Evolution of conspicuousness in defended species involved in Müllerian mimicry

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Abstract

Variation in warning pattern resulting in different levels of conspicuousness is observed within and among chemically-defended prey species. Toxin acquisition and predator avoidance behaviour have been shown to affect the evolutionary processes underlying such warning signal diversity. Predators learn to associate warning colour pattern with unpalatability and this results in a decrease in predation risk for individuals displaying a locally abundant warning pattern. This positive number-dependent selection generated by predators causes evolutionary convergence across defended prey species toward a common warning colour pattern (Müllerian mimicry). Müllerian mimicry has a strong effect on the local diversity of warning patterns in tight connexion with the local abundance of mimetic species. Moreover, because chemical defences often stem from diet, the levels of defences might depend on resource specialisation, therefore impacting species abundance and the evolution of aposematic colour patterns.

To investigate the effect of Müllerian mimicry on the evolution of the conspicuousness of warning signal and unpalatability, we built a single-species model where warning signal and unpalatability can evolve, assuming that (1) predation risk depends on both the number of individuals sharing a warning signal within the studied species and the local abundance of mimetic species and (2) the level of unpalatability depends on resource specialisation, implying that specialists suffer from reduced carrying capacity. We found that Müllerian mimicry can promote the evolution of more conspicuous colouration in cryptic species. Nevertheless, by favouring locally abundant signals, Müllerian mimicry stabilizes the

persistence of mildly conspicuous patterns, explaining for instance the evolution of partially transparent colour patterns in some chemically-defended butterflies. Our model also show that Müllerian mimicry limits the emergence of new aposematic signals associated with reduced unpalatability. Altogether, our theoretical approach highlights complex interplays between resource specialisation, mimicry and predator behaviour on the evolution of aposematic signals and associated defences.

45 **Impact summary**

46 Aposematism, whereby chemically-defended species display conspicuous colouration acting
47 as warning signal is still a debated question, involves the joint evolution of two independent
48 traits, namely colour pattern and chemical defences. Evolution of new conspicuous warning
49 signal is an evolutionary puzzle, because individuals exhibiting increased conspicuousness
50 suffer from increased detection by predators. Convergence in warning pattern is frequently
51 observed among defended prey (*i.e*. Müllerian mimicry), because sharing a common warning
52 signal decreases individual predation risk. Mimicry among defended prey species may
53 therefore profoundly influence the evolution of warning signals conspicuousness and
54 chemical defences both within and among prey species.

55 The origin of variations in chemical defences is still largely unknown for a wide range of prey
56 species, but toxic compounds are frequently sequestered from food intake so that
57 specialized species may be more likely to successfully accumulate toxins from their diet. In
58 turn, such specialization may limit species abundance locally, because of restricted range of
59 resource and have a profound importance on the dynamics of aposematic signals.
60 Understanding the evolution of aposematism therefore requires integrating ecological
61 parameters linked to the evolution of defence levels and species abundance.

62 Here we use a theoretical approach to investigate the evolution of colour pattern
63 conspicuousness in a chemically-defended species, involved in Müllerian mimicry. We
64 explore the impact of ecological parameters, such as composition of local mimetic
65 communities and diet specialisation on the evolution of aposematic signal and chemical

defences. We show that (i) mimetic interactions are a key factor enhancing fixation of new patterns with increased conspicuousness (ii) even mildly conspicuous signals can persist in species involved in Müllerian mimicry and that (iii) the evolution of chemical defences in Müllerian mimics tightly depends on the resource acquisition pathway.

70 **INTRODUCTION**

71 The evolution of warning colour patterns in chemically-defended species (*i. e.* aposematism)
72 has received considerable attention. Aposematism evolution relies on the interplay of three
73 main factors, namely levels of defence, warning colouration, and abundance. Predators can
74 learn to associate a warning colour pattern with unpalatability and subsequently avoid any
75 individual displaying a known warning colour pattern. Predator's' learning generates
76 number-dependent selection favouring the most abundant warning pattern (Chouteau *et al.*,
77 2016). Predators' learning depends on their negative experience associated with attacking a
78 chemically-defended prey, linked to the level of distastefulness of that prey (Alcock, 1970a,
79 1970b; Goodale & Sneddon, 1977). The origins of unpalatability in defended prey are still
80 largely unknown in many defended species, but in aposematic butterflies, one of the best-
81 known examples of aposematic organisms, toxic compounds are frequently synthesized
82 and/or sequestered from diet (Edgar, 1983; Engler-Chaouat & Gilbert, 2006; Zagrobelny *et*
83 *al.*, 2014; de Castro *et al.*, 2017), resulting in variations in the level of defences both within
84 species relying on the same diet, and among species relying on drastically different
85 resources. Specialisation on a given source of toxins might enhance toxin sequestering
86 capacity. For instance, specialist butterfly species *Heliconius sara* and *H. sapho* that
87 sequester toxins from their host-plant *Passiflora auriculata* and *P. pittieri*, respectively, were
88 shown to contain drastically smaller amounts of toxins when reared on other *Passiflora* host-
89 plants, highlighting their increased sequestration capacities linked to host-plant
90 specialisation (Engler-Chaouat & Gilbert, 2006). Nevertheless, compared to generalist
91 species, specialist species have a reduced resource range, which may limit their abundance.

92 By influencing jointly unpalatability and abundance, specialisation on toxin resources may
93 play a complex role in the evolution of warning colour patterns.
94
95 Although higher conspicuous entails higher detectability, it has been shown that
96 when detected conspicuous colour patterns are be less attacked than cryptic patterns often
97 displayed by profitable prey because of innate aversion (Sillén-Tullberg, 1985; Lindström *et*
98 *al.*, 2001), and might also trigger more rapid avoidance-learning due to higher memorability
99 (Roper & Redston, 1987; Ham *et al.*, 2006; Siddall & Marples, 2008). Unpalatability level can
100 impact the evolution of warning colour patterns and *vice versa*. In particular, theoretical
101 models showed that such coevolution should lead to negative or positive correlations
102 between levels of defence and warning pattern conspicuousness. Some models predict a
103 positive correlation between signal conspicuousness and unpalatability (Speed & Ruxton,
104 2005a; Broom *et al.*, 2006, 2008) because warning patterns can act as ''honest" signals of
105 unpalatability, whereby only well-defended individuals display conspicuous pattern
106 associated with elevated attack risk or other fitness costs. Other models predict instead a
107 negative correlation, when defences induce immediate predator deterrence even in the
108 absence of costly conspicuousness (Leimar *et al.*, 1986; Speed & Ruxton, 2005b). Depending
109 on the availability of toxin resources and level of competition, positive and negative
110 correlations between signal conspicuousness and unpalatability can also be expected (Speed
111 & Ruxton, 2007; Blount *et al.*, 2009), so that the directions of such correlation within and
112 across species might differ (Speed, Ruxton, *et al.*, 2010). In empirical studies, positive
113 correlations between conspicuousness and chemical defences have been detected across

