Ecological similarity among co-mimetic species does not favour co-occurrence in the eyes of predators and does not strengthen the benefit of mutualistic mimicry. Consequently, under such homogeneous predation, co-mimetic species do not use more similar micro-habitats or resources than random pairs of species (Fig. A12).

When mimicry diversity is maintained under heterogeneous predation, homomorphic species tend to use more similar micro-habitats than random pairs of species (statistics measuring similarity  $S_{\text{micro-habitat}} > 0$ , Fig. 3d), as shown with assortative mating based on micro-habitat (Fig. 3a). If resource distribution is heterogeneous, however, identifying co-mimetic species from homomorphic species is particularly inaccurate when resources are heterogeneously distributed (all homomorphic species are not co-mimetic; Fig. 4b). This leads to a strong decrease of  $S_{\text{micro-habitat}}$  (Fig. 3d). However, even in this case, increased micro-habitat similarity compared to random species is still detectable (Fig. 3d).

Unlike with micro-habitat use, co-mimetic species do not necessarily use more similar resources than random pairs of species (Fig. 3f), as shown with assortative mating based on micro-habitat (Fig. 3c). Co-mimetic species tend to use more similar resources than random pairs of species  $\hat{S}_{\text{resource}} > 0$  when resource distribution is heterogeneous (statistics measuring similarity  $\hat{S}_{\text{resource}} > 0$ , Fig. 3f). Nonetheless, because of the inaccuracy of the homomorphy criterion (Fig. 4b), similarity in resource use among homomorphic species ( $S_{\text{resource}}$ , Fig. 3e) does not reflect similarity in resource use among co-mimetic species ( $\hat{S}_{\text{resource}}$ , Fig. 3f), leading to erroneous conclusions. Notably, heterogeneity of resource distribution has no effect on  $S_{\text{resource}}$  (Fig. 3e). Here, statistics measured from pairs of homomorphic species are therefore particularly unreliable to dissect the interplay of positive and negative interactions in structuring Müllerian mimetic communities (results are qualitatively different in Fig. 3e and 3f).

Overall, just like with assortative mating based on micro-habitat, co-mimetic species use more similar micro-habitats than random pairs of species (Fig. 3d) and use more similar resources than random pairs of species only when resource distribution is heterogeneous (Fig. 3f). We get qualitatively similar results with a different strength of competition for resources ( $A_{\text{diffres}}$ , Fig. A3) or with both types of assortative mating occurring together (Fig. A4).

## DISCUSSION

Our study highlights the importance of accounting for fine-scale co-occurrence in the eyes of predators if we are to understand the structure of Müllerian mimetic communities. Co-mimetic species are involved in both positive (via mimicry) and negative (via competition) interactions that have antagonistic effects on community structure. Are co-mimetic species close ecologically despite competition? In other words, do mutualistic interactions overcome antagonistic interactions in structuring ecological communities? So far, empirical research tackling this question has produced mixed results, with co-mimetic species being sometimes more similar, and sometimes less similar than expected at random, depending on the ecological axis and the Müllerian mimetic community considered (Willmott and Mallet 2004, Elias et al. 2008, Alexandrou et al. 2011). Here, whatever the type of assortative mating implemented, we showed that convergence among co-mimetic species is not always expected to arise along all ecological axes. Via positive frequency-dependent selection on warning signals, the survival of individuals sharing the warning signal that is predominantly known by the local predator community is increased. Consequently, mutualistic mimicry favours (1) convergence in warning signals among species and (2) increased similarity, through filtering and character displacement (hereafter referred to as 'convergence'), in any ecological trait that promotes co-occurrence in the eyes of predators. By contrast, competition favours ecological dissimilarity (here again, through filtering and character displacement – hereafter referred to as 'divergence'). In particular, we showed that mimicry drives convergence in micro-habitat because such convergence always enhances co-occurrence (as shown empirically and theoretically by Elias et al. 2008 and Gompert et al. 2011, respectively). On the contrary, mimicry does not necessarily drive convergence in resource use. In particular, convergence in resource use does not promote co-occurrence when resources are homogeneously distributed (across micro-habitat or across space at larger scale). Instead, competition (enhanced by co-occurrence linked to mimicry) drives divergence among co-occurring species. Therefore, the extent of heterogeneity of resource distribution with regard to micro-habitat may be a key component in structuring Müllerian mimetic communities, and resource distribution across space could explain why empirical evidence for similarity in resource use among co-mimetic species is mixed (Willmott and Mallet 2004, Alexandrou et al. 2011). Unfortunately, data on resource distribution among micro-habitats is lacking, and empirical studies focusing on interactions between mimetic species should aim at obtaining such data to shed light on the patterns detected.

We used different criteria to identify species that interact positively: a pragmatic criterion, as often used in field studies, homomorphy (similarity in warning signal), and a rigorous criterion, co-mimicry (similarity in warning signal combined with exposure to the same predator community). We showed that the patterns of micro-habitat use and resource use sometimes differ according to the criterion employed. Specifically, statistics based on the pragmatic criterion (homomorphy) may not describe well the underlying forces structuring ecological communities. The reason is simple: homomorphic species that do not co-occur at a fine scale and

therefore do not face the same suite of predators do not effectively interact positively. In our model, assortative mating based on morph allows the maintenance of within-micro-habitat polymorphism, and as a consequence a given morph often occupies multiple micro-habitats. In this case, homomorphic species are often not co-mimetic because they occupy distinct micro-habitats. Therefore, the pragmatic criterion of homomorphy is particularly inaccurate when assortative mating is based on morph identity (e.g., Jiggins et al. 2001, Reynolds and Fitzpatrick 2007). We appreciate that gathering information on the ecology of all species belonging to a community to infer fine-scale patterns of coexistence is tedious. Moreover, sorting species according to their mimicry patterns and using this simple criterion has already proved useful to understand the structure of Müllerian mimetic communities (Beccaloni 1997, DeVries et al. 1999, Willmott and Mallet 2004, Elias et al. 2008, Hill 2010, Alexandrou et al. 2011, Chazot et al. 2014, Willmott et al. 2017). Yet, our study shows that we should be cautious when deriving conclusions from such data. If empirical data show that homomorphic species use more similar micro-habitats or resources than random pairs of species, this is a good indicator of ecological convergence among co-mimetic species. On the contrary, failure to detect convergence among homomorphic species (such as in Willmott and Mallet 2004, Alexandrou et al. 2011) does not necessarily mean that there is no convergence among truly co-mimetic species. Homomorphic species may not use similar resources just because they occupy different micro-habitat, in which case they may not be truly co-mimetic species.

In our study, we made a number of simplifying assumptions about the ecological and evolutionary processes underlying model dynamics. We did not implement shifts in resource use in our model. Implementing the possibility of shifting resources always leads to fully generalist species because resource generalism strongly reduces intraspecific competition for resources. In nature, species often show some degrees of generalism, but such strong degree of generalism is rare. We decided to avoid the implementation of another layer of complexity (intrinsic costs associated to generalism, and various degrees of species generalism), and we assumed that species filtering and character displacement (including 'convergence' in resource use) lead to similar community structures. This remains to be investigated theoretically. We also considered a very simple two-dimensional ecological niche space, determining resource availability (following a Gaussian distribution for each resource) and predation risk (following a beta probability density for each predator community). The distributions determining resource availability and predation risk may seem inconsistent with each other. Gaussian distribution is the most parsimonious distribution and is therefore used to model resource availability. To model predation risk, however, we considered beta probability densities to ensure that encounter probabilities across all predator communities are nearly uniform across micro-habitat space (as in Gompert et al. 2011). Therefore, prey cannot 'escape' predation; this would not have been the case with Gaussian distributions of predation risk. Another caveat is that the maintenance of mimicry diversity, a widespread situation in nature (Briolat et al. 2019) and a necessary condition to investigate the interplay between mimicry and competition, is very sensitive to the parameters linked to predation and to population

dynamic (as in Aubier et al. 2017). We therefore restricted our sensitivity analysis to a set of parameters where mimicry diversity is maintained under heterogeneous predation (see Gompert et al. 2011 for a detailed sensitivity analysis regarding the maintenance of mimicry diversity). Nonetheless, we showed that our predictions on the effects of resource distribution on community structure are robust to variations of the parameters determining resource competition and mating behaviour.

The interplay between positive and negative interactions in Müllerian mimetic communities can conceivably have cascading effects on species diversification. Divergence in warning signal in *Heliconius* and Ithomiini butterflies via mimicry of other species is key for reproductive isolation and speciation, due to selection against non-mimetic hybrids and assortative mating for colour pattern (Jiggins et al. 2001, Jiggins et al. 2006, McClure et al. 2019). In addition to this direct effect on speciation rate, mutualistic mimicry should theoretically affect the macro-evolutionary pattern of diversification at the clade level, through its effect on spatial range (Aubier et al. 2017). However, our understanding of the evolutionary process of species diversification remains incomplete unless we jointly consider positive and negative interactions (Fontaine et al. 2011, Jones et al. 2012). The macro-evolutionary pattern derived from divergence in warning signals is intimately linked to other types of interactions because mimicry is likely to cause speciation through cascading effects on incipient species' biology (via ecological convergence) (as suggested by Elias et al. 2008). Our model does not investigate directly the implications of competitive interactions for species diversification in mimetic communities. Yet, we show that such 'cascading effects' may not occur along all ecological axes consequently to a shift in mimicry pattern. Our model suggests that macro-evolutionary patterns of diversification driven by ecological convergence may be intimately linked to fine-scale patterns of co-occurrence. A model precisely investigating such indirect effects on ecological convergence and speciation should be tailored to have an integrated view (across multiple trophic levels) of the process of diversification of mimetic species (e.g., with the theoretical framework of Aguilée et al. 2013).

Interspecific interactions often drive phenotypic diversification and species phenotypes in turn influence species interactions (Gause 1934, MacArthur and Levins 1967). Consequently, several phylogenetic comparative methods have recently been deployed with the goal of elucidating how interspecific interactions drive (or are driven by) trait evolution (Manceau et al. 2017). Statistical tools to fit process-based models of phenotypic evolution including within- and between-clade interspecific interactions may greatly improve our understanding of the determinant of trait evolution along phylogenies, although such methods are still in their infancy (Drury et al. 2018). Our model highlights, however, that trait evolution relies on spatial (and, by extension, temporal) co-occurrence and vice-versa, for the simple reason that ecological interactions driving trait evolution occur among co-occurring species. Trait evolution affects co-occurrence among species and, in turn, co-occurrence defines the strength of ecological interactions among species. Of course, the deployment of those statistical tools already faces strong methodological challenges. Those methods already include a term to specify which lineages co-occur at any given time-point in the phylogeny. This co-occurrence term can

be inferred by biogeographical reconstruction. Our predictions suggest that those statistical tools would certainly gain much power if they account for fine-scale co-occurrence as a link between ecological interactions and trait evolution.

