Rapid life-history evolution reinforces competitive asymmetry between invasive and resident species

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ABSTRACT

Biological invasions by phylogenetically and ecologically similar competitors pose an evolutionary challenge to native species. Cases of character displacement following invasions suggest that they often respond to this challenge by shifting their traits. However, the actual impact of such shifts on competition are seldom studied. Here, we study competition between two freshwater snails from Guadeloupe (French Antilles), the native *Aplexa marmorata* and the introduced *Physa acuta*; the former has responded to invasion by rapid life-history evolution towards an apparently more colonization- and less competition-oriented syndrome. We observe negative impacts of both species on each other, though *P. acuta* is dominant and over generations largely displaces *A. marmorata* from co-cultures. In addition, *A. marmorata* populations having experienced competition by *P. acuta* for sufficient time in nature, have evolved to become even less tolerant to it. Though apparently paradoxical, this result supports the hypothesis that rapid life-history evolution has allowed this species not to resist competition, but to avoid it by specializing into a colonizer lifestyle. This example illustrates how evolution, in accordance with metacommunity coexistence theory, sometimes takes other ways than specialization into distinct types of resource or habitats to ensure coexistence between related species inhabiting the same landscape.

Keywords: invasion, competition, asymmetry, character displacement, laboratory, freshwater snails

Introduction

It is now commonplace to describe biological invasions as long-term, natural experiments (Sax et al., 2007; Davis, 2009) providing the opportunity to study the consequences of interspecific interactions on community dynamics and evolution. An invasive species develops a new network of interactions with residents, through for example predation, competition or habitat transformation (Carroll 2007; Davis, 2009; Prentis et al., 2008), thereby affecting their demography, abundance and selection regime (Simberloff 2013; Weber & Strauss, 2016). We here focus on competition, highlighting two important aspects with regard to species interactions. First, the strongest effects of competition are expected when the phenotypic and ecological similarity between invasive and resident species is high, for example when an invasive species meets with a phylogenetically related resident (the limiting similarity hypothesis; Duncan & Williams, 2002; Jeschke & Erhard, 2018). Second, biological invaders do not often wipe out the native species through competition, and most of the spectacular examples of extinctions following invasions are rather explained by predation or ecosystem engineering (Sax et al., 2007; Gallardo et al., 2016; David et al., 2017). Instead, introduced competitors will, most of the time, lead to a reduced abundance (Gallardo et al., 2016) and/or a narrowing of the niche of resident species (e.g., Duyck et al., 2006; Sidorovich et al., 2010). These two aspects make competition between related invasive and resident species a good situation to observe rapid evolutionary responses and their impact on community composition, combining a strong change in selection pressure and enough time to evolve. Phenotypic shifts due to microevolution and/or plasticity may then contribute to modify the intensity of reciprocal competitive impacts between invasive and resident species, as shown in plants (Huang et al., 2018; Germain et al., 2020). However most experimental studies generally look at trait changes and do not directly measure competition (Stuart et al., 2014; Alexander et al., 2015; Hart et al., 2019). Here we study under laboratory conditions the competition between two related species, one invasive and one resident, and how previously documented evolutionary changes in traits during invasion (Chapuis et al. 2017) modify this competition.

At least two general predictions have been proposed on the impacts of competitive interactions between invasive and resident species based on the idea that coevolution of competing species contributes to long-term coexistence (Lankau, 2009; 2011; Faillace & Morin, 2016). A first prediction is the existence of an initial competitive asymmetry when two generalists, related, invasive and resident species first come into contact. The species have not had the opportunity to coevolve and mitigate their reciprocal impacts (for example, through some form of niche specialization or character displacement; Freckleton & Watkinson, 2001), so that one of the two may often largely dominate the other on the most abundant resource, an interaction more asymmetrical than would be expected in a pair of long-term sympatric competitors. However, among all possible candidate invaders, those that are competitively superior to the resident will invade with a greater probability (the 'invasion filter': David et al., 2017; Graiger et al., 2019). As a result, we might expect that successful invaders will often be largely dominant over their related competitors, possibly restricting them to marginal resources or niches that they are unable to exploit themselves (Lagos et al., 2017). The second prediction, which is a consequence of this initial asymmetry, is that the strongest selection pressure is expected to bear mostly (though not exclusively; see Jones & Gomulkiewicz, 2012) on the resident species. Two evolutionary trajectories can then be envisaged: (i) to evolve to resist competition, for example to become more competitive on the resource occupied by the invasive species (Germain et al., 2020); (ii) to evolve to avoid competition, through ressource shift and character displacement (Pfennig & Pfennig, 2009). These two possible evolutionary trajectories (resistance and avoidance) can also be related to the two broad mechanisms, equalizing and stabilizing, promoting species coexistence in Chesson's theory (Chesson, 2000). Equalizing mechanisms tend to reduce average fitness differences between species within their common environment, while stabilizing mechanisms are present when intraspecific competition exceeds interspecific competition, e.g. because species specialized on different resource ranges, resulting in negative frequency-dependence and preventing competitive exclusion. Interestingly, resisting and avoiding competition may require different sets of traits in trade-off with each other, or different values of the same trait, suggesting disruptive selection towards either traits promoting tolerance, or traits promoting avoidance. The direction taken by the evolutionary response partly depends on the initial

asymmetry (Jones & Gomulkiewicz, 2012). Under a very asymmetrical interaction (invasive very dominant), the probability of resistance is low and the most likely response will be avoidance, while a small initial asymmetry would increase the probability to evolve resistance (Huang et al., 2018; Germain et al., 2020).

Phenotypic evolution in pairs of competing species has classically been studied through the concept of character displacement (Tobias et al., 2014). Such studies mostly focus on traits linked to the classical niche concept, i.e., traits involved in the exploitation of different food resources (e.g., beak morphology in Darwin's finches; Grant & Grant, 2006) or different microhabitats (e.g., limb structure in *Anolis* lizards; Feiner et al., 2021). A relatively under-explored category of traits, though potentially very important in this context, are life-history traits. These traits may be subject to rapid evolution after contact beween invasive and resident species both because they often have a high genetic variance and evolvability relative to morphological traits (Houle 1992), and because modern coexistence theory has highlighted their potential to promote coexistence on the same type of resource, through metapopulation mechanisms, such as the colonization-competition trade off (Higgins & Cain, 2002) or the competition-persistence trade-off (Muller-Landau, 2010). Accordingly, some life histories can favor persistence when the resource is weak and stable, while others favor colonisation and population growth in patches of abundant and ephemeral resources. For example, in plants, the life-history trade-off theory has been used to study traits linked to seed dispersal (Turnbull et al., 2004; Cadotte et al., 2006). In the context of coexistence theory based on life-history trade-offs, the alternative between resistance to competition *versus* avoidance of competition translates into convergence versus divergence of life-history profiles along the colonization-competition gradient.

Here we test these predictions (resistance/avoidance) by focusing on a pair of generalists, related species (freshwater snails), one invasive and the other resident. We previously observed that populations of the resident species have recently evolved towards a life-history profile that seems less competition- and more colonization-oriented, after contact with the invasive (Chapuis et al., 2017). We measure the competitive interactions between these species in the laboratory to test (i) whether the invasive species is indeed competitively dominant (competitive asymmetry), (ii) whether the evolution of life-history traits in the resident has modified competitive impacts and in which direction and (iii) is to assess whether the competitive interaction has evolved in a population-specific way or not. Theses 3 main hypothesis are summarized in Table 1, first column.