114 populations of the Asian ladybird *Harmonia axyridis* (Bezzerides *et al.*, 2007; María Arenas *et*
115 *al.*, 2015), the poison frog *Dendrobates pumilio* (Maan & Cummings, 2012) and the paper
116 wasp *Polistes dominula* (Vidal-Cordero *et al.*, 2012) or across species of Dendrobatidae frogs
117 (Summers & Clough, 2001; Santos & Cannatella, 2011), ladybirds (María Arenas *et al.*, 2015)
118 and Opisthobranchia (marine gastropods) species (Cortesi & Cheney, 2010). However
119 empirical investigations across species have also revealed negative correlation between
120 conspicuousness and unpalatability, across poison frog *Epipedobates* species (Darst &
121 Cummings, 2006), Nudibranch (marine gastropods) species (Winters *et al.*, 2018) and burnet
122 moth (Briolat *et al.*, 2019).

123 In many cases, warning patterns are shared across defended species living in
124 sympatry (Mallet & Gilbert, 1995): because of the positive number-dependent selection
125 acting on colour patterns, evolutionary convergence of warning colour pattern among
126 species within the same locality is favoured, a phenomenon described as Müllerian mimicry
127 (Müller, 1879; Guilford, 1988; Sherratt, 2008; Joron, 2009). Mimetic interactions with other
128 defended species can influence the evolution of warning patterns and unpalatability .For
129 instance, defence levels in *Limenitis archippus* 'viceroy' butterfly tend to increase when the
130 co-mimetic species *Danaus gilippus* is less abundant (Prudic *et al.*, 2019). In this case, the
131 observed variations of unpalatability are independent from variations in host-plant toxic
132 compounds, suggesting direct selection on unpalatability, linked to the decreased
133 abundance of co-mimetic species. Warning patterns may also evolve in response to
134 variations in unpalatability displayed by co-mimics: Franks et al. (2009) showed theoretically
135 that the evolution of aposematic signals can be promoted in a defended species, if the

136 abundance of a palatable, parasitic mimetic species (*i. e.* Batesian mimics) is high. Different
137 mimicry patterns may vary in their conspicuousness, resulting in contrasted warning colour
138 patterns observed even between closely related species. A striking example is the
139 neotropical butterfly tribe Ithominii, whereby some species exhibit brightly coloured wing
140 patterns while others harbour transparent wings patterns (Beccaloni, 1997; Arias *et al.*,
141 2019). The evolution of new colour patterns with a different level of conspicuousness is not
142 straightforward, as individuals with new colour patterns may suffer from reduced fitness. In
143 addition to fitness reduction incurred by potential metabolic cost of pigmentation (Hill,
144 1996; McGraw *et al.*, 2005) and possible increased attack rates stemming from higher
145 detectability for more conspicuous patterns or from higher resemblance to profitable prey
146 for more cryptic patterns (Arias. et. 2019), the initially low abundance of new patterns limits
147 number-dependent advantages linked to predation avoidance learning (Greenwood *et al.*,
148 1989; Lindstrom *et al.*, 2001). However, when the local community contains multiple
149 mimetic species, including species with different colour patterns as often observed in
150 aposematic butterfly communities (*e. g.*, Willmott et al. 2017), the emergence of new
151 patterns within a species can be facilitated if it resembles a warning pattern already
152 displayed by other defended species. Therefore, mimetic interactions between species need
153 to be taken into account when investigating the evolution of conspicuousness in defended
154 species.

155 Here we used a theoretical approach to investigate the evolution of conspicuousness
156 and unpalatability as heritable traits, in a population of a defended species involved in
157 Müllerian mimicry. In particular, we investigate whether the presence of a diverse

158 community of mimetic prey species can facilitate the evolution of new colour pattern, even
159 in the absence of direct deterrence provided by more conspicuous colour pattern (*i. e.*,
160 innate aversion against conspicuousness) and unpalatability. Contrary to other studies, in
161 our model prey do not survive an attack whatever its unpalatability level. We considered
162 that mutant warning patterns that differ in conspicuousness from the wild-type pattern can
163 either (i) be recognized as the same signal as the ancestral pattern or (ii) be considered as a
164 new warning signal, distinguished by predators from the ancestral pattern. In the latter case,
165 ancestral and emergent patterns could then match local mimicry rings (community of
166 individuals living in sympatry and sharing the same warning pattern) of various abundances,
167 and therefore benefit from enhanced protection. We assumed that conspicuousness
168 enhances not only detectability by predators but also signal memorability, and therefore
169 influences predator's learning process in associating a given warning colour pattern with
170 unpalatability. Finally, because unpalatability is linked to resource specialisation in some
171 prey species (*e. g.*, butterflies), we assume that increase in unpalatability stems from
172 specialisation towards a limited type of resources, thereby restricting population size. This
173 hypothesis contrasts with classical assumption assuming a physiological cost of
174 unpalatability that might limit investment in costly pigments. We also assumed no direct
175 effect of enhanced unpalatability on predator deterrence, so that the effect of unpalatability
176 only impacts individual protection because of predator learning.
177

178 **MATERIAL AND METHODS**

179 **General model**

180 Using ordinary differential equations, we model a single population of chemically-defended
181 species, initially composed of a number of wild-type individuals N_{wt}. Wild-type individuals
182 have a fixed unpalatability u_{wt} and display a warning colour pattern with a level of
183 conspicuousness c_{wt} and a basal predation rate p_{wt}, which depends on the abundance of co-
184 mimetic species (see table 1). We introduce a small number of mutant individuals N_m
185 harbouring either the same or a different warning colour pattern as the wild-types. Mutant
186 individuals may have different conspicuousness c_m, basal predation rate p_m or unpalatability
187 u_m as compared to wild-type (see table 1). We then track the evolution of the number of
188 wild-types and mutants through time.
189 The evolution of these numbers of wild-types and mutants through time follows the general
190 equations [1] and [2], respectively:

191 $$\frac{dN_{wt}(t)}{dt} = \frac{dR_{wt}(t)}{dt} + \frac{dP_{wt}(t)}{dt} \quad [1],$$

192 and $$\frac{dN_m(t)}{dt} = \frac{dR_m(t)}{dt} + \frac{dP_m(t)}{dt} \quad [2],$$