We obtained insights into the joint effect of mutualistic and competitive interactions on the structure of Müllerian mimetic communities. In particular, we showed that the structure of mimetic communities greatly depends on the mimetic environment that has emerged. By promoting co-occurrence, mutualism sets the stage for competitive interactions among mutualistic species. Competition is therefore a critical factor of the evolutionary dynamics linked to mutualism, and vice-versa (Jones et al. 2012). Ecological network research has recently explored networks including different types of interspecific interactions (e.g., Kéfi et al. 2016). In recent theoretical works, the diversity of interactions is a key determinant for community stability (Lee and Inouye 2010, Mougi and Kondoh 2012), as well as for the link between network structure and community stability (Sauve et al. 2014, Kéfi et al. 2016). Yet, our study on mimetic communities highlights that network theory applied to ecological communities is incomplete unless the effects of those interactions on fine-scale co-occurrence is considered. In our model, the same antagonistic interaction (competition) has different outcomes on the community structure depending on how this antagonistic interaction affects co-occurrence. Of course, mutualism and competition between same-guild species can take various forms (Crowley and Cox 2011, Jones et al. 2012) (e.g., competition for the commodities that mutualists produce and competition between mutualists and exploiters) and our theory may not hold for all of them. In particular, mutualistic interactions can stem from competition for food (e.g., group-foraging in cichlid fishes causes environment disturbance and increases food intake, Yuma 1994). To capture the implication of such complex competition-mutualism interactions, our model should be deeply modified.

In conclusion, we suggest an explanation for the mixed empirical evidence on ecological convergence driven by mutualistic interactions in Müllerian mimetic communities. The nature of ecological axes involved must be clearly defined, as well as their link to co-occurrence. For instance, convergence in resource use among co-mimetic species is unlikely to occur if resources are homogeneously distributed across micro-habitats (or across space at larger scale). More generally, our predictions highlight the importance of fine-scale co-occurrence to understand how positive and negative interactions are structuring ecological communities.

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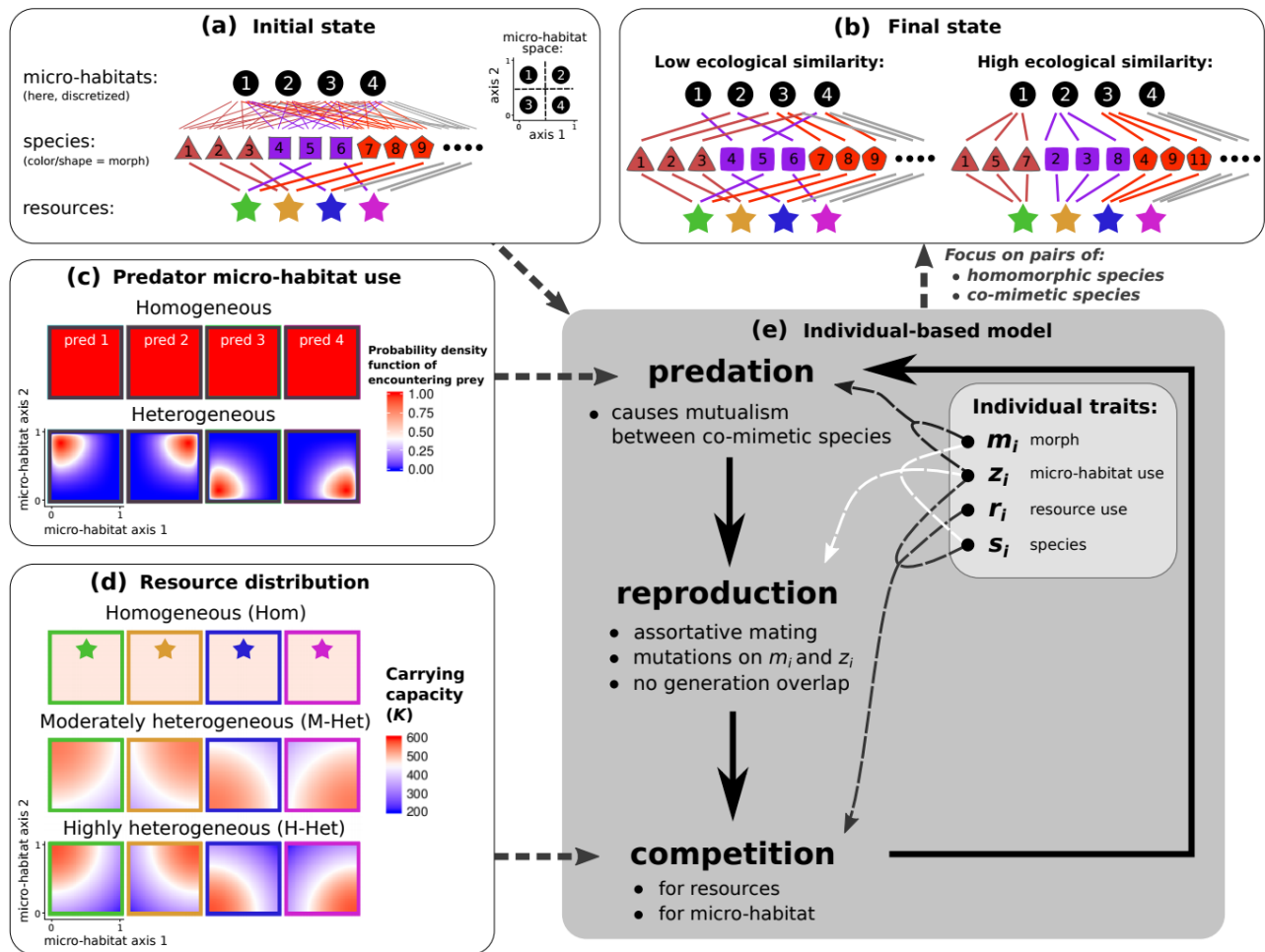
## TABLE

**Table 1:** Notations and numerical values

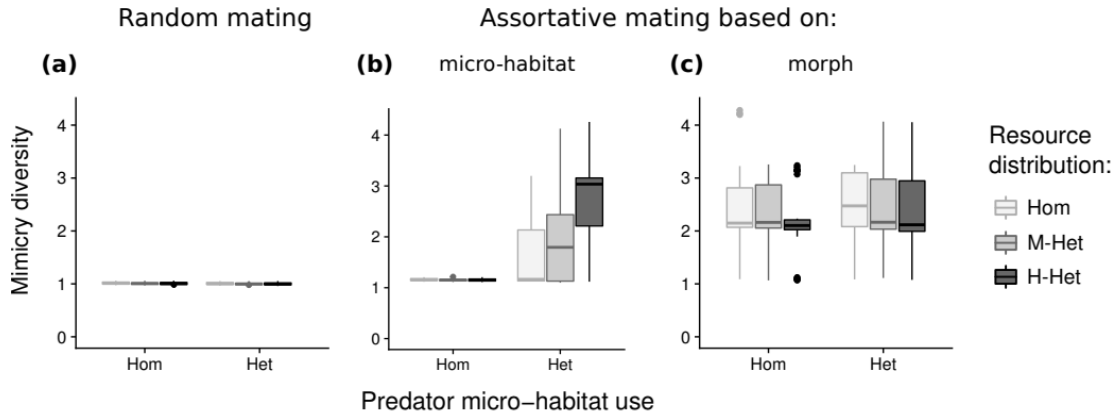
Notation	Description	Range/Value
<b>State variables</b>		
$z_i = (x_i, y_i)$	Micro-habitat occupied by individual $i$	$(x_i, y_i) \in [0, 1]^2$
$m_i$	Morph of individual $i$	$m_i \in \{1, 2, \dots, N_{\text{morph}}\}$
$r_i$	Resource used by individual $i$	$r_i \in \{1, 2, \dots, N_{\text{resource}}\}$
$s_i$	Species of individual $i$	$s_i \in \{1, 2, \dots, N_{\text{species}}\}$
<b>Parameters</b>		
$N_{\text{species}}$	Number of species	20
$N_{\text{morph}}$	Number of possible morphs	10
$N_{\text{resource}}$	Number of available resources	4
$N_{\text{predator}}$	Number of predator communities	4
$N_s$	Number of prey encountered by each predator community per time step	500
$(\alpha_1^p, \beta_1^p, \alpha_2^p, \beta_2^p)$	Parameters of the beta predation function $B$ for predator community $p$	$[1, 4]^4$

$n_k$	Number of prey of each morph eaten by each predator community per time step	15
$b$	Number of offspring per individual	2
$(a_h, a_m)$	Strength of assortative mating based on micro-habitat or morph	$(0,0)$ , $(5,0)$ , $(0,0.5)$
$K_{\max}$	Maximum of the carrying capacity function	$\{575, 550, 500\}$
$\sigma_K$	Standard deviation of the carrying capacity function	$\{1, 1.5, \infty\}$
$\sigma_c$	Standard deviation of the competition kernel	1
$A_{\text{diffsp}}$	Maximum competition term between different species	0.05
$A_{\text{diffres}}$	Maximum competition term on different resources	0.5
$z_r^*$	Ecological optimum for resource $r$	$[0,1]^2$
$\sigma_z$	Variance between parent and offspring micro-habitat use	0.05
$m_{\text{morph}}$	Mutation rate to an alternative morph	0.01