We take advantage of the spatial structure of the invaded region, with sites 'anciently' versus 'recently or not yet invaded', at the time of sampling – the latter acting as evolutionary controls. However, spatial structure potentially adds another source of complexity: competition is by definition a local interaction and, if gene flow is too slow to homogenize populations at the time scale considered here (a few generations or tens of generations), evolution may take place, to some extent, independently in different invaded populations so that competitive interactions might differ depending on whether we confront invasive and resident populations from the same site versus from different sites.

We tested these three ideas based on laboratory experiments conducted with a pair of pulmonate freshwater snails of the same family (*Physidae*). In Guadeloupe (Lesser Antilles) the native species (*Aplexa marmorata*) occupies a network of freshwater ponds that have been recently invaded by the ecologically and phylogenetically (Wethington & Lydeard, 2007) related species *Physa acuta*, a cosmopolitan invasive species (Bousset et al., 2004; Ebbs et al., 2018). Owing to a long-term yearly metacommunity survey we have a very detailed knowledge of invasion of new sites by *P. acuta* since 2001, allowing us to contrast long-invaded versus not or recently invaded sites. Metapopulation models on presence/absence data (Dubart et al., 2019; Pantel et al., 2022), time-series of changes in species abundance within sites (Chapuis et al., 2017) and joint species-distribution models at the metacommunity scale (Dubart et al., 2019) all detected negative and reciprocal impacts of competition in the field between *P. acuta* and *A. marmorata* during the 2001-2017 period. No loss of neutral genetic variability was detected at invasion front in *P. acuta*, but it decreases in *A. marmorata* populations that have been confronted to *P. acuta* for a longer time (Jarne et al., 2021). In addition, as mentioned previously, a common-garden experiment showed that life-history traits in *A. marmorata* evolve in a few years (less than two) after a population is reached by *P. acuta*, becoming mature sexually earlier and more fecund

(Chapuis et al., 2017). We conducted laboratory competition experiments with the same set of populations.

Table 1 – Main hypotheses and associated predictions in our experiments. They are discussed in Introduction, and how the experimental tests were conducted in Material and methods. Note that Front and Core populations of *Physa acuta* showed relatively little trait differences, except for a slight decrease in fecundity (Chapuis et al. 2017) in the Front populations, assumed to reflect temporary founder effects. We therefore do not have clear expectations about differences in the outcomes of competition experiments – Front populations might be less harmful competitors than Core ones to the resident species. We nevertheless kept the Front / Core distinction in the statistical analysis to check for a possible effect.

Hypotheses	Predictions
(i) Initial competitive asymmetry favouring the introduced species => *P. acuta* dominates.	The impact of *P. acuta* on fitness traits of *A. marmorata* is more negative than the reverse. Changing the identity of the competitor (*P. acuta* instead of *A marmorata*) tends to decrease fitness traits of both species. The relative recruitment of *P. acuta* in mixed populations is higher than that of *A. marmorata*, so that the frequency of *P. acuta* increases over the generations.
(ii) Trait evolution in the resident species *A. marmorata* reflects an avoidance of competition rather than an increased tolerance to competition.	Fitness traits of Experienced populations (E) of *A. marmorata* are more negatively affected by *P. acuta* than those of Naive populations (N): Experienced are less tolerant to competition than Naive.
(iii) *A. marmorata* and *P. acuta* have locally coevolved.	Fitness is more (less) depressed by interspecific competition in sympatric than in allopatric pairs, IF coevolution results in higher (lower) competition impacts / lower (higher) tolerance to competition.

Material and methods

Biological model

Our field sites are freshwater ponds or intermittent creeks located in Grande-Terre and Marie-Galante (Guadeloupe; see Figure 1). The native species *A. marmorata*, and the invasive *P. acuta* belong to a community of around 25 species of freshwater snails, all detritivorous and herbivorous, that collectively constitute the most important biomass of the macrobenthos in these habitats (Pointier, 2008; Pantel et al. 2022, Dubart et al. 2022). *Physa acuta* was first detected in the late 1970s and has recently experienced a spectacular spread from two sites occupied in 2001, to more than 80% in 2020 of the ca. 280 sites that we survey in Guadeloupe. The first report of *P. acuta* in Marie-Galante is more recent (2010). The native *A. marmorata* also occupies a large fraction of these sites with limited temporal decrease in this fraction, but a significant one in population density (Chapuis et al. 2017). This hermaphroditic species self-fertilizes at rates exceeding 90% in natural populations (Dubois et al*.,* 2008; Escobar et al*.,* 2011), while *P. acuta* is mainly outcrossing. In both species sexual maturity of isolated individuals is reached at about four to five weeks under laboratory conditions (24°C, 12 hours of light; Chapuis et al., 2017). Egg capsules include up to 30 eggs inserted in a gelatinous matrix, and are laid on hard surfaces (e.g., branches or stones in natural populations, box walls in the laboratory). Juveniles hatch after about a week. Growth is continuous, and adults reach a size of about 10-15 mm in shell length. The generation time under natural conditions is estimated to be around two months, meaning 5-6 generations per year. Individuals can live up to six months under laboratory conditions.