193 including a reproduction term given by $\frac{dR_{wt}(t)}{dt}; \frac{dR_m(t)}{dt}$ and a predation term given by
194 $\frac{dP_{wt}(t)}{dt}; \frac{dP_m(t)}{dt}$ described below.
195

196 **Reproduction and resource specialisation**

197 Wild-types and mutants belong to the same species. As such, they have equal growth rate
198 (r), compete for same resources and have the same carrying capacity (K) (see table 1).
199 We consider no physiological cost associated with unpalatability u, but we assume that
200 increased unpalatability (u_{wt} and u_m for wild-type and mutant respectively) stems from

201 higher resource specialisation, so that unpalatability affects the range of available resources
202 and thus modulates the carrying capacity (see equation [3] and [4]). We implement a
203 parameter α to specifically investigate the effect of resource dependence on unpalatability
204 acquisition in the species: when α=0, level of unpalatability is independent from resource
205 and unpalatability has no effect on carrying capacity; the higher α, the stronger the
206 dependence between unpalatability and resource specialisation and therefore the impact on
207 carrying capacity. Changes in numbers of wild-type and mutant individuals due to
208 reproduction (R_{wt} and R_m respectively) are thus described as follows:

209 $$\frac{dR_{wt}(t)}{dt} = r * N_{wt}(t)\left[1 - \frac{N_{wt}(t)+N_m(t)}{K\left(\frac{1}{1+u_{wt}*\alpha}\right)}\right] \quad [3],$$

210 $$\frac{dR_m(t)}{dt} = r * N_m(t)\left[1 - \frac{N_{wt}(t)+N_m(t)}{K\left(\frac{1}{1+u_m*\alpha}\right)}\right] \quad [4].$$

211

212 **Predation and mimicry**

213 We assume that the predation risk decreases as the number of individuals sharing the same
214 warning colour pattern in the population increases, as classically assumed in models of
215 Müllerian mimicry (e. g., Joron & Iwasa, 2005). In case of mimicry with other species, the
216 basal level of predation applied to the wild-type and the mutant (p_{wt} and p_m respectively*)*
217 depend on the abundances of their respective co-mimetic species. Predation risk faced by
218 wild-type and mutant individuals then depends on their warning colour pattern
219 conspicuousness *c*, the signal abundance and their unpalatability *u*.

220 Conspicuousness has two opposite effects on predator's behaviour, detectability and
221 memorability. Detectability is described as the direct effect of conspicuousness on predation

222 rate, assuming more conspicuous warning colour patterns are more likely to be detected and
223 attacked. Cryptic individuals (c=0) have the lowest level of detectability by predators (but
224 even those individuals are detectable to some extent). Memorability is then described as an
225 indirect effect on the number-dependent advantage associated with mimetic signals: we
226 assume that more conspicuous signals might be easier for predators to remember and
227 therefore enhance protection brought by mimicry, as in previous models of Sherratt, 2002
228 and Broom *et al.*, 2006. We introduce a parameter β that modulates the effects of
229 conspicuousness on detectability compared to memorability. Specifically, for a given
230 memorability effect, low values of β incur a low detectability, while high values incur a high
231 detectability. By investigating the effect of parameter β, we investigate the relative effect of
232 conspicuousness on the balance between detectability and memorability.

233 First, we investigate the evolution of conspicuousness assuming that variations in
234 conspicuousness are generalized by predators, so that wild-type and mutant individuals
235 share the same warning signal ('single signal hypothesis' hereafter), (equations [5] and [6]).
236 We thus assume that warning colour patterns exhibited by wild-type or mutant individuals
237 belong to the same mimicry ring (and therefore face the same basal predation rate, p_{wt}=p_m)
238 and benefit from the same number-dependent advantage, but that they can differ in their
239 conspicuousness level. Under the single signal hypothesis, changes in numbers of wild-type
240 and mutant individuals due to predation (P_{wt} and P_m respectively) are thus described as
241 follows:

242 $$\frac{dP_{wt}(t)}{dt} = \frac{-p_{wt}(1+\beta*c_{wt})N_{wt}(t)}{1+(u_{wt}*c_{wt}*N_{wt}(t)+u_m*c_m*N_m(t))} \qquad [5],$$

243 $$\frac{dP_m(t)}{dt} = \frac{-p_m(1+\beta*c_m)N_m(t)}{1+(u_{wt}*c_{wt}*N_{wt}(t)+u_m*c_m*N_m(t))} \quad [6].$$

244

245 Alternatively, variations in conspicuousness can result in warning signal recognized as
246 different by predators and thus do not share the cost of predator's learning process ('two-
247 signal hypothesis' hereafter) (equations [7] and [8]). Other mimetic species in the
248 community are not explicitly modelled, but we assume that differences of abundances
249 between mimicry rings result in different basal predation rates p_{wt} *and* p_m. Under the two-
250 signals hypothesis, changes in numbers of wild-type and mutant individuals due to predation
251 (P_{wt} and P_m respectively) are thus described as follows:

252 $$\frac{dP_{wt}(t)}{dt} = \frac{-p_{wt}(1+\beta*c_{wt})N_{wt}(t)}{1+(u_{wt}*c_{wt}*N_{wt}(t))} \quad [7],$$

253 $$\frac{dP_m(t)}{dt} = \frac{-p_m(1+\beta*c_m)N_m(t)}{1+(u_m*c_m*N_m(t))} \quad [8].$$

254

255 **Testing the evolution of conspicuousness and unpalatability using simulations**

256 We investigate the evolution of conspicuousness and unpalatability by running numerical
257 simulations in Python ("Python Release Python 3.6.5," 2018). We do not investigate co-
258 evolution pattern between conspicuousness and unpalatability, as always one out the two is
259 fixed and the other varies. We first model a population of wild-type individuals and let them
260 reach equilibrium, (*i. e.*, a stable population size). Then, we introduce mutant individuals in
261 proportion of 0.01% of the wild-type. We assess whether the mutant colour pattern invades
262 the population or not, after 100,000 time steps. We specifically focus on four main
263 questions, investigating the evolution of conspicuousness and unpalatability, implementing

264 the same default values for global carrying capacity K=1000 and growth rate r=2 and
265 exploring a range of values for the other parameters, depending on the addressed question
266 (table 1). Notably, for all four questions investigated, we systematically test the effect of our
267 hypotheses regarding the link between unpalatability and resource specialisation (α) and the
268 detectability/memorability balance (β) on the evolutionary outcomes.
269