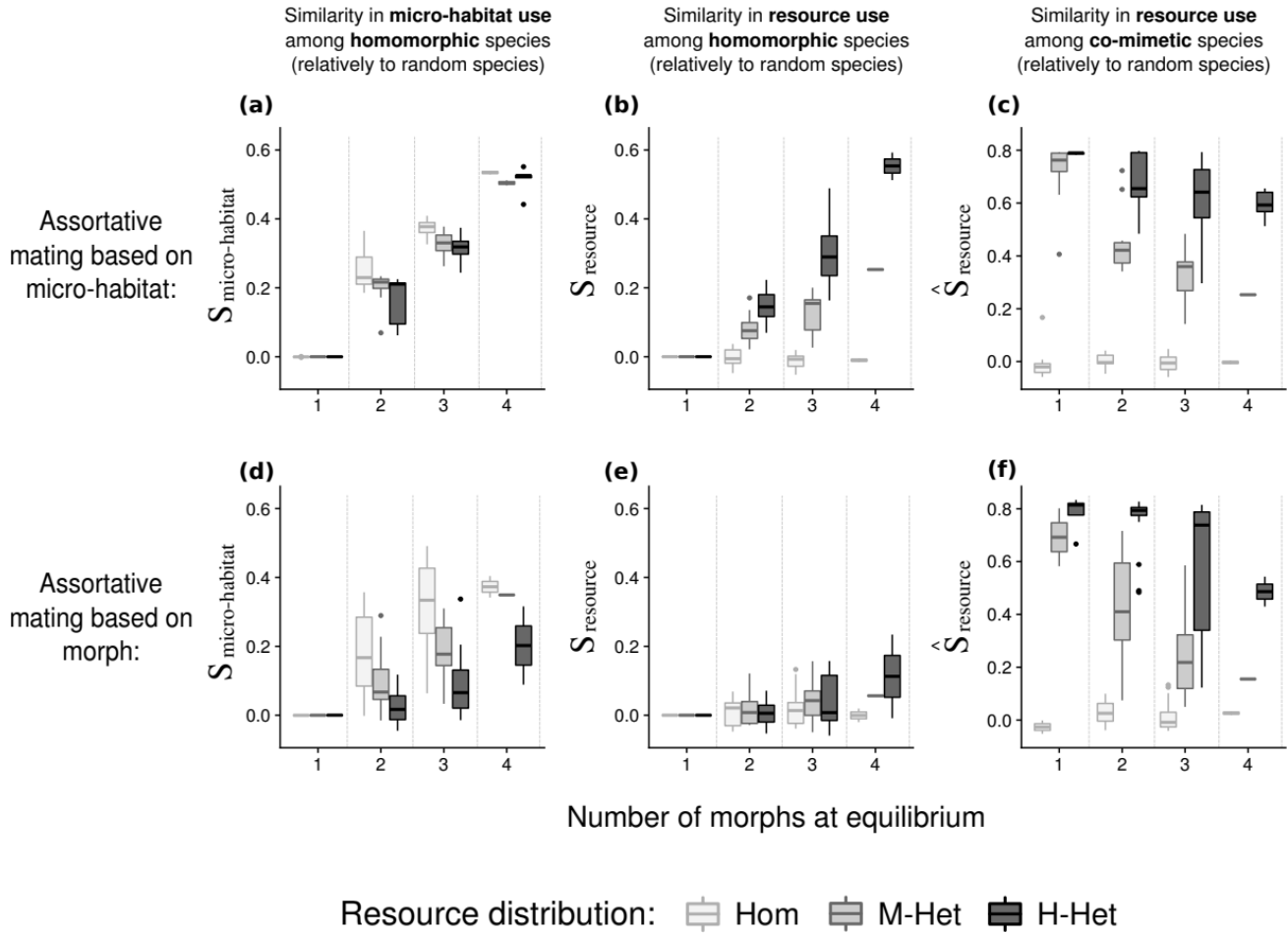
# FIGURES



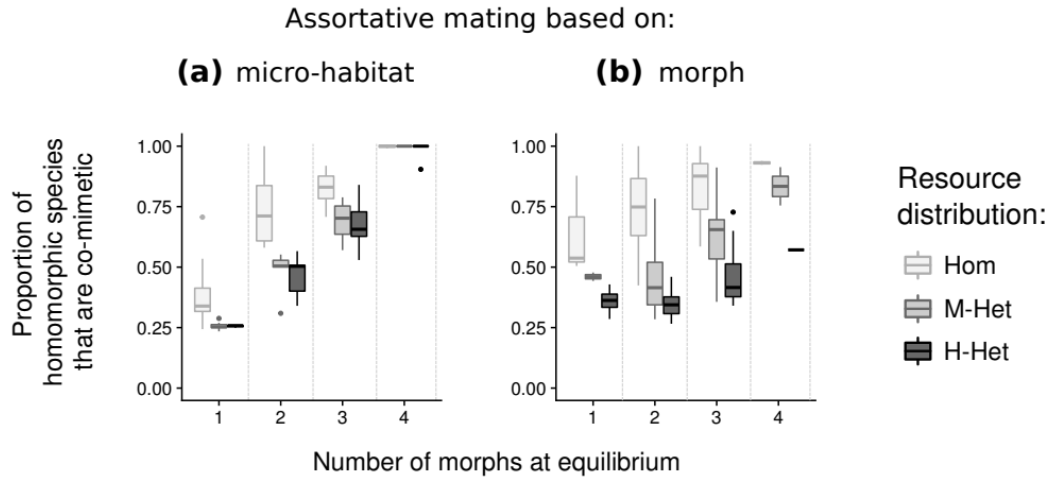
**Figure 1:** Individual-based model. (a) Schematized prey community at initial state with monomorphic species occupying the entire micro-habitat space (represented by circles) and using a single resource (represented by stars). (b) Predator micro-habitat use; the probability of a given predator community to encounter prey is either homogeneous or heterogeneous across micro-habitat space. (c) Resource distribution across micro-habitat space; the carrying capacity for each individual is a function of its micro-habitat occupancy and its resource use. The four resources can be homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het) across micro-habitat space. (d) Schematized prey community at final state; the ecological similarity is measured among pairs of homomorphic or co-mimetic species. The networks represent cases where pairs of homomorphic/co-mimetic species are more similar, in term of both micro-habitat use and resource use, than random pairs of species (right) or not (left). (e) Flowchart of the model with the three processes occurring at each time step. Dashed arrows are showing which model inputs and individual traits affect those processes.



**Figure 2:** Maintenance of mimicry diversity. After 1,000 generations, we measure the remaining mimicry diversity. Mating is random ( $a_h=0, a_m=0$ ) (a) or assortative based on micro-habitat ( $a_h=5, a_m=0$ ) or morph ( $a_h=0, a_m=0.5$ ) (b). In different simulations, predator micro-habitat use is either homogeneous (Hom) or heterogeneous (Het). Resource distribution among micro-habitat is homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). Parameter values: see Table 1.



**Figure 3:** Ecological similarity among homomorphous or co-mimetic species under heterogeneous predation. Resource distribution among micro-habitat can be homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). Mating is assortative based either on micro-habitat ( $a_h=5, a_m=0$ ) (a, b, c) or on morph ( $a_h=0, a_m=0.5$ ) (d, e, g). After 1,000 generations, we assess the level of similarity in micro-habitat use ( $S_{\text{micro-habitat}}$ ) (a, d) and in resource use ( $S_{\text{resource}}$ ) (b, e) among homomorphous species compared to all species pairs. We also assess the level of similarity in resource use among co-mimetic species compared to all species pairs ( $\hat{S}_{\text{resource}}$ ) (c, f). For each combination of parameters, simulations are classified according to the number of morphs that remain in the community. If similarity statistics are equal to 0, pairs of homomorphous (or co-mimetic) species are as similar as pairs of randomly selected species in terms of resource use or micro-habitat use. If similarity statistics are positive, homomorphous (or co-mimetic) species are ecologically more similar than expected at random along the ecological dimension considered. Parameter values: see Table 1.



**Figure 4:** Accuracy of the homomorphic criterion. Proportion of homomorphic species (sharing the same morph) that are co-mimetic (i.e., that also face the same predator community) under heterogeneous predation. Resource distribution among micro-habitat can be homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). Mating is assortative based either on micro-habitat (  $a_h=5, a_m=0$  ) (a) or on morph (  $a_h=0, a_m=0.5$  ) (b). After 1,000 generations, we assess the proportion of homomorphic species that are co-mimetic – i.e., that face the same predator community because they use a similar micro-habitat (Euclidean distance between their micro-habitat  $< 0.3$ ). For each combination of parameters, simulations are classified according to the number of morphs that remain in the community. If the proportion statistics are close to 1, homomorphic species are always faced with the same predator community, i.e., they are always co-mimetic species. Parameter values: see Table 1.

Oikos

**OIK-06789**

Aubier, T. G. and Elias, m. 202. Positive and negative interactions jointly determine the structure of Müllerian mimetic communities. –

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Appendix 1



Table A1. Parameter values ( $\alpha_1^p, \beta_1^p, \alpha_2^p, \beta_2^p$ ) for predation functions (Equation 1). Unlike in Gompert et al. (2011) (see references at the end of the supplementary information), mimicry diversity is not maintained in our simulations with moderately heterogeneous predator micro-habitat use (e.g. (1, 2, 1, 2)) (not shown). This difference lies in the fact that competition for resources, which makes the maintenance of mimicry diversity more difficult, was not accounted in Gompert et al.'s model.

<b>Predator micro-habitat use</b>	<b>Predators 1</b>	<b>Predators 2</b>	<b>Predators 3</b>	<b>Predators 4</b>
Homogeneous	(1, 1, 1, 1)	(1, 1, 1, 1)	(1, 1, 1, 1)	(1, 1, 1, 1)
Heterogeneous	(4, 1.5, 4, 1.5)	(4, 1.5, 1.5, 4)	(1.5, 4, 4, 1.5)	(1.5, 4, 1.5, 4)