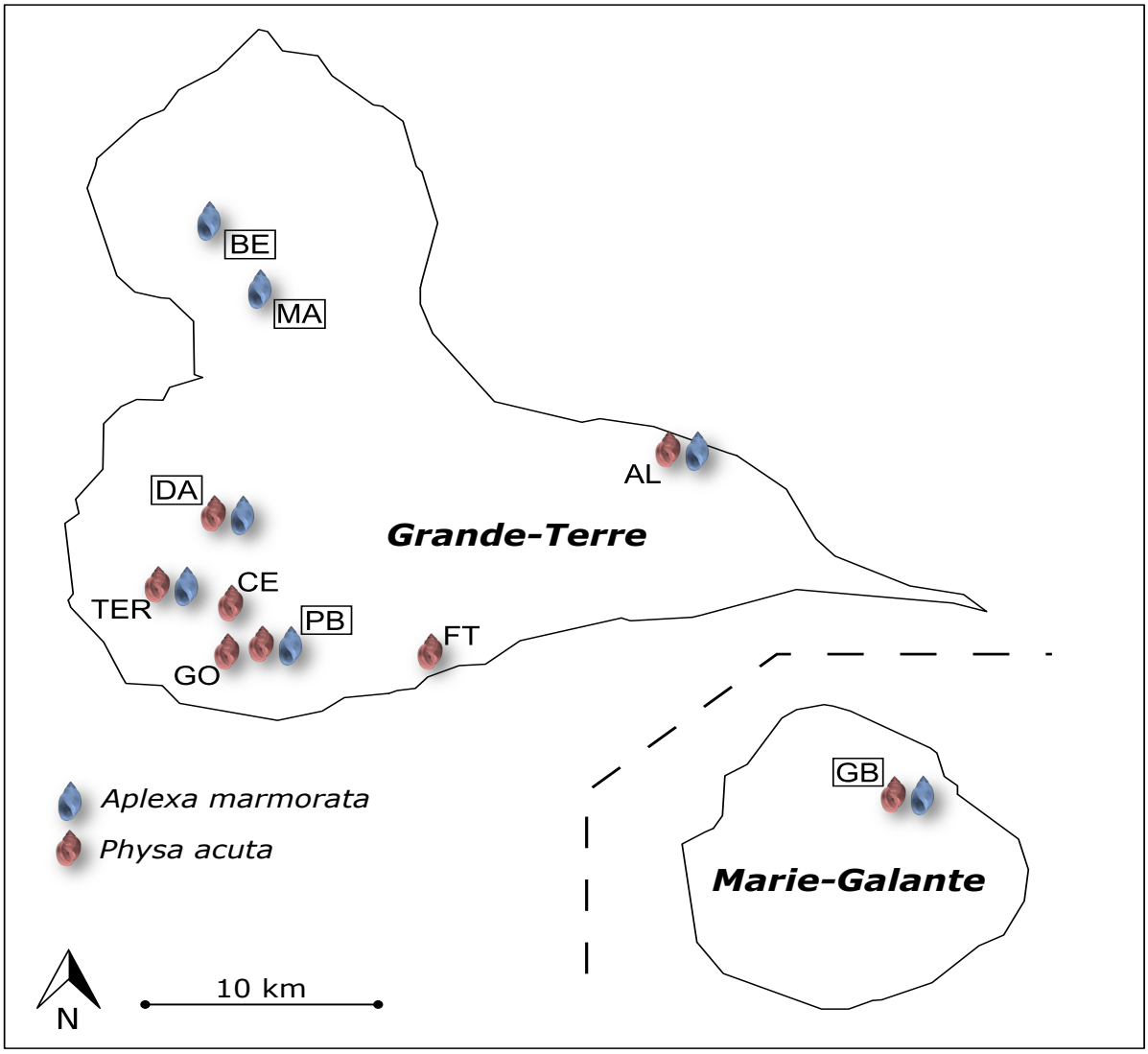


Figure 1 - Distribution of the 10 sites sampled in Guadeloupe for our experiment. Snail populations are represented by colored pictograms: blue for *Aplexa marmorata* and red for *Physa acuta*. N (never or newly-invaded) populations of *A. marmorata* are indicated by a box. See Table 1 for the acronyms of population names. The islands of Grande-Terre and Marie-Galante are exaggeratedly close but are in reality distant by around 30 km.

Field collection

We sampled G_0 snails from 10 sites: TER, AL, GB, DA, CE, MA, FT, PB, G0, BE (Figure 1, Table 2 and Chapuis et al., 2017 for more details on populations). Seven sites harboured populations of *A. marmorata* and eight *P. acuta*, with five were occupied by both species. Sampling was done in January 2010. Individuals were brought back to the laboratory in Montpellier (France) and the experiment was carried out on the second laboratory generation in constant conditions (12/12 photoperiod and 25°C). Populations of *A. marmorata* were classified into two types depending on when/whether *P. acuta* invaded the site, based on previous analyses (Chapuis et al., 2017): 'naive' (N) refers to populations where, at the time of sampling, *P. acuta* had never been observed or had been observed only recently (less than two years) and 'experienced' (E) to populations that have evolved in presence of interspecific competition as the first observation of *P. acuta* had taken place more than two years before sampling (Table 2). On the

other hand, populations of *P. acuta* can be classified as 'front' (invasion front, F) for populations present for less than two years in a site and 'core' (C) when present for more than two years (Table 2). Note that the contrast between F and C populations in *P. acuta* is of a different nature from that between N and E populations. In *P. acuta*, F populations are younger (founded more recently) than C populations, while N and E populations in *A. marmorata* are all anciently established. In addition, F populations are not 'naive' as their ancestors have been exposed to the same history of interspecific competition as C populations (they were recently founded, but the founders were coming from C populations). An additional distinction refers to the fact that competing populations in mixed cultures could have been sampled in the same site (hereafter 'sympatric') or in different sites ('allopatric') - we referred to this effect as origin of the competitor.

Table 2 - The 10 sites in which *A. marmorata* (native) and *P. acuta* (invasive) were sampled. The year during which *P. acuta* was first detected is given in the 'first detection' column ('never' indicates that *P. acuta* was never detected). The invasion status is given for each population (N for naive, E for experienced in *A. marmorata*; F for front and C for core in *P. acuta*, details in text). Hyphens (--) in the last two columns indicate that the species was not sampled in this site.

Site	Acronym	First detection of *P. acuta*	*A. marmorata*	*P. acuta*
Belin	BE	Never	N	--
Malakoff	MA	Never	N	--
David	DA	2010	N	F
Grand-Bassin	GB	2010	N	F
Port Blanc	PB	2010	N	F
Fond Thezan	FT	2007	--	C
Alleaume Nord	AL	2004	E	C
Caraque Est	CE	2004	--	C
Goudenave	GO	2004	--	C
Terrasson	TER	2004	E	C

Laboratory experiment

We collected individual (G_0) from each population in January-February 2010, and they were brought back to the laboratory in Montpellier to lay eggs (G_1). These G_1 individuals were used in a previous experiment (Chapuis et al., 2017) and their offspring (G_2) were used for the following experiment. The G_2 individuals were raised separately in 80 mL plastic boxes from hatching to three weeks (Chapuis et al., 2017). The competition experiment took place in June-August 2010 as follows: five three-week old G_2 individuals from a given population of each species were set together in a 1L tank (so 10 individuals per tank). Once mixed, snails of the same species could no longer be identified individually, but interspecific differences were sufficient to distinguish adult individuals from each species. Among all possible pairs of populations, we were able to make 15 pairs (see Table 3). We chose to set up both allopatric and sympatric pairs when possible (sympatry is when the two populations originated from the same site, and allopatry when they originated from different sites). It should be noted that, by definition, it is not possible to establish sympatric pairs for *A. marmorata* populations that have never been invaded by *P. acuta*. Among the allopatric pairs, we could make E/C, N/C, and N/F combinations. However, the low number of *A. marmorata* E populations and of *P. acuta* F populations did not allow us to make the E/F combination. For each population and each species, control tanks were set up and included 10 individuals from only one species and population. Two replicates were made for each type of tank, giving a total of 60 experimental tanks (Table 3).

Table 3 - Combinations of populations (for acronyms see Table 2) used in the interspecific competition experiment. The 15 pairs (indicated by A or S) included seven *Aplexa marmorata* populations and eight *Physa acuta* populations. A = allopatric pair and S = sympatric pair; N for naive, E for experienced in *A. marmorata*; F for front and C for core in *P. acuta* as in Table 2. Cells are shaded for the pairs that were not constituted

Physa acuta	AL (C)	TER (C)	CE (C)	FT (C)	GO (C)	GB (F)	PB (F)	DA (F)
Aplexa marmorata								

AL (E)	S	A						
TER (E)	A	S			A			
GB (N)						S	A	
PB (N)						A	S	A
DA (N)								S
BE (N)			A	A				
MA (N)			A	A				

First stage of the competition experiment

The experiment was initiated using three-week old individuals (i.e*.,* before sexual maturity which occurs around 4-5 weeks under our laboratory conditions; Chapuis et al., 2017), and consisted of two successive stages. The first stage (from grouping to 35 days / five full weeks later) mostly focused on the effects of competition on adult life-history traits. G_2 individuals of both species interacted freely for five weeks and were then discarded. In snails, growth and other traits depend on population density (Dan and Railey, 1982; Dillon, 2000) so the same initial density of 10 individuals per tank was used for all tanks including intraspecific controls. However, once the experiment started, we chose not to replace dead individuals to mimic "natural situations". Shell length was measured two and five weeks after the initial grouping. The number of surviving G_2 adults of each species was counted at week 5. At that time, G_2 adults had started to reproduce and were living together with their progeny (egg masses or hatchlings). Adults tend to monopolize resources and inhibit the growth of juveniles, and were then removed at week 5.