270 *1- Evolution of conspicuousness within the same warning signal (single-signal)*
271 Assuming the same fixed level of unpalatability in wild-type and mutant (u_{wt}=u_m), we study
272 the evolution of the level of conspicuousness of a given warning colour pattern, *i.e.* under
273 the single signal hypothesis, and assuming the same basal predation rate (p_{wt}=p_m=0.5). Wild-
274 type and mutant individuals thus have the same warning signal but differ in their
275 conspicuousness (c_{wt}≠c_m).
276

277 2- *Evolution of conspicuousness among different mimetic warning signals (two-signal)*
278 Assuming again a fixed level of unpalatability (u_{wt}=u_m), we explore scenarios where
279 variations in conspicuousness evolution results in a distinct warning signal in mutants (*i. e.*
280 two-signal hypothesis). We consider a mutant whose warning colour pattern is recognized as
281 different from that exhibited by the wild-type, where initially rare mutant colour patterns do
282 not benefit from protection gained by resemblance with numerous wild-type individuals.
283 We consider that wild-type and mutant belong to two distinct mimicry rings, that can have
284 either similar (*i.e.* p_{wt}=p_m=0.5), or uneven abundances, with more abundant mimicry ring

285 resembling wild-type individuals (p_{wt}=0.5 and p_m=0.75) or mutant individuals (p_{wt}=0.5 and
286 p_m=0.25).
287
288 *3- Evolution of unpalatability within the same warning signal*
289 Then we investigate the evolution of unpalatability assuming that wild-type and mutant
290 individuals shared the same warning colour pattern (single signal hypothesis), therefore
291 following predation equation [5] and [6] and assuming p_{wt}=p_m and c_{wt}=c_m.
292 In these simulations, we thus assume that wild-type and mutant individuals can differ in
293 their level of unpalatability (u_{wt}≠u_m).
294
295 *4- Evolution of unpalatability among different mimetic warning signal*
296 Finally, we explore the evolution of unpalatability (u_{wt}≠u_m) assuming that wild-type and
297 mutant individuals display different warning colour patterns (two signals hypothesis), but
298 with similar basal predation rate and level of conspicuousness p_{wt}=p_m and c_{wt}=c_m.
299
300 **RESULTS**
301 **1- Decrease in conspicuousness is favoured in populations displaying a single warning**
302 **signal**
303 We explore the evolution of conspicuousness in a population of individuals sharing the same
304 warning colour pattern (single signal hypothesis). Overall, less conspicuous colour patterns
305 are advantaged in unpalatable populations (Fig.1A). Predators recognize wild-type and
306 mutant patterns as the same warning signal, so that mutants and wild-types both benefit

307 from the same number-dependent protection, brought by the strength in number. However,
308 less conspicuous individuals also benefit from reduced detection by predators and therefore
309 benefit from a low predation rate. Because the signal is generalized by predators whatever
310 the level of conspicuousness, conspicuousness of warning signal tends to decrease. By
311 modulating the effect of conspicuousness on detectability/memorability (β), we confirmed
312 that the selective advantage of decreased conspicuousness is due to reduced detection by
313 predators, limiting predation (Sup. fig. 1.).

314 For high levels of unpalatability, we observed that less conspicuous mutants are not
315 fixed after 100,000 generations when wild-type individuals are highly conspicuous (Fig. 1B).
316 By increasing the number of generations in our simulations, less conspicuous warning colour
317 patterns still invade the population (Sup. Fig. 2), confirming that the selection coefficient
318 associated with less conspicuous mutants is still positive. In that case, predation pressure on
319 wild-type individuals is very low because number-dependent advantage is increased by high
320 unpalatability; consequently, selection favouring less conspicuous colour patterns is weak
321 such that more time is needed to reach fixation.

322 When unpalatability has no cost, our model suggests that decrease in
323 conspicuousness might be favoured within a single warning colour pattern because more
324 cryptic individuals benefit from both reduced detectability and protection brought by
325 mimicry. As previously suggested by theoretical models (*e.g.* Puurtinen & Kaitala, 2006), our
326 study highlights that the effect of conspicuousness on detectability should be precisely
327 characterized to understand the evolution conspicuousness within warning signal.

328

329 **2- Mimicry promotes the persistence of midly conspicuous warning colour pattern**

330 We then investigate invasion probability of mutants harbouring a different colour pattern
331 from that of the wild-type (two-signal hypothesis). In defended population, mutants
332 displaying a new warning signal rarely invade (Fig. 2), even when less conspicuous than the
333 wild-type signal, because wild-type individuals benefit from a stronger number-dependent
334 selection. Nevertheless, more conspicuous signals can invade when wild-type individuals
335 display a very cryptic signal (Fig. 2). Such invasion of a new signal with higher
336 conspicuousness is favoured when the basal predation rate of mutants (p_m) decreases, *i. e.*
337 when the new signal mimics warning patterns displayed by an abundant local community of
338 defended species (Fig. 2). New signals with increased conspicuousness can be favoured by
339 greater memorability; by diminishing the effect of conspicuousness on detectability while
340 maintaining the same level of memorability (low β), we observe an increase in the invasion
341 range of the more conspicuous mutant (Sup. fig. 3). When the effect of conspicuousness on
342 detectability decreases, its positive effect on memorability further facilitates the invasion of
343 an - initially rare - new conspicuous signal.

344 Our model therefore suggests that a more conspicuous signal matching a local
345 mimetic community can be advantaged in a population of cryptic prey, but mostly fails to
346 invade populations where wild-type individuals already display a mildly to strongly
347 conspicuous signal. This might explain the persistence of signals with mild conspicuousness
348 in Ithomiini butterflies, whereby many species harbour partly transparent mimetic colour
349 patterns (Beccaloni, 1997; Willmott *et al.*, 2017) despite their high levels of chemical
350 defences (Brown, 1984; Trigo *et al.*, 1996; Trigo, 2010). Transparency in Ithomiini results in a

351 decrease in detectability by avian predators (Arias *et al.*, 2019). But these mildly conspicuous
352 colour patterns might still be advantaged by their level of conspicuousness (providing both
353 low detectability but sufficient memorability) and the abundance of their mimicry ring.
354

355 **3- Less unpalatable mutants are advantaged in population displaying a single warning**
356 **signal**

357 We explored the evolution of unpalatability within a population where all individuals display
358 the same warning colour signal (single-signal hypothesis). When unpalatability stems from
359 increased resource specialisation ($\alpha \neq 0$), mutants with lower unpalatability invade the
360 population (Fig. 3A, C) because they share the same warning colour pattern with more
361 unpalatable wild-type, while bearing a lower cost due to resource specialisation. As a
362 consequence, when unpalatability becomes independent from resource specialisation ($\alpha = 0$),
363 mutant with lower unpalatability no longer invade (Fig. 3B, D). Less unpalatable mutants are
364 favoured as soon as unpalatability is linked to resource specialisation, regardless of
365 conspicuousness level (Sup. fig. 4). For instance, in aposematic butterflies, the origin of
366 unpalatability, sequestered and/or synthesized from host-plants, therefore impacts the
367 evolution of the level of chemical defences, stressing the need to consider not only
368 variations in chemical defences within mimicry rings but also the ecological pathway
369 enabling these variations.
370