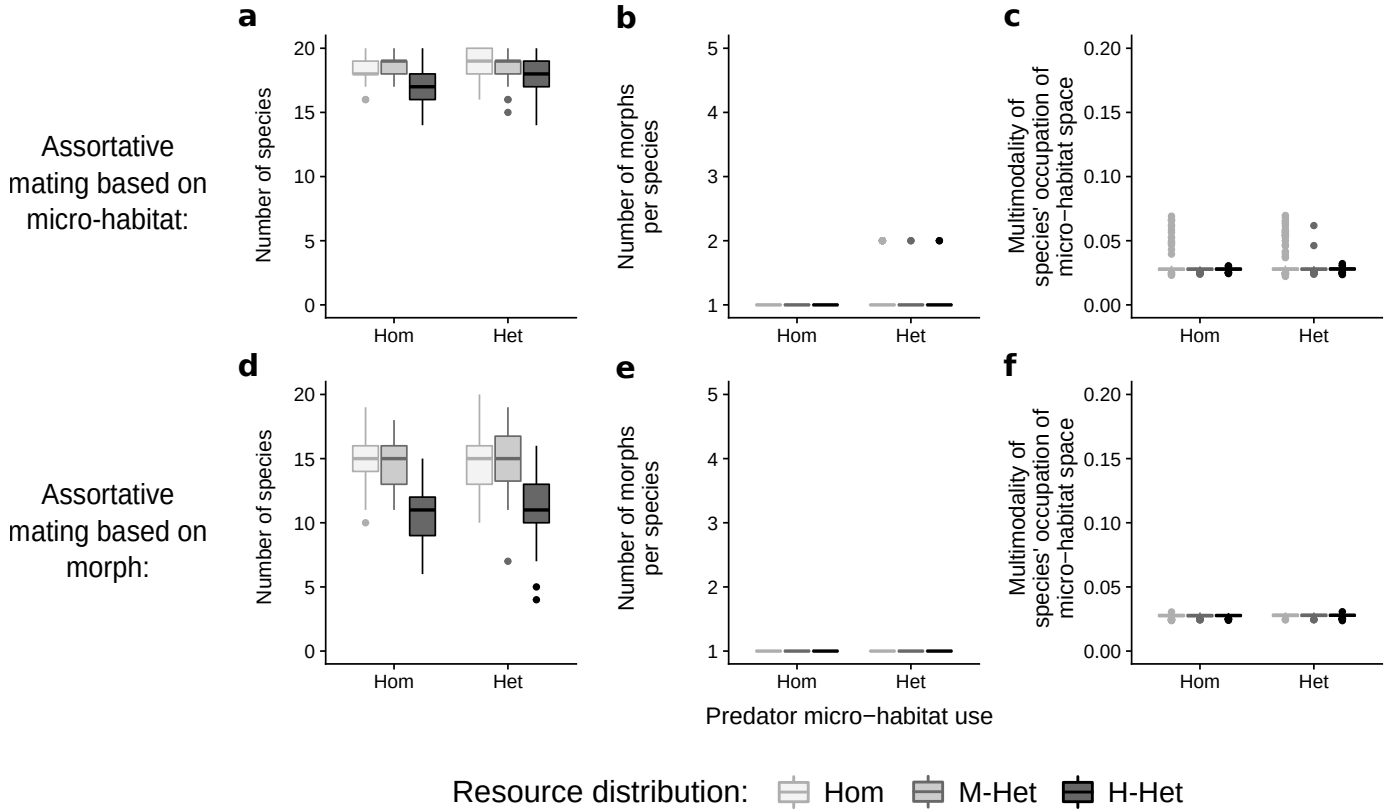


Figure A1. Species diversity and species characteristics. Mating is assortative based either on micro-habitat ( $a_h = 5$ ,  $a_m = 0$ ) (a, b, c) or on morph ( $a_h = 0$ ,  $a_m = 0.5$ ) (d, e, g). After 1,000 generations, we record the number of remaining species (a, d), the number of morphs carried by each species (b, e) and the multimodality of species' occupation of micro-habitat space (c, f). In each species, we count the number of morphs carried by more than 10 individuals (b, e) to increase the likelihood that the morphs observed at the end of the simulation are not transient (morphs generated by recent mutations that would have been eliminated by selection if simulations had continued). To analyze how species use the micro-habitat space, we measure the pairwise Euclidean distances between the individuals position in the two-dimensional micro-habitat space. We then compute the Hartigans' dip statistic (Hartigan and Hartigan, 1985; Freeman and Dale, 2013) to assess the multimodality intensity in the distribution of pairwise micro-habitat distances within species. When species' occupation of the micro-habitat space is unimodal, then the dip statistics of the distribution of the pairwise micro-habitat distances is close to 0. The dip statistic increases when individual distribution throughout the micro-habitat space departs from unimodal expectations, resulting in clustered, multimodal coverage of micro-habitat space. In other words, this statistics is high for species using multiple micro-habitats. In different simulations, predator micro-habitat use is either homogeneous (Hom) or heterogeneous (Het). Resource distribution among micro-habitat is homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). We record some species extinctions in our simulations (a, d). Additionally, almost all species are monomorphic (b, e) and use a restricted micro-habitat (c, f) (except some outlier species). Parameter values: see Table 1.

## Assortative mating based on micro-habitat and heterogeneous predation

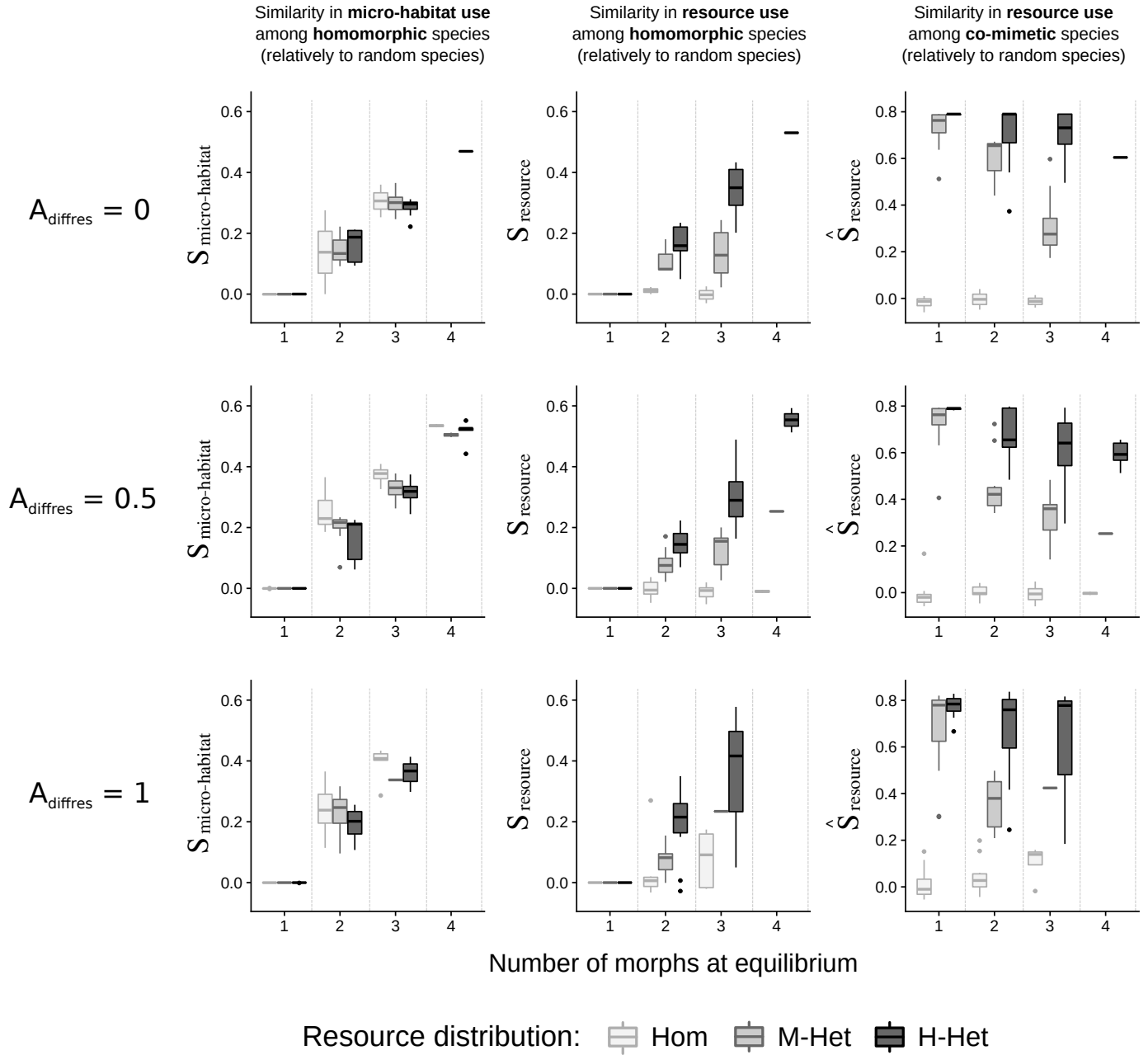


Figure A2. Ecological similarity among homomorphic or co-mimetic species under heterogeneous predation for different values of the resource-based competition parameter  $A_{\text{diffres}}$ . Mating is assortative based on micro-habitat ( $a_h = 5$ ,  $a_m = 0$ ). Resource distribution among micro-habitat can be homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). See caption of Fig. 3 for details. For  $A_{\text{diffres}} = 1$ , competition between species using the same or different resources is even. Note that, among the 40 runs performed per combination of parameters, we do not observe the maintenance of high mimicry diversity (number of morph at equilibrium = 4) for some combinations of parameters. For all conditions tested, similarity in resource use among co-mimetic species occur if resources are heterogeneously distributed (because it promotes co-occurrence among co-mimetic species). Parameter values: see Table 1.