Second stage of the competition experiment

In the second stage (weeks 5 to 16), we focused on relative recruitment of the two species under interspecific competition. To this end, we kept only aquaria where the two species had been initially introduced. Juveniles of both species developed under intense competition, both within and among species. Competition went on for 11 weeks, after which we measured the number of G_3 snails recruited for each species within each aquarium (week 16). Before they reach a certain size, snails cannot easily be identified to the species level (~4 mm). We therefore decided to consider only individuals over this threshold size as recruited in the next generation. Note that some of the recruited G_3 snails may have already started to reproduce at week 16. The relative recruitment of *P. acuta* and *A. marmorata* within each aquarium represents an integrative outcome of competition over two generations (i.e., relative population growth rate, accounting for interspecific differences in fecundity, juvenile survival, and growth).

Data analysis

Our data (Chapuis, 2023a) were used to test our main predictions (see Introduction and Table 1) based on statistical analyses conducted separately for each species (Chapuis, 2023b). The software R and the "lme4" package in R (Bates et al., 2015) were used for all statistical analyses (R Core Team, 2019).

Shell size (week 2 and 5) was analysed in two steps. In the first step, we focused on competition asymmetry (difference in size under intraspecific versus interspecific competition), and its potential dependency on the status of the population (N versus E for *Aplexa marmorata*; F versus C for *Physa acuta*). We fitted linear mixed models with fixed effects "type of competition" (intraspecific in control tanks, interspecific in mixed tanks), population status, and their interaction. Population (in interaction with type of competition) and replicate (nested within population-by-competition combination) were included as random effects. Model simplification and likelihood-ratio tests were used to test the significance of fixed effects (keeping random effects unchanged). When the interaction was significant the effect of type of competition was tested within each status separately. In the second step, we kept only mixed tanks (i.e., interspecific competition) and focused on possible differences in competitive impact depending on coevolutionary history (allopatric versus sympatric pairs of populations, i.e., sampling site effect). We fitted linear models with a single fixed sampling site effect; random effects were again population (in interaction with sampling site) and replicate. The same two-step analysis was performed on survival at week 5, using a generalized linear mixed model (GLMM) with binomial error, with here the random 'replicate' effect accounting for overdispersion (i.e., excess of residual variance among aquaria).

The recruitment of juveniles of the two species (after 16 weeks) was measured only in mixed aquaria. First, we analysed, for each species separately, the number of juveniles recruited using GLMMs with Poisson error, with status (E/N or F/C depending on species), sampling site and their interaction as

fixed factors, and population and replicate as random factors (the replicate factor accounts for overdispersion, as previously). Second, we focused on relative recruitment of juveniles of the two species using binomial GLMMs on the numbers of recruits per species. The fixed factors included were the same as previously, while the random factors were population pair and replicate.

Results

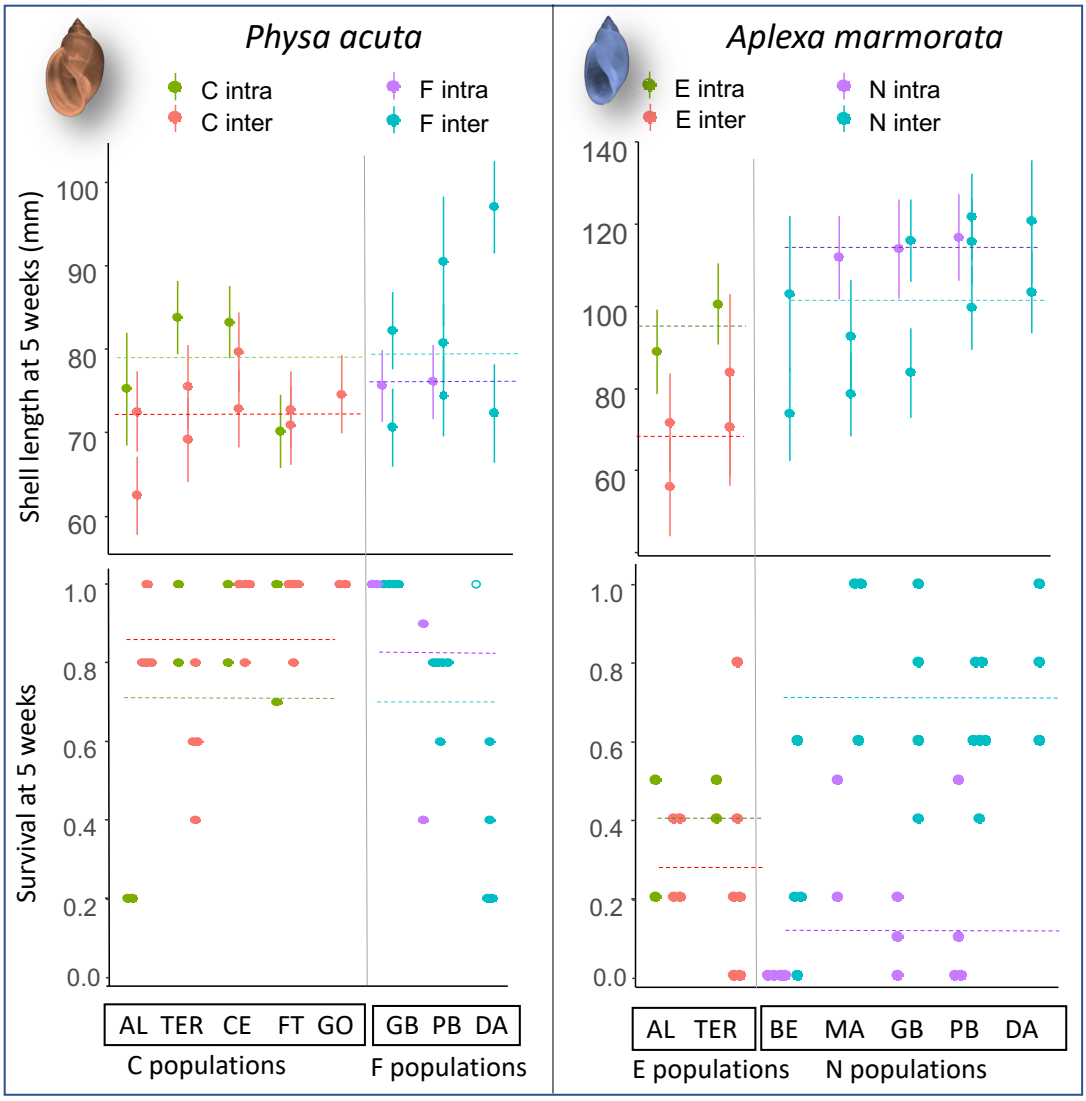
Body size

Physa acuta

In *P. acuta,* we found a (marginally) significant status effect on shell length at both week 2 and week 5, as individuals from F were slightly larger than individuals from C populations. Individuals exposed to interspecific competition were, on average, similar in size to those exposed to intraspecific competition (Table 4; Figure 2). However, the outcome of interspecific competition depends on the origin of *A. marmorata* competitors (Origin effect; Table 4): snails exposed to sympatric competitors grew smaller than those exposed to allopatric competitors (Figure 3).