371 **4- Müllerian mimicry limits the emergence of new signal associated with reduced defence**

372 Finally, we investigate the evolution of unpalatability when mutants and wild-types display
373 distinct warning signals (two-signal hypothesis) but similar level of conspicuousness. Here we
374 assume that level of unpalatability is positively linked to resource specialisation ($\alpha \neq 0$), so
375 that more unpalatable individuals suffer from increased competition for resource. Mutants
376 with increased unpalatability can invade only in wild-type populations that are fully palatable
377 (Fig. 4A). Otherwise, only mutants with drastically lower level of unpalatability compared to
378 wild-type individuals can invade as (Fig. 4A). In that case, individuals displaying a new colour
379 pattern suffer from increased predation risk as compared to wild-type individuals, which
380 benefit from number-dependent advantage. Nevertheless, because high unpalatability
381 results in a reduction in abundance (Fig. 4C), mildly unpalatable mutant individuals can
382 quickly reach a higher abundance and replace highly unpalatable wild-type individuals (Fig.
383 4A). When relaxing the hypothesis linking unpalatability to resource specialisation (*i. e.*
384 assuming $\alpha=0$), mutants with decreased unpalatability no longer invade (Fig. 4B), confirming
385 the role of resource specialisation in the evolution of new warning signal associated with
386 decreased unpalatability. This trend is observed whatever the values of conspicuousness
387 (Sup. fig. 5).

388 Because resource specialisation is likely to reduce abundance, it has a strong impact
389 on the evolution of aposematic signal, enabling for instance signal associated with lower
390 unpalatability to settle in mimetic population with high unpalatability. This might explain
391 why generalist species, such as the mimetic butterfly *Heliconius erato*, can be found in large
392 abundances despite displaying a low level of toxins (Arias et al. 2016). This low unpalatability
393 level contrasts with the high unpalatability levels observed in closely related specialist

394 species like *H. sara* (Arias *et al.*, 2016), displaying a different signal and often living in
395 sympatry.
396

397 **DISCUSSION**

398 **Evolution of conspicuousness depends on mimetic interactions**

399 Overall, our model highlights that the evolution of increased conspicuousness is not possible
400 when assuming no direct effect of unpalatability or colour pattern conspicuousness on
401 predator deterrence. In this case, we showed that more conspicuous warning colour
402 patterns cannot evolve unless considering Müllerian mimicry. Within species harbouring a
403 single warning signal, protection brought by number-dependent selection facilitates the
404 emergence of less conspicuous warning colouration.

405 By contrast, our theoretical approach highlights that the emergence of more
406 conspicuous warning colour patterns can be favoured by mimetic interactions with local
407 community. When a diverse mimetic environment is considered and the mutant pattern
408 belongs to another mimicry ring in the community, we showed that more conspicuous
409 warning colour patterns can be favoured over cryptic patterns, but not over an already
410 conspicuous one. This suggests that mildly conspicuous signals can still provide efficient
411 protection against predation. This might explain the diversity of levels of conspicuousness of
412 warning colour pattern in closely-related species, such as transparent and opaque patterns
413 in Ithomiini butterflies (Elias *et al.*, 2008; Chazot *et al.*, 2014). Considering mimetic
414 community opens a new angle to explain the evolution of the wide diversity of colour

415 patterns: even if number-dependent selection favours the most abundant signals within
416 population, its effect can be modulated by variation in the conspicuousness of the different
417 signals.

418 Nevertheless, some cognitive biases in predators might favour the invasion of more
419 conspicuous warning colour patterns in unpalatable species, on top of mimicry: innate
420 memorability, direct deterrence, diet conservatism or neophobia have indeed been shown
421 to promote the emergence of new warning patterns (Marples & Kelly, 1999; Marples *et al.*,
422 2005; Aubier & Sherratt, 2015). Moreover, in our model, conspicuousness variations within a
423 given warning colour pattern do not affect the predator's generalization behaviour.
424 However, when difference of conspicuousness becomes very high, predators may be less
425 likely to generalize, leading to mutant individuals losing protection from the strength in
426 number.

427 Environmental variations and stochasticity could also favour the settlement of new
428 warning colour patterns in defended species. For instance, some colour pattern might
429 benefit from crypsis in a given habitat by matching the local background but habitat change
430 might then enhances the evolution of conspicuousness (Merilaita & Tullberg, 2005; Speed &
431 Ruxton, 2005a; Tullberg *et al.*, 2005; Speed, Brockhurst, *et al.*, 2010). Stochastic events,
432 including colonization of new environments, have been predicted to facilitate the
433 emergence of new colour patterns (Sherratt et al 2006; Mallet, 2010), and may allow more
434 conspicuous patterns to arise. Such emergence of conspicuous colour pattern can also be
435 enhanced by gregariousness, which generate an initial number-dependent advantage
436 (Leimar *et al.*, 1986).

437

438 **The balance between detectability and memorability can modify the emergence of new**
439 **mimicry pattern**

440 Evolution of warning colour patterns relies on the evolution of conspicuousness: defended
441 prey benefit from aposematism only if predators are able to associate the colour pattern
442 with chemical defences. More specifically, our model highlights that memorability of
443 warning signal has an important influence on predator's behaviour, as it reduces predation
444 probability (Gittleman & Harvey, 1980; Ham *et al.*, 2006). Warning patterns might thus have
445 a different evolutionary fate depending on signal memorability. In the mimicry literature,
446 models exploring the emergence and persistence of multiple mimetic signals (Sherratt et al
447 2006, Mallet 2010) usually consider that all mimetic signals have the same predation risk,
448 and that the attack rate then depends on local number-dependent selection. Here we
449 highlight that the evolution of mimetic signals in defended species results from complex
450 interactions between signal abundance and unpalatability but also on the
451 detectability/memorability balance of the different mimetic colour patterns.