## Assortative mating based on morph and heterogeneous predation

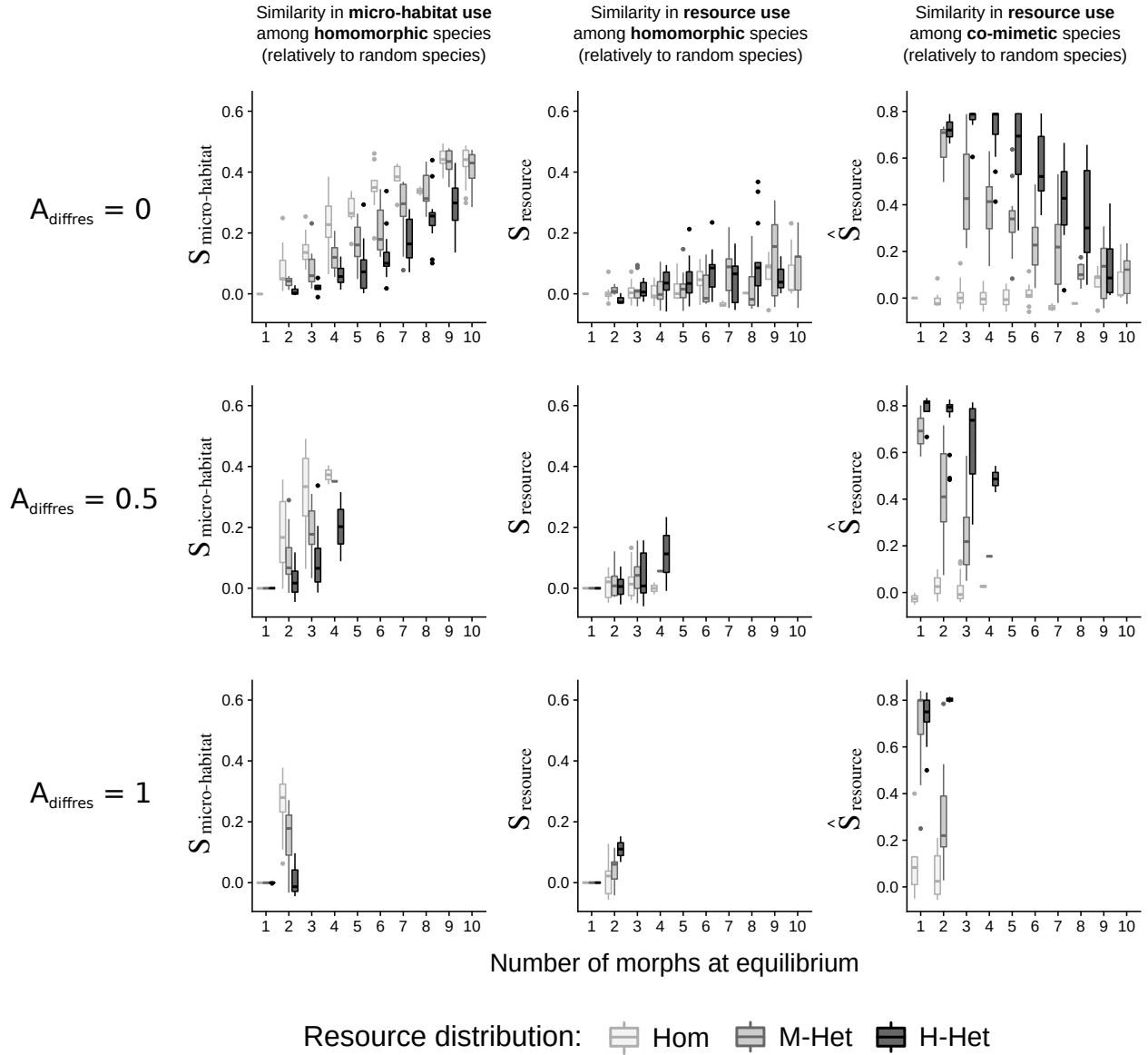


Figure A3. Ecological similarity among homomorphic or co-mimetic species under heterogeneous predation for different values of the resource-based competition parameter  $A_{\text{diffres}}$ . Mating is assortative based on morph ( $a_h = 0$ ,  $a_m = 0.5$ ). Resource distribution among micro-habitat can be homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). See caption of Fig. 3 for details. For  $A_{\text{diffres}} = 1$ , competition between species using the same or different resources is even. When low mimicry diversity is maintained (number of morphs at equilibrium  $< 4$ ), similarity in resource use among co-mimetic species occur if resources are heterogeneously distributed (because it promotes co-occurrence among co-mimetic species). When high mimicry diversity is maintained (number of morph at equilibrium  $> 4$ ), species that are not co-mimetic are faced to the same predator community, weakening the effects of positive interactions on ecological similarity in resource use ( $\hat{S}_{\text{resource}}$  decreases with mimicry diversity at equilibrium). For all values of  $A_{\text{diffres}}$  tested, similarity in micro-habitat ( $S_{\text{micro-habitat}}$ ) or resource use ( $S_{\text{resource}}$ ) among homomorphic species do not reflect the importance of positive interactions in structuring Müllerian mimetic communities. Overall, however, co-mimetic species use more similar micro-habitats than random pairs of species ( $S_{\text{micro-habitat}} > 0$ , left column) and use more similar resources than random pairs of species if resource distribution is heterogeneous ( $\hat{S}_{\text{resource}} > 0$ , right column). Parameter values: see Table 1.

## Assortative mating based on micro-habitat and morph, and heterogeneous predation

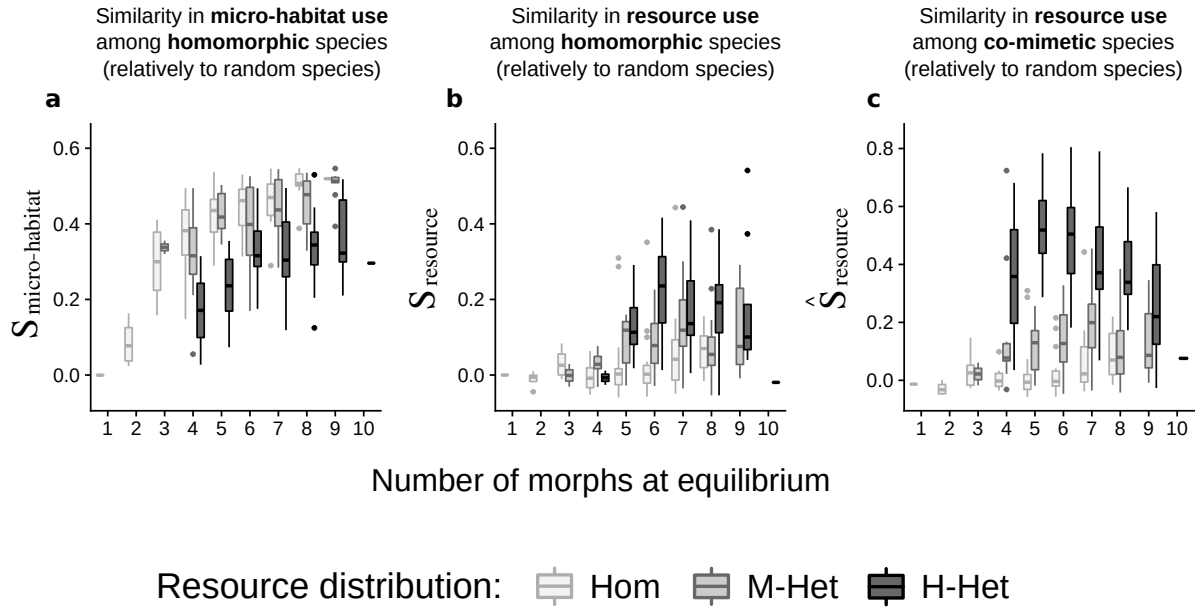


Figure A4. Ecological similarity among homomorphic or co-mimetic species under heterogeneous predation when mating is assortative based on micro-habitat and morph ( $a_h = 5$ ,  $a_m = 0.5$ ). Resource distribution among micro-habitat can be homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). See caption of Fig. 3 for details. For  $A_{\text{diffres}} = 1$ , competition between species using the same or different resources is even. Here, assortative mating based on morph favours the maintenance of multiple morphs despite positive frequency-dependent predation. When high mimicry diversity is maintained (number of morphs at equilibrium  $> 4$ ), species that are not co-mimetic are faced to the same predator community, weakening the effects of positive interactions on ecological similarity in resource use ( $\hat{S}_{\text{resource}}$  decreases with mimicry diversity at equilibrium, c). Moreover, similarity in resource use ( $S_{\text{resource}}$ , b) among homomorphic species weakly reflects the importance of positive interactions in structuring Müllerian mimetic communities. Overall, however, co-mimetic species use more similar micro-habitats than random pairs of species ( $S_{\text{micro-habitat}} > 0$ , a) and use more similar resources than random pairs of species if resource distribution is heterogeneous ( $\hat{S}_{\text{resource}} > 0$ , c). Parameter values: see Table 1.

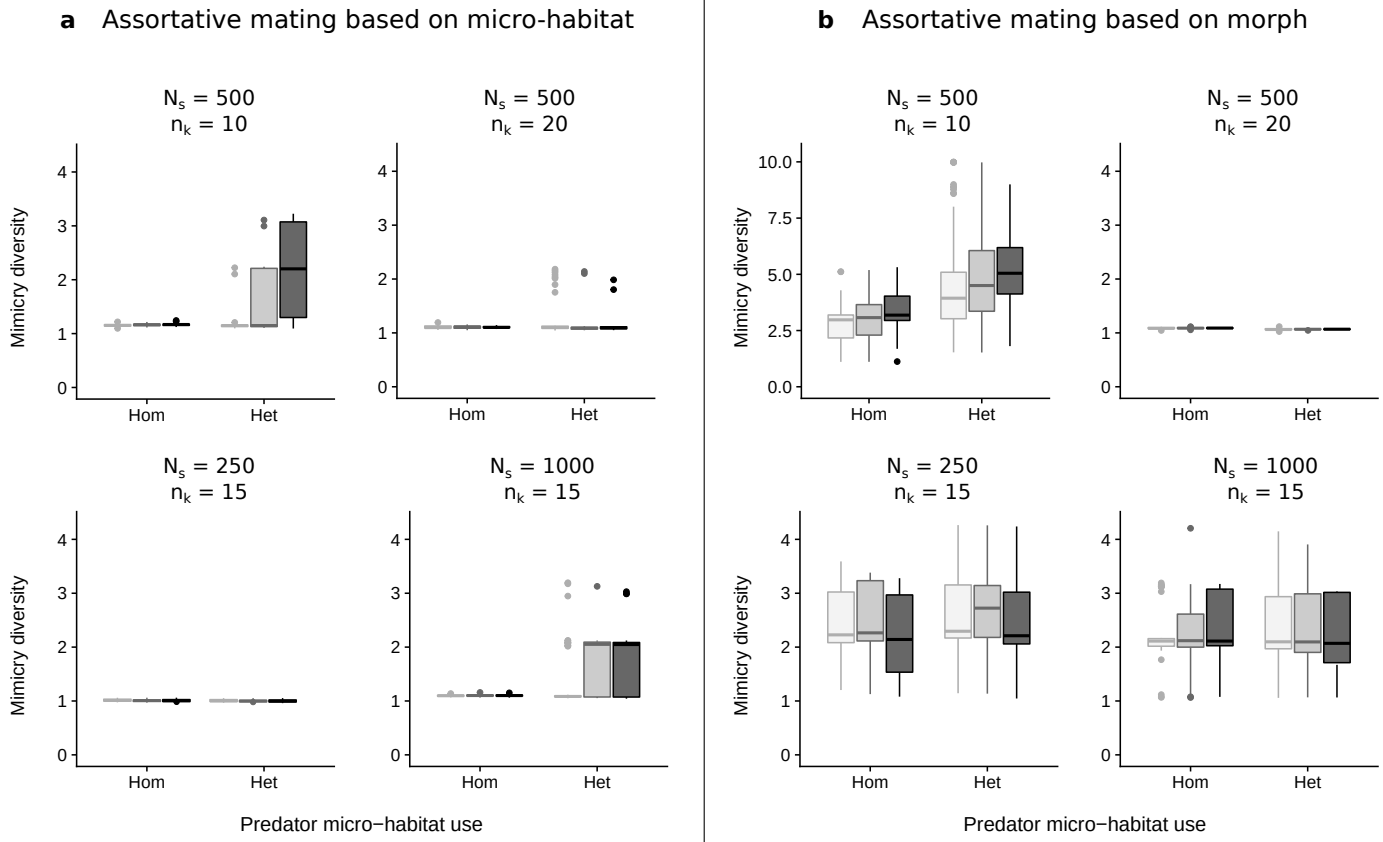


Figure A5. Maintenance of mimicry diversity and sensitivity to  $(N_s, n_k)$ . After 1,000 generations, we measure the remaining mimicry diversity. Mating is assortative based on micro-habitat ( $a_h = 5, a_m = 0$ ) (a) or morph ( $a_h = 0, a_m = 0.5$ ) (b). In different simulations, predator micro-habitat use is either homogeneous (Hom) or heterogeneous (Het). Resource distribution among micro-habitat is homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). The conditions favouring the maintenance of mimicry are very limited. In the main analysis, we therefore implement parameters favouring the maintenance of mimicry diversity ( $N_s = 500, n_k = 15$ ). As long as mimicry diversity is maintained, we get qualitatively the same results concerning the structure of ecological communities (Fig. A6). Other parameter values: see Table 1.