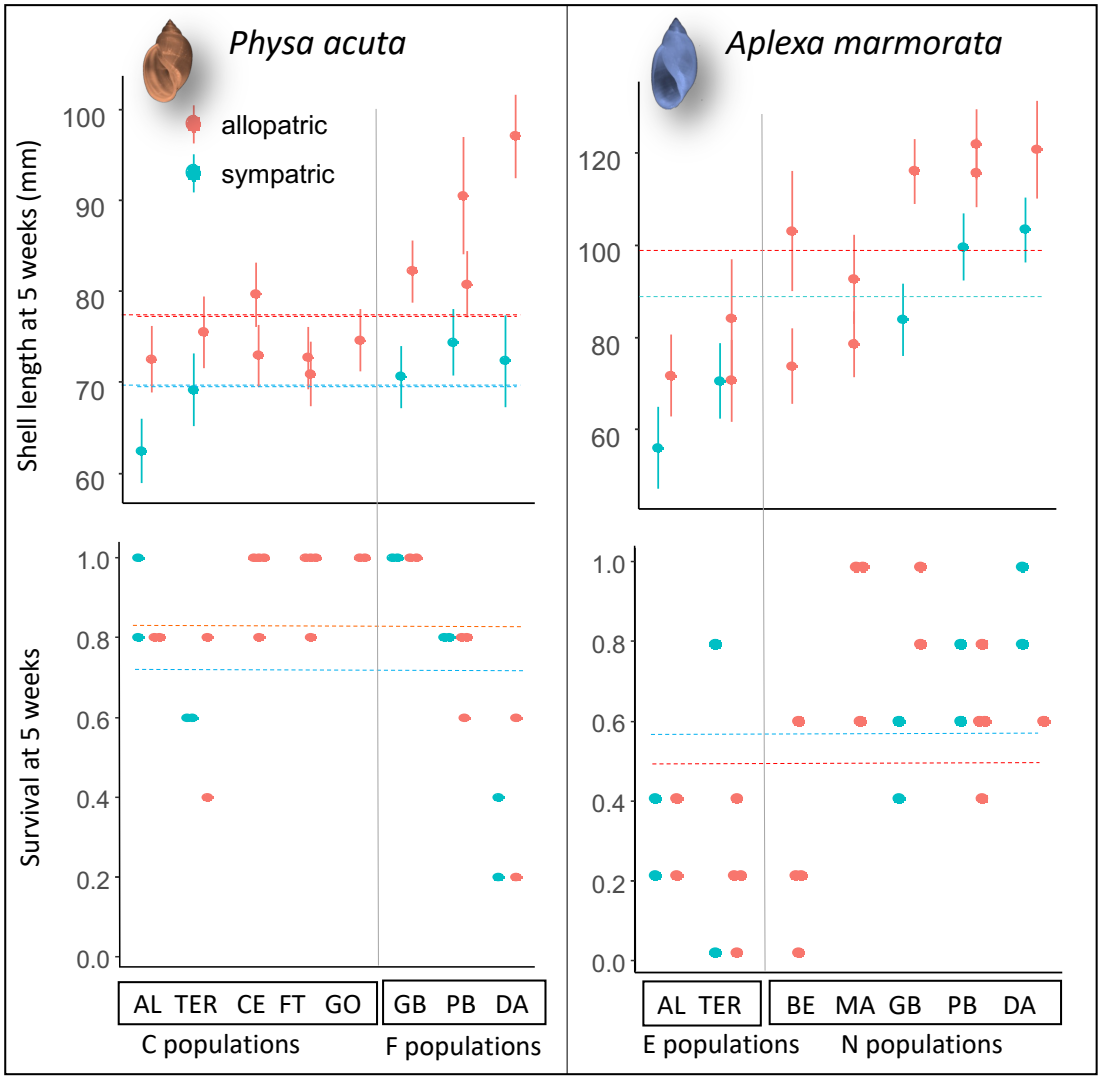
Table 4 - Statistical tests on size and survival of G_2 individuals in the two species studied. Size was estimated at week 2 and 5, and survival between weeks 0 and 5. In model 1, we considered all experimental units (one- and two-species cultures), their status (core and front in *P. acuta*, and naive and experienced in *A. marmorata*), the competition type (intra- and interspecific) and their interaction. N and E refer to values in naive and experienced populations. Only two-species cultures were considered in Model 2, testing for the effect of the origin of the competitor. All linear and generalized linear mixed models included population and replicate as random factors. Size was modelled with a Gaussian distribution, and survival with a Binomial one. We report the value of the chi-square test (X^2) with the associated probability value (P). All tests with one degree of freedom. In bold, P<0.05.

Species	Trait	Model 1						Model 2	
		Status		Competition type		Interaction		Origin	
		X^2	P	X^2	P	X^2	P	X^2	P
Physa acuta	Size (2 w)	3.921	0.048	3.087	0.088	1.927	0.165	7.512	**0.006**
	Size (5 w)	4.330	**0.037**	1.6456	0.120	1.730	0 .190	6.707	**0.009**
	Survival	2.341	0.126	1.436	0.231	1.445	0.229	0.448	0.490
Aplexa marmorata	Size (2 w)	2.977	0.085	0.032 1.193 (N) 5.375 (E)	0.086 0.275 **0.020**	5.471	**0.019**	1.021	0.312
	Size (5 w)	7.31	**0.007**	6.87	**0.009**	0.556	0.456	6.705	**0.01**
	Survival	0.906	0.341	4.310 7.879 (N) 0.121 (E)	**0.038** **0.005** 0.728	8.438	**0.004**	0.004	0.984


Physa acuta
C intra
C inter
F intra
F inter
Aplexa marmorata
E intra
E inter
N intra
N inter
Shell length at 5 weeks (mm)
Survival at 5 weeks
AL TER CE FT GO
GB PB DA
C populations
F populations
AL TER
BE MA GB PB DA
E populations
N populations

311

312 **Figure 2** - Effect of population status and competition type (intra- versus interspecific) on G_2 shell size (at week 5) and
313 survival of the two snail species. Status and type are separated by a vertical line for each species. Populations are indicated
314 at the bottom of each graph (pooled by status: N for naive, E for experienced in *A. marmorata*; F for front and C for core in
315 *P. acuta* as in Table 2), and their full names are given in Table 2. For both traits, see Table 2 for the one to three combinations
316 of population pairs for each population in interspecific interactions. For shell length, each point represents the two
317 replicates of a given combination of populations, pooled together in order to increase clarity. For survival, each replicate is
318 represented as a separate point. The horizontal dotted lines represent the means for each status and competition type.
319 Note the difference in scale between the two species for shell size. Species are represented by artificially colored
320 pictograms: in blue for *Aplexa marmorata* and in red for *Physa acuta*. The vertical axis is used to separate populations and
321 statuses



322
323 **Figure 3** - Effect of origin site (sympatric versus allopatric) on G_2 shell size (at week 5) and survival of the two snail species
324 under interspecific competition. Populations are indicated at the bottom of each graph (pooled by status), and their full
325 names are given in Table 2. For both traits, see Table 2 for the one to three combinations of population pairs for each
326 population in interspecific interactions. For shell length, each point represents the two replicates of a given combination of
327 populations, pooled together in order to increase clarity. For survival, each replicate is represented as a separate point. The
328 horizontal dotted lines represent the means for each status and competition type. Note the difference in scale between
329 the two species for shell size. The vertical axis is used to separate populations and statuses. The data represented here are
330 a subset of those in Figure 2 (interspecific interactions only).
331
332 *Aplexa marmorata*

At 5 weeks, shell size was significantly affected by both population status and the type of competition in *Aplexa marmorata* (Table 4; Figure 2): snails from N populations were bigger than snails from E populations, and snails grown under interspecific competition were smaller than snails grown in single-species cultures. The effect of interspecific competition was more pronounced, with smaller snails when competitors were sympatric than when they were allopatric (Table 4; Figure 3). As for *P. acuta,* this difference was observed in each of the five populations where the comparison could be made. The same tendencies were already observed at week 2, but weaker. For example, the effect of competition type was significant only in N populations, resulting in a significant competition-by-status interaction, and the effect of allopatry versus sympatry was not significant (Table 4).