452

453 **Unpalatability evolution is underpinned by resource specialisation.**

454 We showed that selection favours individuals with lower unpalatability level, because of the
455 link between unpalatability and resource specialisation assumed in our model. Within a
456 single warning colour pattern, less unpalatable mutants strictly invade the population
457 because they benefit from the same number-dependent selection as wild-types. By
458 considering a diverse mimetic community, mutants with a colour pattern belonging to a

459 different mimicry ring lose this advantage, which inhibits the invasion of less unpalatable
460 mutants. In our model, as in some prey species such as butterflies, unpalatable metabolites
461 are either synthesized and/or sequestered from specialised resources (*e. g.*, butterfly larval
462 hostplants), and unpalatability is considered as an heritable trait linked to capacities to
463 survive and acquire toxins from defended resources. This assumption has important impact
464 on the evolution of unpalatability within and among mimetic signals. The origin of
465 unpalatability variations in conspicuous prey, their dependence to local resources and the
466 link between resource specialisation and prey carrying capacity thus needs to be empirically
467 investigated to improve our understanding of the evolution of mimetic warning patterns.
468 Furthermore, co-mimetic species sometimes share the same resources (Willmott & Mallet,
469 2004; Elias *et al.*, 2008; but see Alexandrou *et al.*, 2011), such that resource competition
470 might be more important within mimicry ring. If level of unpalatability is linked to resource
471 specialisation, the co-evolution between conspicuous mimetic signal and unpalatability
472 would therefore be shaped by both mutualistic and competitive interactions between co-
473 mimetic species.
474

DATA ACCESSIBILITY

AUTHOR'S CONTRIBUTIONS

V.L designed the study, T.G.A and L.M wrote the code, O.S ran simulations. O.S wrote the manuscript with contributions from all authors. All authors participated in constructive discussions and approved manuscript final version.

COMPETING INTERESTS

We declare no competing interests.

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641

642 **TABLE LIST**

643 **Table 1**: Summary of parameters used in the model, with their biological meaning and
644 explored range values.

Parameter	Range explored	Description
$N_{wt}(t)$, $N_m(t)$	-	Number of individuals sharing wild-type or mutant warning colour pattern at time *t*
u_{wt}, u_m	[0;1]	Unpalatability associated with wild-type or mutant warning colour pattern
c_{wt}, c_m	[0;1]	Conspicuousness of wild-type or mutant warning colour pattern
p_{wt}, p_m	[0;1]	Basal predation rate exerted on wild-type or mutant warning colour pattern, depending on the abundance of their respective mimetic communities.
α	[0;1]	Effect of unpalatability on resource specialisation
β	[0;1]	Effect of conspicuousness on detectability
K	1000	Global carrying capacity
r	2	Growth rate

645

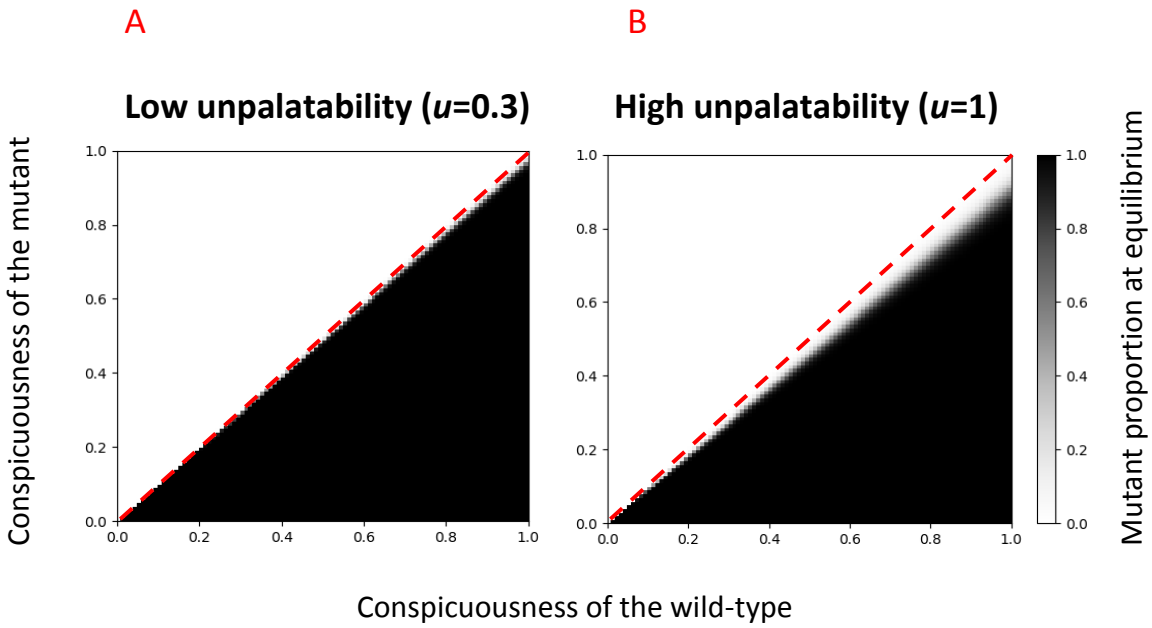

Figure 1: **Evolution of conspicuousness within the same mimicry ring; wild-type and mutant have the same warning colour pattern but with a different conspicuousness.**

Frequency of mutant and wild-type individuals after 100,000 generations, assuming different levels of conspicuousness c_{wt} of wild-type individuals (x-axis) and c_m of mutant individuals (y-axis). Colour scale indicates frequency of mutant individuals, with white representing 0% (100% wild-type individuals) and black being 100% (0% wild-type individuals). Red dashed line shows diagonal, where $c_{wt}=c_m$. Here the value of resource specialisation, α, do not influence the invasion pattern. Warning colour pattern are detectable, β=1, thus suffer greater predation. Predation functions followed equations [5] and [6], assuming basal predation rates $p_{wt}=p_m=0.5$. Toxicity values are fixed within each simulation, **A**) $u_{wt}=u_m=0.3$, **B**) $u_{wt}=u_m=1$.