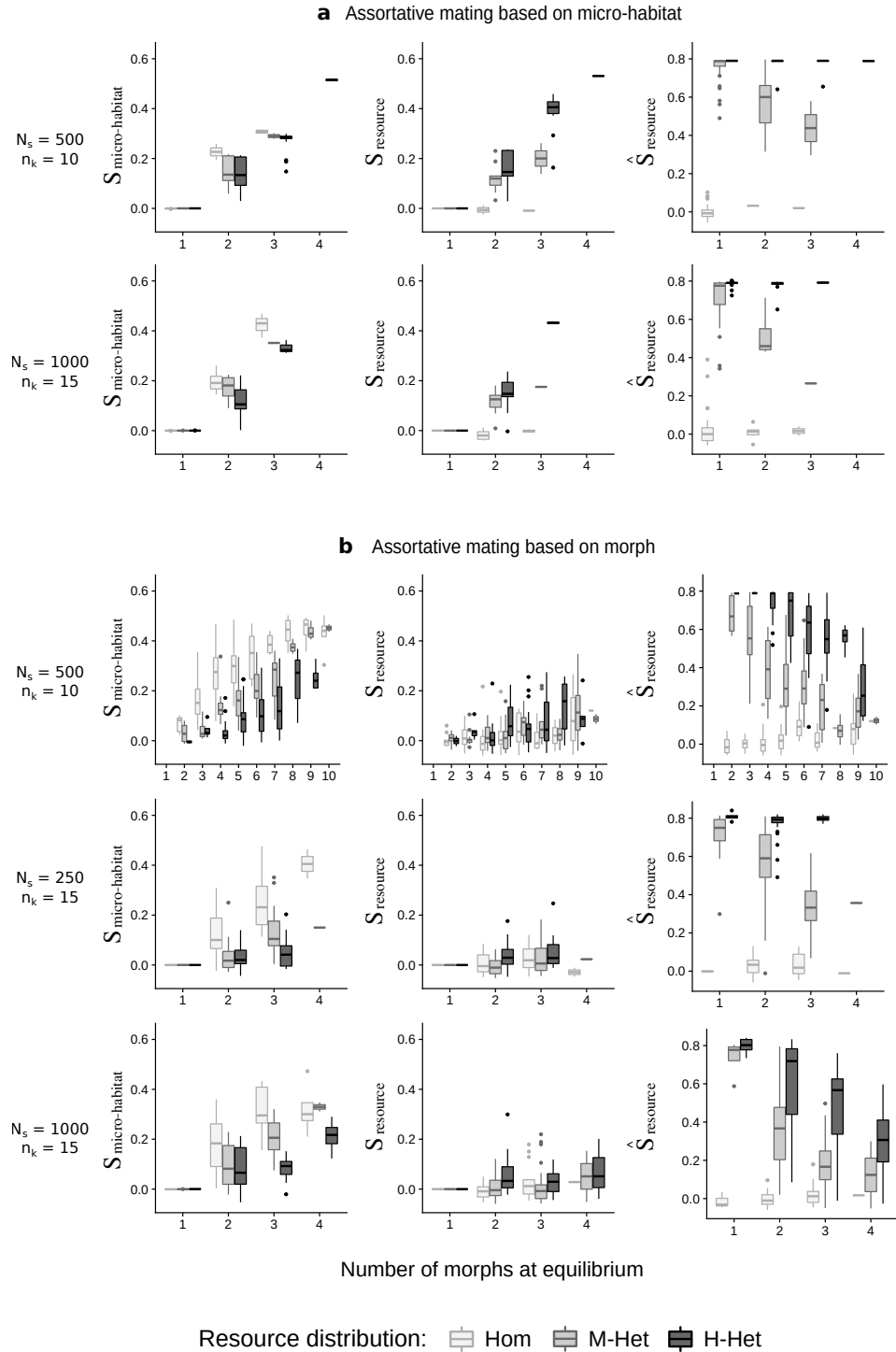


Figure A6. Ecological similarity among homomorphous or co-mimetic species under heterogeneous predation, and sensitivity to  $(N_s, n_k)$ . After 1000 generations, we assess the level of similarity in micro-habitat use ( $S_{\text{micro-habitat}}$ ) and in resource use ( $S_{\text{resource}}$ ) among homomorphous species compared to random pairs of species. We also assess the level of similarity in resource use among co-mimetic species compared to random pairs of species ( $\hat{S}_{\text{resource}}$ ). For each combination of parameters, simulations are classified according to the number of morphs that remain in the community. Here we implement combinations of parameters  $(N_s, n_k)$  that lead to the maintenance of mimicry diversity (Fig. A5). We get qualitatively the same results concerning the structure of ecological communities (shown in Fig. 3). Other parameter values: see Table 1.

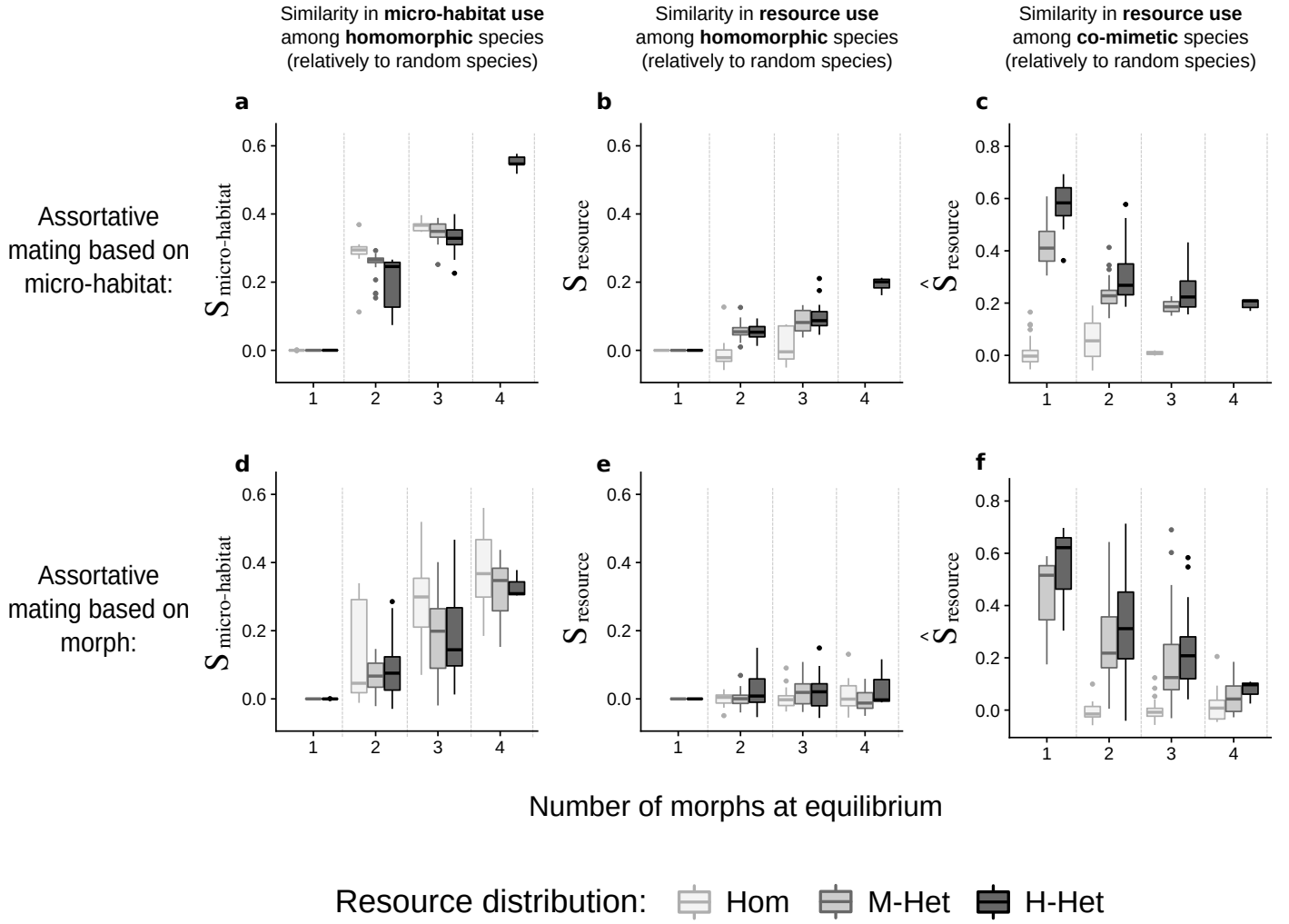


Figure A7. Ecological similarity among homomorphic or co-mimetic species under heterogeneous predation within a three-dimensional niche space (with  $N_{\text{resource}} = 8$  and  $N_{\text{predator}} = 8$  organized as in the two-dimensional case, i.e. as in Fig. 1b-c). Resource distribution among micro-habitat can be homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). Mating is assortative based either on micro-habitat ( $a_h = 5$ ,  $a_m = 0$ ) (a, b, c) or on morph ( $a_h = 0$ ,  $a_m = 0.5$ ) (d, e, g). See caption of Fig. 3 for details. Parameter values: see Table 1.