Survival and recruitment

Physa acuta

In *P. acuta*, the survival of the adult G_2 individuals was not significantly affected by population status, type of competition, or the allopatric versus sympatric origin of competitors (Table 4; Figures 2 and 3). The number of G_3 recruits of *P. acuta* at the end of the experiment in mixed cultures was not significantly affected by the origin of competitors, but the status effect was marginally significant (Table 5), as C populations recruited on average more offspring than F populations (although recruitment was highly variable in both cases; Figure 4).

Table 5 - Effect of population status (detailed in text and in Table 2), origin of the competitor (allopatric versus sympatric) and interaction of both on the recruitment of G_3 individuals at week 16 in two-species cultures. Population and replicate were included as random factors. Models were Poisson-distributed GLMMs, and we report the value of the chi-square test (X^2) with the associated probability value (P). All tests with one degree of freedom. In bold, P<0.05.

Species	Status		Origin		Interaction	
	X^2	P	X^2	P	X^2	P
Physa acuta	4.375	**0.036**	1.500	0.221	1.545	0.214
Aplexa marmorata	0.058	0.801	0.003	0.954	1.498	0.221

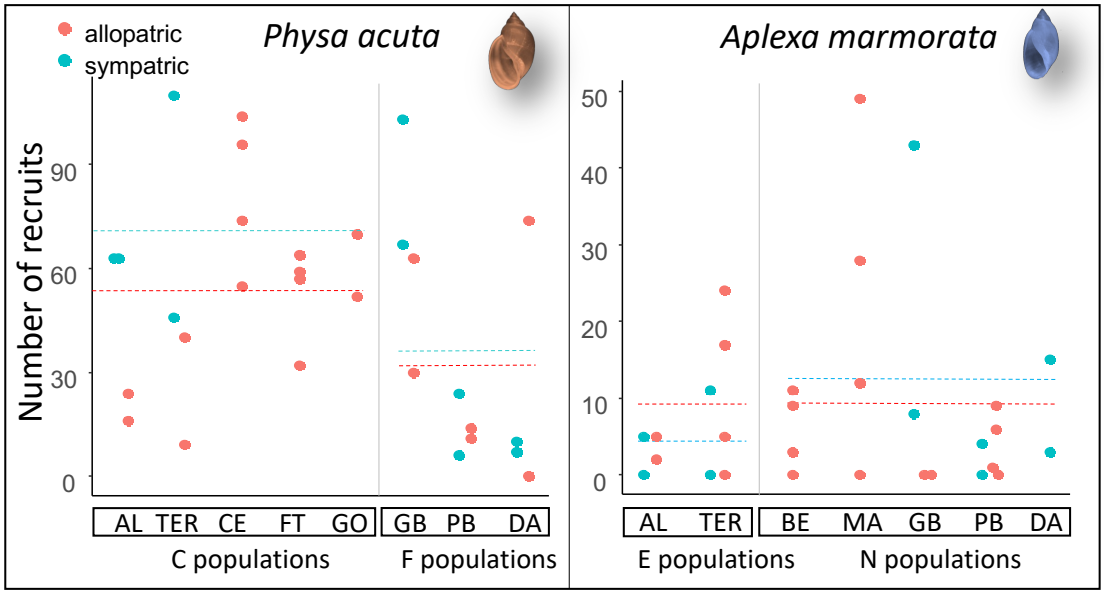


Figure 4 - Effect of population status and sampling site (sympatric versus allopatric) on recruitment (at week 16) of the two snail species under interspecific competition. Populations are indicated at the bottom of each graph (pooled by status), and their full names are given in Table 2. For both traits, see Table 2 for the one to three combinations of population pairs for each population. Each point represents a replicate. The horizontal dotted lines represent the means for each status and

competition type. Note the difference in scale between the two species for shell size. The data represented here are a subset of those in Figure 2 (interspecific interactions only).

Aplexa marmorata

In *A. marmorata* the survival of G_2 individuals at week 5 was affected by the type of competition, but the effect differed depending on population status (significant interaction in Table 4). In E populations, *A. marmorata* survived at similar rates whether in intra or interspecific competition, while in N populations, they survived better under interspecific competition than in pure cultures (Table 4; Figure 2). Under interspecific competition, there was no difference in survival depending on whether the competitors were allopatric or sympatric (Table 4; Figure 3). The recruitment of G_3 individuals did not depend on population status or the origin of competitors (Table 5; Figure 4).

Relative survival and recruitment of both species in mixed cultures

The relative proportion of *P. acuta* in the G_2 survivors at week 5, and in the G_3 recruits at the end of the experiment, did not significantly depend on the allopatric *versus* sympatric nature of the pair of competing populations (X^2_{1df} = 0.787 and 0.021 for survivors and recruits respectively, both P > 0.05), nor on the combination of statuses of the *A. marmorata* and *P. acuta* populations (X^2_{3df} = 7.177 and 5.072, both P > 0.05). However, these results must be taken with caution given the low number of population pairs in each category. The proportion of *P. acuta* significantly exceeded ½ (intercept > 0 in logit scale in the binomial models) both in the G_2 survivors (X^2_{1df} = 6.241, P = 0.012) and in the G_3 recruits (X^2_{1df} = 20.702, P < 0.001) over all population pairs. The proportions fitted by the models were 0.62 +/- 0.043 in G_2 and 0.92 +/- 0.035 in G_3, corresponding to odd-ratios of 1.61 and 11.14 in favor of *P. acuta* for survival and recruitment respectively, and the corresponding raw means (+/- SE over experimental units) were 0.63 +/- 0.038 and 0.80 +/- 0.044 (odd-ratios of 1.72 and 4.10). Note that estimates and raw means differ because of the inclusion of random effects in the logit-scale binomial model. Frequencies of *P. acuta* in G_2 at week 5 and in G_3 recruits at week 16 were not significantly correlated across replicates (Spearman's rho= 0.015, P > 0.05).

Discussion

We studied competitive interactions between the freshwater snails *A. marmorata* and *P. acuta* under laboratory conditions, and adressed three questions (exposed in Table 1): (i) Is there a competitive asymmetry between the two species, and more specifically is the introduced species competitively dominant on the resident? (ii) Does the resident species manage to resist competition, or does it avoid it through trait variation? (iii) Is there a population-specific component of coevolution between the two species within each site, so that sympatric populations of both snails would tolerate each other better or worse than allopatric ones?