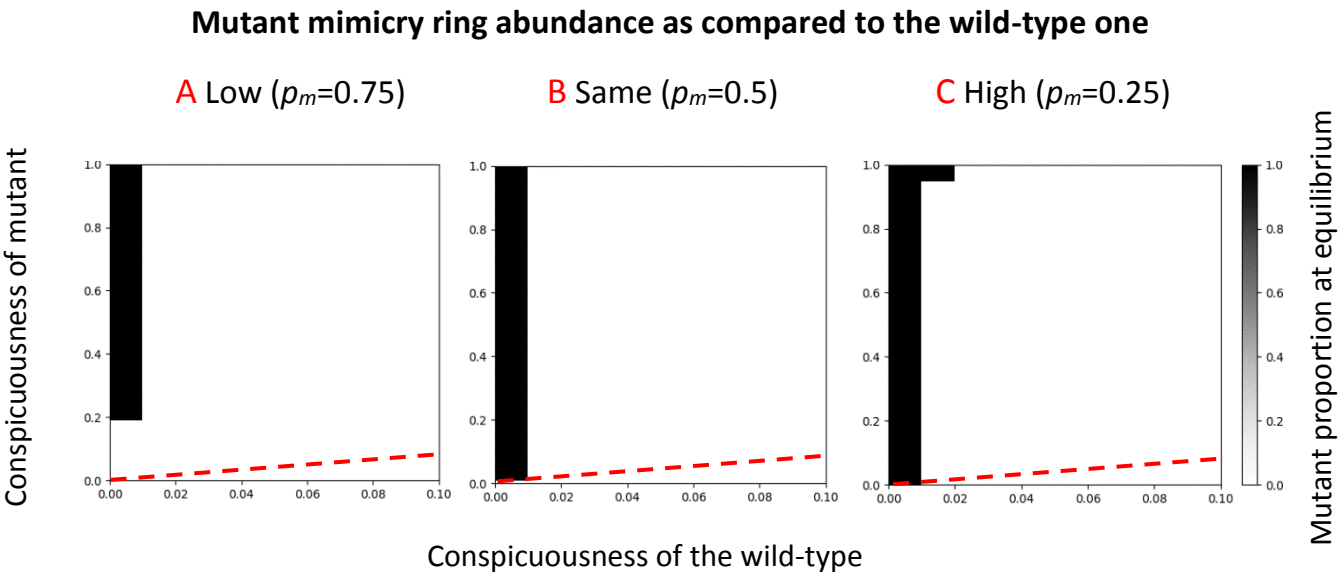

Figure 2: **Evolution of conspicuousness among different mimicry rings; wild-type and mutant have a different warning colour pattern under various predation risks.** Frequency of mutant and wild-type individuals after 100,000 generations, assuming different levels of conspicuousness c_{wt} of wild-type individuals (x-axis) and c_m of mutant individuals (y-axis). The x-axis scale is cropped for visual comfort. Colour scale indicates frequency of mutant individuals, with white representing 0% (100% wild-type individuals) and black being 100% (0% wild-type individuals). Red dashed line shows diagonal where c_{wt}=c_m. Parameter modulating resource specialisation α=1 but variations in α, gives similar results on invasion pattern. Here, warning colour pattern is detectable, β=1. Unpalatability value is fixed within each simulation, here u_{wt}=u_m=1 (high unpalatability). Predation functions followed equations [7] and [8]. Various basal predation rates modelling mutant morph belonging to **A**) a rare mimicry ring (p_{wt}=0.5, p_m=0.75), **B**) a mimicry ring of same abundance as the wild-type morph (p_{wt}=p_m=0.5), and **C**) an abundant mimicry ring (p_{wt}=0.5, p_m=0.25).

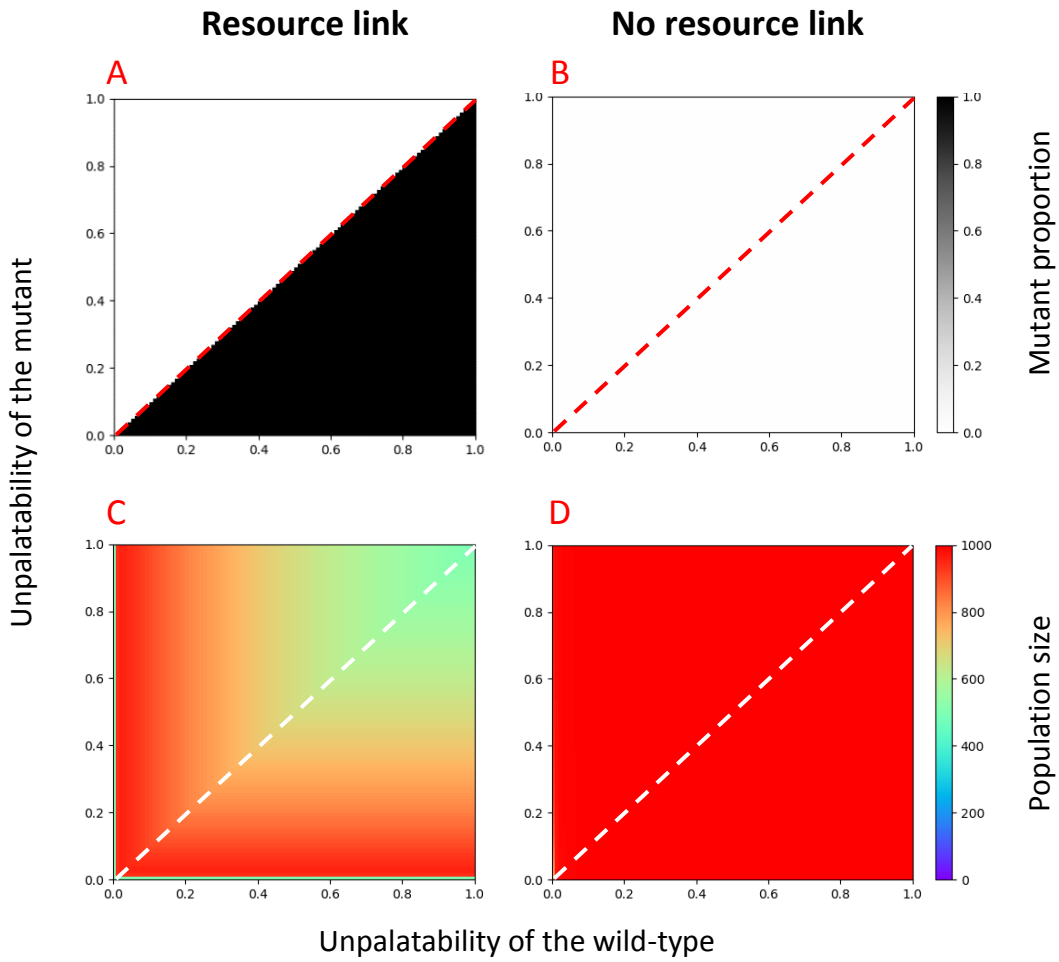

Figure 3: Evolution of unpalatability within the same mimicry ring. Only resource specialisation controls invasion pattern and population size. Frequency of mutant and wild-type individuals after 100,000 generations, assuming different levels of unpalatability u_{wt} of wild-type individuals (x-axis) and u_m of mutant individuals (y-axis). Red and white dashed lines show diagonal where $u_{wt}=u_m$. **A-B)** Mutant proportion at equilibrium. Colour scale indicates proportion of mutant individuals fixed, with white representing 0% (100% wild-type individuals) and black representing 100% (0% wild-type individuals). **C-D)** Population size at equilibrium. Colour scale indicates number of individuals ($N_{wt}+N_m$), with dark blue

representing 0 (extinct population but never reached) and red representing 1000 (saturation of the carrying capacity K=1000, but never observed).