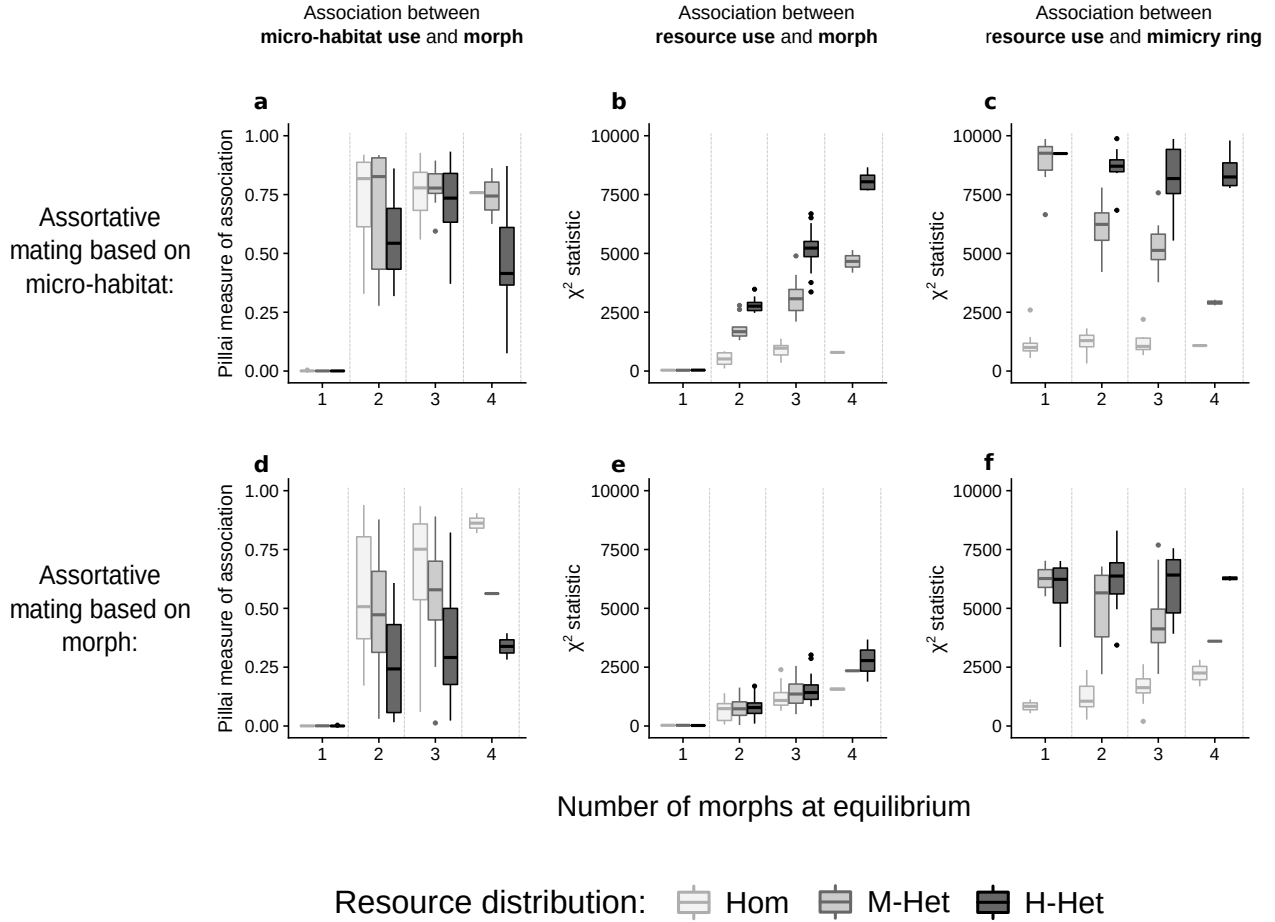


Figure A8. Ecological similarity among homomorphic or co-mimetic individuals under heterogeneous predation using statistics measuring strength of association within population. Resource distribution among micro-habitat can be homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). Mating is assortative based either on micro-habitat ( $a_h = 5$ ,  $a_m = 0$ ) (a, b, c) or on morph ( $a_h = 0$ ,  $a_m = 0.5$ ) (d, e, g). Mimicry ring is here defined using the co-mimicry criterion: individuals belonging to the same mimicry ring have the same morph and occupy the same micro-habitat (descretized as in Fig. 1a). We measured the association between morph/mimicry group and the two niche scores of each individual by calculating Pillai's trace statistic in a multivariate analysis of variance framework. Pillai's trace is analogous to the coefficient of determination. We measured the association between morph/mimicry group and the resource use of each individual by calculating the  $\chi^2$  statistic (i.e. a measures of goodness of fit). Using those statistics accounting for the variance within population lead to qualitatively similar results than with our measures of similarity ( $S_{\text{micro-habitat}}$ ,  $S_{\text{resource}}$ ,  $\hat{S}_{\text{resource}}$ ) at the species level (Fig. 3). See caption of Fig. 3 for other details. Parameter values: see Table 1.

## Heterogeneous predation and homogeneous resources

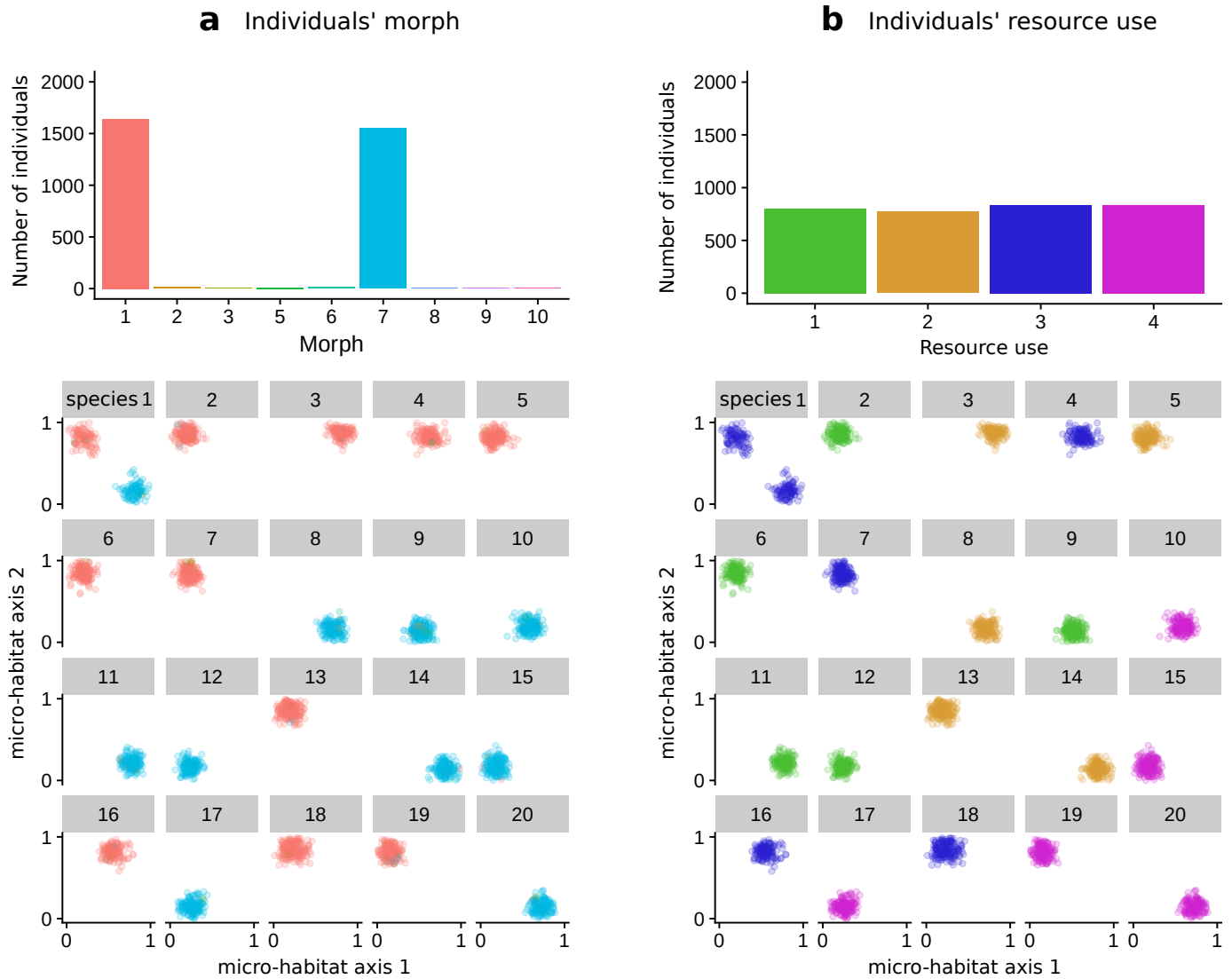


Figure A9. Example of ecological community with heterogeneous predator micro-habitat use and homogeneous resources after 1000 generations. Individuals' morph (a) and resource use (b) are shown. We represent the number of individuals with each trait value (graphs at the top), as well as the micro-habitat use of each individual from all 20 remaining species (graphs at the bottom). Each colour corresponds to a morph value or a resource use value. Here, mimicry diversity is maintained via heterogeneous predator micro-habitat use. Homomorphous species often use similar micro-habitats (a), but may differ in their resource use (b). Mimicry is linked to ecological similarity along the micro-habitat axis, but not along the resource axis. Parameter values: see Table 1.