Asymmetrical competition, life-history syndromes and invasion

Our results first show that *A. marmorata* might be less resistant to competition than *P. acuta*. Individuals of the former were indeed more affected by interspecific than by intraspecific competition, especially with regard to growth, and no effect was detected in the latter. In addition, over the passage of generations (G_2 and G_3), the frequency of *A. marmorata* relative to *P. acuta* decreased in co-cultures*;* the former was even eliminated in some cases. This was due to a combination of higher adult survival and higher per-capita recruitment in *P. acuta*.

Competitive dominance reflects interspecific differences in traits that affect how they exploit resources and/or interfere with each other (Keddy, 2001). For instance, in plants, species growing faster to large size tend to monopolise light and outcompete slow-growing species (Hautier et al., 2009). We have previously shown that life-history traits differ between our two snail species in non-competitive laboratory conditions (Chapuis et al., 2017; a summary of these results is given in Appendix 1): compared to *A. marmorata, P. acuta* individuals are sexually mature slightly later but more fecund, and survive much longer once adults, although their juvenile survival is lower. In freshwater snails, adults move faster and consume food more efficiently than juveniles (e.g., Selck et al., 2006). Thus, they efficiently inhibit the recruitment of juveniles in crowded conditions, which is why we usually propagate snails by separating

clutches from their parents (pers. obs.). In our co-cultures, juvenile recruitment reflects the 5-week accumulation of many eggs with low individual chances of survival, chances that increased with time as adults progressively died out and were finally removed. Adults *P. acuta* appear to monopolize resource, decreasing the growth of *A. marmorata* (hence, probably, their egg production); they also outlive *A. marmorata,* thus laying more eggs over time. Although *A. marmorata* eggs exhibit a higher hatching rate and survival in non-competitive conditions (Chapuis et al., 2017), this advantage seems insufficient to counterbalance the advantage of *P. acuta* during the adult phase. Our study thus corroborates the hypothesis (Chapuis et al., 2017) that the life-history strategy of *P. acuta* provides an advantage in exploitative competition (a "K lifestyle").

The conditions in our experiment (high density, single food source and unstructured aquarium environnement) probably amplify the impacts of competition compared to natural situations. However, field data support the existence of asymmetrical effects of *P. acuta* on *A. marmorata* in Guadeloupe. First, population density in the latter decreased quickly in the Guadeloupe metacommunity after *P. acuta* arrival (Chapuis et al., 2017). Second, the presence of *P. acuta* in a site decreases its probability of colonization by *A. marmorata* (Dubart et al., 2019) during the following year. Reciprocally, in the same study, the rate of local extinction of *P. acuta* was increased by the presence of *A. marmorata* in the site – this negative reciprocal effect was recovered using a different statistical approach (Dubart et al., 2022). However, this rate remained lower than that of *A. marmorata*, resulting in a form of pre-emption at metacommunity / landscape scale: *P. acuta* colonizes new sites less often, but persists longer in each, and once established, tends to prevent recolonization by *A. marmorata*. As a consequence, stationary landscape occupancy by *A. marmorata* was predicted to decrease in Guadeloupe following the spread of *P. acuta*, though remaining far from the extinction threshold (Dubart et al., 2019).

Traits promoting competitive dominance therefore characterize the invasive *P. acuta*. The search for traits promoting biological invasion has been going on for a long time, with ambiguous results (e.g., Kueffer et al., 2013; Perkins & Nowak, 2013). This mixed outcome may be related to mixing different situations in which invasion is limited, or not, by competition (Krafts et al., 2007). Classical models of population growth (Elton 1946, Pimm 1991), have inspired the hypothesis that "fast" or "r-selected" lifestyles should be associated with invasion success- as suggested recently in amphibians, reptiles and mammals (Allen et al., 2017; Capellini et al., 2015). However, this may be the case only when rapid population growth is the only important limiting factor, i.e., in an "empty niche" situation. In the presence of a resident competitor, the limiting factor is to increase in frequency under competitive conditions- and the associated trait syndrome should promote competitive dominance, at least relative to the resident species. For example, invasive birds tend to prioritize adult survival, and delay reproduction (review by Sol et al., 2012). Our snail example belongs to this category. Similar cases of asymmetric competition between related invasive and resident species (that may be themselves native or previously established invaders) have been observed in *Anolis* lizards (Culbertson et al., 2019) and fruit flies of the family Tephritidae (Duyck et al., 2006).

David et al. (2017) noticed that if negative species interactions, such as competition, act as important filters for potential invaders, those invasions that succeed are expected to have, on average, large negative impacts on resident species. As mentioned above, in the *P. acuta / A. marmorata* pair, such negative impacts are observed in the field (Dubart et al., 2019; 2022), though they seem relatively moderate compared to the outcome of laboratory experiments: *A. marmorata* does not seem to be at risk of extinction in Guadeloupe (while it does in our laboratory co-cultures). This situation may not be unusual, as secondary extinctions due to competition by invasive species appear relatively rare compared to those resulting from predation or ecosystem engineering (Shine, 2010; however, similarly, a more recent report from the IPBES (2019) suggests that competition may play a somewhat lesser role than the combined effects of predation and herbivory). Instead of extinction, the outcome of invasive-resident competition is often niche partitioning. For example, resident Tephritid flies in the island of La Reunion were replaced by invaders in the most abundant resource (cultivated fruits in the lowland, e. g. mango) but persisted in marginal niches (peculiar families of fruits such as Solanacae, or highlands; Duyck et al., 2006; David et al., 2017; Facon et al., 2021). Similarly, in *Anolis* lizards, a native and an invasive species can co-exist owing to behavioral differences that promote differences in microhabitat use (Dufour et al., 2018). The generalist diet of freshwater snails (they basically graze on periphyton and exploit decayed organic matter) makes them little prone to specialization on different food sources – a form of

specialization that has never been demonstrated in this group, though this would definitely deserve more research (see Dillon, 2000). The kind of 'niche partitioning' that protects *A. marmorata* from extinction after invasion by *P. acuta* is more likely due to divergence in life-histories. The traits of *A. marmorata* (fast reproduction, high juvenile survival in the absence of competition, self-fertilization) allow it to exploit ephemeral patches of resources (e.g., associated to macrophyte growth in ponds) before *P. acuta* numbers grow enough to outcompete it, which may happen in places with stable resource levels. At the metapopulation level, the same traits may explain why *A. marmorata* more efficiently colonizes empty sites, but is more prone to local extinction, than *P. acuta* (Dubart et al., 2019; 2022).