Here the effect of conspicuousness on detectable, β, has no effect. Conspicuousness value is fixed within each simulation, here c_{wt}=c_m=1, and same results are observed for every tested value. Predation functions following equations [5] and [6], assuming basal predation rates p_{wt}=p_m=0.5.

A-C) Individuals rely partly on resources to acquire unpalatable metabolites. Here α=1 but same invasion pattern is observed as long as α≠0. Individual can sequester and synthesize their unpalatable compounds. **B-D)** There is no link between unpalatability and resources, α=0. Individual can only synthesize their unpalatable compounds.

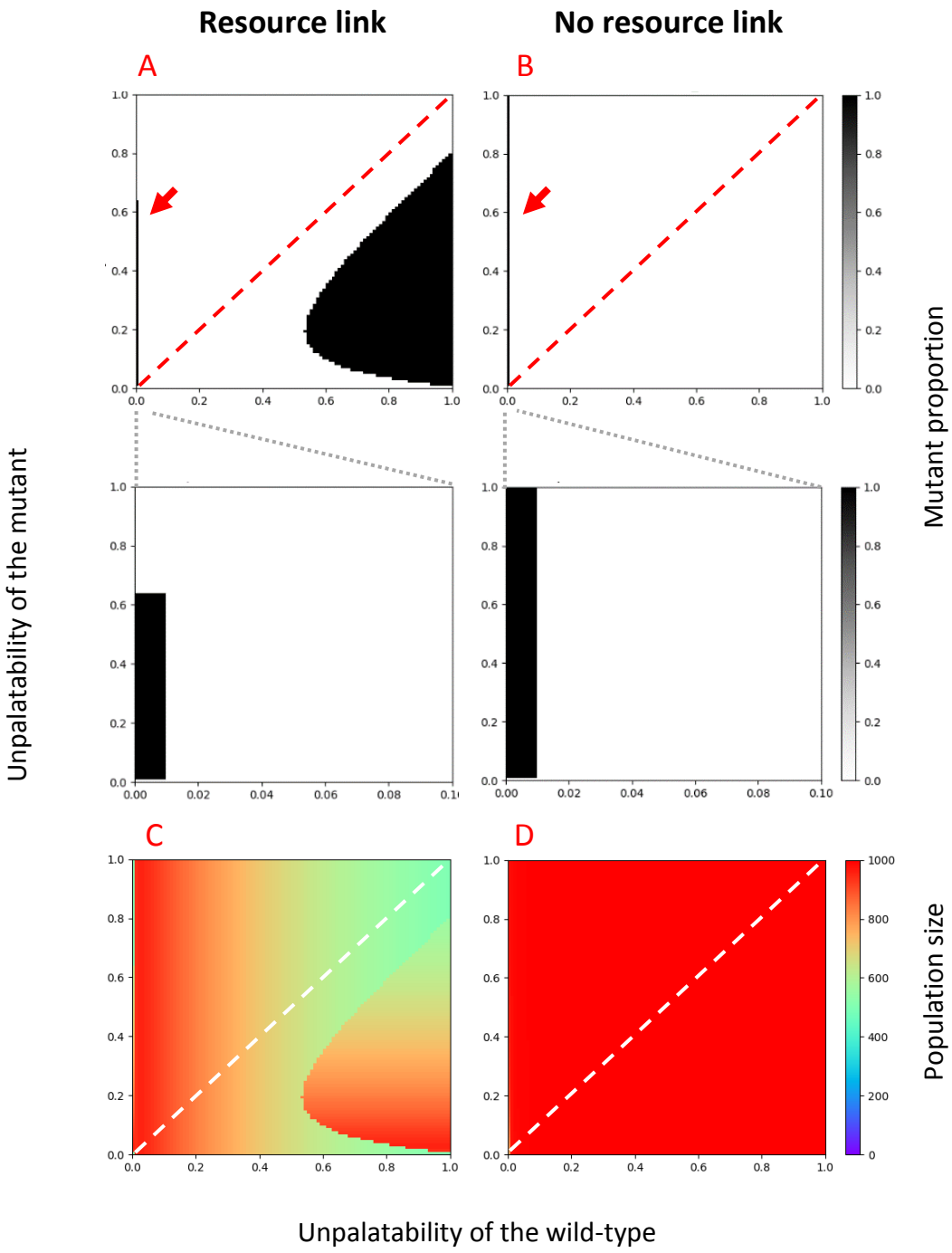
Resource link
No resource link
A
B
C
D
Unpalatability of the mutant
Mutant proportion
Population size
Unpalatability of the wild-type

Figure 4: Evolution of unpalatability between individuals displaying a different warning signal. Only resource specialisation controls invasion pattern and population size. Frequency of mutant and wild-type individuals after 100,000 generations, assuming different levels of unpalatability u_{wt} of wild-type individuals (x-axis) and u_m of mutant individuals (y-axis). Red and white dashed lines show diagonal where $u_{wt}=u_m$. **A-B)** Mutant proportion at equilibrium. Colour scale indicates proportion of mutant individuals fixed, with white representing 0% (100% wild-type individuals) and black representing 100% (0% wild-type individuals). Red arrows point out mutant invasion when the wild-type is palatable ($u_{wt}=0$), and these areas are zoomed for better visualisation. **C-D)** Population size at equilibrium. Colour scale indicates number of individuals ($N_{wt}+N_m$), with dark blue representing 0 (extinct population but never reached) and red representing 1000 (saturation of the carrying capacity $K=1000$, but never observed). Detectability ($\beta=0$ or $\beta=1$) do not influence invasion pattern. Conspicuousness value is fixed within each simulation, here $c_{wt}=c_m=1$, and similar results are observed for every tested value. Predation functions following equations [7] and [8]. We tested various predation risks modelling mutant morph belonging to a rare mimicry ring ($p_{wt}=0.5$, $p_m=0.75$), a mimicry ring of same abundance as the wild-type morph ($p_{wt}=p_m=0.5$), and an abundant mimicry ring ($p_{wt}=0.5$, $p_m=0.25$). Here we present results for $p_{wt}=p_m=0.5$, as other conditions are similar. Red arrows point out mutant invasion when the wild-type is palatable ($u_{wt}=0$).

A-C) Individuals rely partly on resource to acquire unpalatable metabolites, $\alpha=1$. Individual can sequester and synthesize their unpalatable compounds. **B-D)** There is no link between unpalatability and resource, $\alpha=0$. Individual can only synthesize their unpalatable compounds.