## Heterogeneous predation and highly heterogeneous resources (example 1)

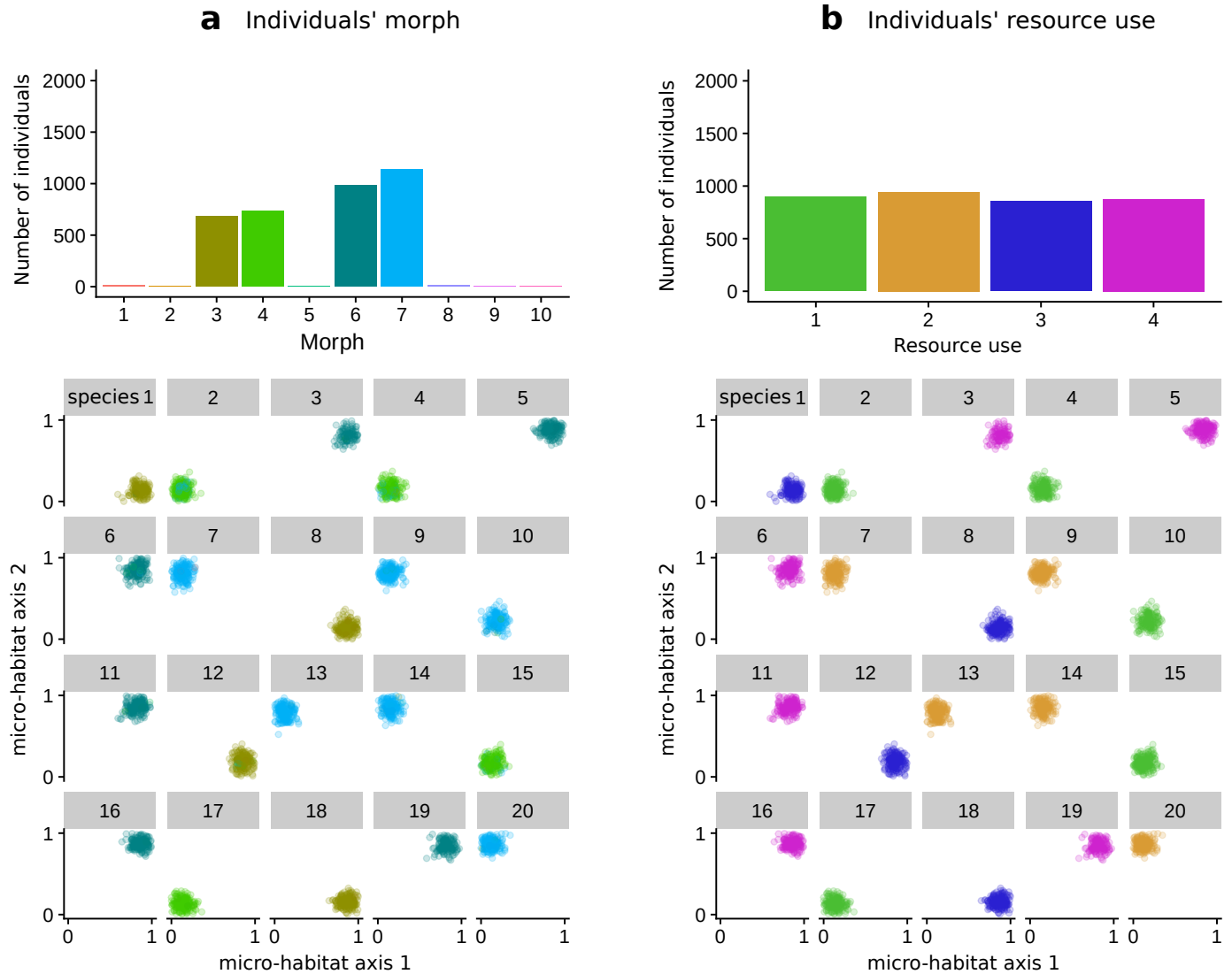


Figure A10. Example of ecological community with heterogeneous predator micro-habitat use and highly heterogeneous resources after 1000 generations. See caption of Fig. A9 for details. Again, mimicry diversity is maintained via heterogeneous predator micro-habitat use. Homomorphic species often use similar micro-habitats (a), and the same resource (e.g. species 1, 8, 12 and 18) (b). Mimicry is linked to ecological similarity along the micro-habitat and resource axes. Parameter values: see Table 1.

## Heterogeneous predation and highly heterogeneous resources (example 2)

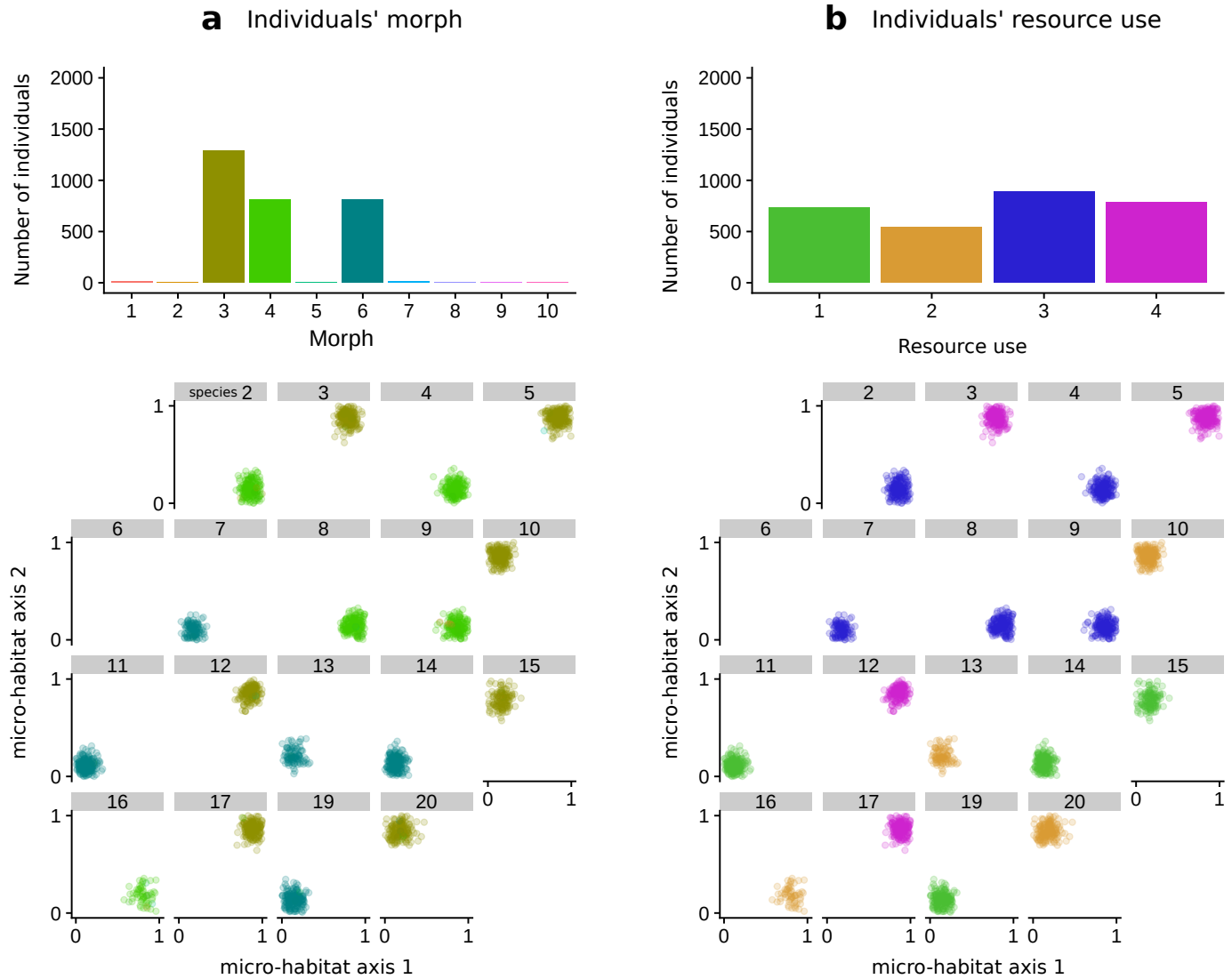


Figure A11. Same conditions than in Fig. A10, but this time with the maintenance of only three morphs at equilibrium. Note that individuals carrying morph 3 use both the top-left and top-right corners of the niche space. Homomorphic species are not all co-mimetic species facing the same predator community.

## Assortative mating based on morph and homogeneous predation

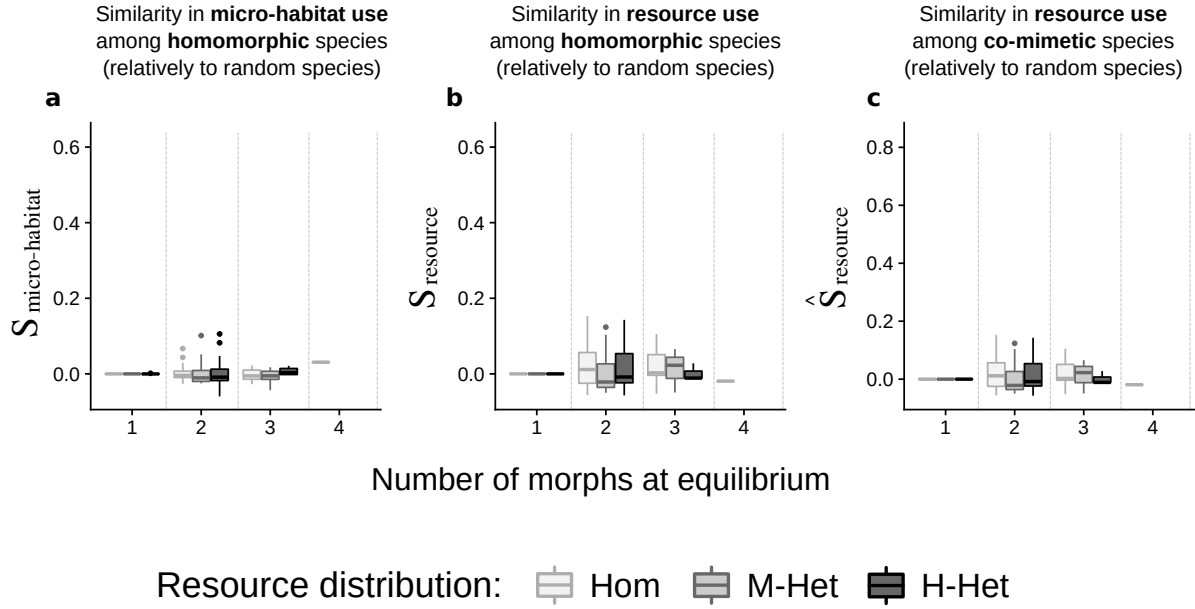


Figure A12. Ecological similarity among homomorphous or co-mimetic species under homogeneous predation. Mating is assortative based on micro-habitat ( $a_h = 5$ ,  $a_m = 0$ ). Resource distribution among micro-habitat can be homogeneous (Hom), moderately heterogeneous (M-Het) or highly heterogeneous (H-Het). See caption of Fig. 3 for details. For  $A_{\text{diffres}} = 1$ , competition between species using the same or different resources is even. Here, all species are faced to the same community of predators (homomorphous species are necessarily co-mimetic) and assortative mating based on morph favours the maintenance of multiple morphs despite positive frequency-dependent predation. Compared to the case with heterogeneous predation (Fig. 3d-f), there is little ecological similarity in micro-habitat use or resource use among co-mimetic species (statistics  $S_{\text{micro-habitat}}$ ,  $S_{\text{resource}}$  and  $\hat{S}_{\text{micro-habitat}} \simeq 0$ ) when predation is homogeneous. Parameter values: see Table 1.

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