Life history evolution and competition between resident and invasive species

Rapid evolution has been observed in several instances of interactions betwen invasive and resident species (Maron et al., 2004; Stuart et al., 2014; Chapuis et al., 2017). Competition can promote character displacement, i.e., trait evolution in response to selection to minimize impacts of competition between species, a process that occurs naturally during adaptive radiation (e.g., divergence in beak size among Darwin's finches, Schluter & McPhail, 1992; Grant & Grant, 2006), as well as after invasion. For instance, in Dominica, the introduced lizard *Anolis cristatellus* and the native *Anolis oculatus* (Losos, 1990, Schluter & McPhail, 1993) diverged in body size after introduction, limiting niche overlap (review in Losos, 2009). However, laboratory environments offer highly simplified conditions and competition experiments usually do not reproduce the diversity of resources or niches that may promote character displacement in nature. This may lead to apparent contradictions between field and laboratory data. For example, in mosquitoes, different species were competitively dominant in the field (with litter as main food source) and in the laboratory (with artificial diet based on liver powder and yeast, Juliano, 1998). Similarly, reversed competitive dominance was observed in laboratory and field trials between thrips (*Frankliniella occidentalis* and *Thrips tabaci*), due to the differential susceptibilities of the species to insecticides present only in the field (Zhao et al., 2017). Thus, we might not necessarily expect that if the traits of our snail species had evolved to differenciate their niches and decrease competition in nature, they would also do so in our experimental conditions, with only one food source and a stable, unstructured environment. Our previous study has shown that *A. marmorata* life-history traits have rapidly evolved in populations invaded by *P. acuta* (Chapuis et al., 2017): evolution favours traits associated with rapid population growth in non-competitive situations rather than exploitative competition, as their juvenile survival is enhanced while at the adult stage their body size is smaller and their life span shorter (Appendix 1). Our competition trials appear to validate this idea: the adult survival of experienced populations of *A. marmorata* is inferior to that of naive populations specifically when in competition with *P. acuta.* Thus *A. marmorata*, when reached by the *P. acuta* invasion, has evolved to become less competitive (at least in standard laboratory conditions). This apparent paradox, however, is solved under the hypothesis that the niche differenciation that allows *A. marmorata* and *P. acuta* to coexist is not a matter of resource type, but of ability to exploit bursts versus low, stable levels of resource (see above). In invaded populations, the latter may be monopolized by *P. acuta*, and *A. marmorata* may have evolved to better exploit its residual niche (i.e., competition-free microhabitats) as mentioned in the first section of the Discussion paragraph. This situation could be considered as character displacement along the r-K gradient. More generally, it illustrates the idea that interactions with invasive species may lead resident species to avoid rather than resist such interactions - another example is snakes that evolved a smaller gape to avoid predating poisonous invasive cane toads in Australia (Shine, 2010). Note, however, that similar recent studies in plants have found an evolution towards higher competitivity of the resident species (Germain et al., 2020) or an increase in allelopathy (Huang et al., 2018), suggesting that the direction of evolution (becoming more or less competitive) may vary depending on the context. More studies are needed to assess whether these different outcomes of rapid evolution in resident species following invasion are generally related to differences in the initial degree of niche similarity and/or initial competitive asymmetry as expected from models (Godoy et al., 2014).

Invasive species may also evolve in response to interaction with residents, but our design is not able to detect this, as we do not have the "unevolved" states. Indeed, all the *P. acuta* populations, be they recent (front) or ancient (core), have been founded by ancestors exposed to *A. marmorata* during the spread of *P. acuta* in Guadeloupe. Chapuis et al. (2017) did not detect important life-history differences between front and core populations – the small differences could be interpreted as possible impacts of

temporary founder effects (invasion load; Colautti et al., 2006). In line with this finding, we only observed small differences between front and core populations of *P. acuta*, but no impact on competition: both population types were equally insensitive to the presence of *A. marmorata*, and outcompeted it in mixed cultures.

Coevolution in sympatry

One of our most intriguing results is the stronger reduction in growth in both species by heterospecific competitors when the latter come from the same site (sympatry) than when they come from another invaded site (allopatry). This suggests that some specific evolution has taken place in one or both species within each site, which locally increases the impact of competition between the two. This coevolution pattern contrasts with the only other similar study (Germain et al., 2020), as in their plant system, the 'foreign' versus 'local' nature of the competitors (allopatric versus sympatric pairs in our study) did not influence the outcome.

We must acknowledge that we do not have a straightforward explanation for this local coevolution. Local environmental conditions seem to favor a common phenotype in both species, although this phenotype may vary from site to site due to specific conditions. This could be explained by the limiting similarity hypothesis. Character displacement theory predicts that local populations of resident and invasive species locally diverge in resource use and minimize their reciprocal competitive impacts (Pfennig & Pfennig, 2009), rather than reinforce it. In addition, given that we provided a single food source, the evolution of resource exploitation efficiency cannot specifically affect the local population of competitors. Instead of exploitation, interference competition (Amarasekare, 2002; Huang et al., 2018) might be involved. This hypothesis is still speculative (pending further experiments), but Physids are known to alter their growth in reponse to scents of predators or congeners eaten by predators (Turner, 1997), such that they may also be able to chemically influence the growth of heterospecific competitors.

Whatever the mechanism, the result of local evolution in our study system increased local competition impacts. This is in agreement with the hypothesis developed above, that the maintenance of the resident species in invaded ponds depends on its performances in occasional non-competitive situations rather than on withstanding interspecific competition in patches where the invasive species is well established.

Conclusion

In natural metacommunities, species coexistence may constantly be fine-tuned by evolution, promoting either stabilizing mechanisms ('niche-based' sensu lato), or equalizing mechanisms (i.e., low competitive asymmetry, up to neutrality) (Vanoverbeke et al., 2015; Leibold et al., 2019; Thompson et al., 2020). However, this sort of eco-evolutionary coupling is not easy to detect empirically, and is likely to proceed via small, population-specific trait changes (Leibold et al., 2019). In contrast, species invasions induce large-scale perturbations that may trigger large demographic and evolutionary adjustments, especially in resident species competing with newcomers (Haeuser et al., 2019). Our study provides an example where the competition between invasive and resident species is largely asymmetrical, in favor of the former, as expected from the phylogenetic and trophic similarity between the two, and the hypothesis of a competition filter to invasion. Contrary to other examples (Huang et al., 2018; Germain et al., 2020), rapid evolution in the resident species has tended to reinforce the initial competitive asymmetry. This is consistent with a mode of coexistence based on a form of niche partitioning along the colonization-competition ('r-K') axis, whereby the resident species specializes in exploiting ephemeral low-competition situations (such as resource availability peaks just after floods when communities are reestablishing), being otherwise outcompeted by the invasive species. This is akin to cases of character displacement observed in other animals, except that the displaced characters are life-history traits rather than traits (e.g., morphological) related to the exploitation of different resource types (Chapuis et al., 2017). As in most published examples of invasive-resident interactions, we have no reason to believe that evolution was absolutely necessary for the resident to persist in the presence of its new competitor (i.e., evolutionary rescue sensu stricto: Carlson et al., 2014); but several other examples suggest that rapid evolution of competitive interactions is commonplace after invasions (Huang et al., 2018; Germain et al., 2020). Understanding under which conditions evolution tends to promote resistance to competition (such

as in plants: Huang et al., 2018; Germain et al., 2020) versus its avoidance (as in snails) is a worthwile goal for future research.

Appendix

Appendix 1 - Mean values (sd) of several phenotypic traits studied in non-competitive laboratory conditions in Chapuis et al. (2017). SM = sexual maturity. The biovolume was estimated based on an ellipsoid considering shell length and width meaured as estimates of its height and diameter respectively, and fecundity was estimated over two weeks.

	Age at SM (days)	Body length at SM (mm)	Biovolume at SM (mm^3)	Fecundity (egg number)	Age at death (days)	Juvenile survival (%)
Aplexa marmorata	28.14 (4.82)	6.70 (0.84)	39.74 (15.12)	135.63 (40.72)	52.60 (26.83)	74.92 (24.40)
Physa acuta	30.77 (3.18)	6.23 (0.65)	40.91 (13.15)	171.64 (72.17)	78.30 (22.96)	52.46 (26.85)

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Data, scripts, code, and supplementary information availability

Data are available online: https://doi.org/10.5281/zenodo.10041280
Scripts and code are available online: https://doi.org/10.5281/zenodo.10041345

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

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