Sex in the kitchen: non-additive effects of competition for food and reproductive interference on coexistence outcomes between closely related species.

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Authorship Statement

MC, VS, OG, SM and FZ designed the experiments. MC collected data. MC, IF, OG and FZ performed modelling work and analysed data. MC and FZ wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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Conflict of interest

The authors declare that they have no conflict of interest with the content of this article.

Data availability

All datasets and R scripts are available at Zenodo (https://doi.org/10.5281/zenodo.10086125).

Abstract

Competition for food and negative interspecific sexual interactions (reproductive interference) have been identified as major drivers of species exclusion. These interactions likely do not act independently, as they often involve the same actors and may be modulated by the same underlying traits. However, how they determine competitive dominance when acting in combination has not yet been studied. Here, we address this issue using two closely related species, the spider mites *Tetranychus urticae* and *T. cinnabarinus*. First, by measuring species interactions in small-scale experiments, we revealed that the strength and symmetry of reproductive interference between species changed in presence of food competition. Next, using a population model, we showed that such non-additive effects induce significant changes in predicted competitive outcomes, specifically, a change in priority effects from favouring the inferior competitor for food in the sole presence of reproductive interference to favouring the superior competitor instead. Finally, we confirmed the accuracy of the model predictions for short-term population dynamics in a large-scale experiment. Together, these lines of evidence show that food competition and reproductive interference have non-additive effects on the population dynamics of interacting species, and highlight the necessity of incorporating both mechanisms to better predict competitive outcomes.

Introduction

Competitive interactions between organisms, be they for food, mates, or hosts, shape population dynamics and affect species distributions. Indeed, all these interactions generally have negative consequences for population growth of one or both species involved. They are also often modulated by the same underlying traits. For example, size is a mediator of competition for food, but also for mates[1–4]. Still, despite all the potential for interaction among these types of competition, they have mostly been addressed in disparate bodies of literature[5].

The impact of competition for food (*i.e.*, exploitative competition) in shaping species coexistence has been predicted and analysed by means of modern coexistence theory[6–10]. This framework posits that two species can coexist when niche differences, arising when intraspecific competition exceeds interspecific competition, are greater than fitness differences (*i.e.*, differences in species' intrinsic growth rate weighted by their overall sensitivity to competition). Otherwise, the species with higher fitness outcompetes the inferior competitor. Alternatively, priority effects can occur when species limit their competitor's growth more than their own (negative niche differences). In that case, the species that arrives first in a community, or is at an initial higher frequency, dominates it locally[7,11].

Although the validity of this framework to predict the population dynamics of interacting species has been shown in a wide variety of biological systems[12–16], it has largely overlooked competition for other types of resource beyond food. This is at odds with the fact that other types of competition can arise between those same individuals that are competing for food. For instance, closely related species are likely to engage in competition for food, due to sharing similar niches[17], and they can also compete for mates. This can result in reproductive interference, *i.e.*, any sexual interaction between genetically differentiated organisms with negative fitness consequences for at least one of them, ranging from signal jamming to hybrid infertilty[18,19]. Several laboratory[20] and field studies[21–23] have shown that reproductive

interference is an important mechanism driving exclusion, precluding interacting species from long-term persistence[21,24,25]. Indeed, species are increasingly affected by reproductive interference as they become rarer due to reduced encounter rates with conspecifics[19]. Theoretically, reproductive interference is thus predicted to cause priority effects, thereby leading to the exclusion of the initially less common species[26]. However, theoretical studies also predict that the outcome of reproductive interference may change depending on its interplay with trophic interactions[20,26,27].

It is thus clear that the integration of trophic interactions such as competition for food and sexual interactions such as reproductive interference is key to our understanding of species dynamics and distribution[28]. Some theoretical and empirical developments have been done in this direction[20,29–32]. They predict that both interactions may act synergistically to accelerate exclusion, but if both processes are asymmetric in opposite directions (such that the species most affected by food competition is equally less affected by reproductive interference and vice-versa), coexistence is possible[26,33]. However, these theoretical models assumed that food competition and reproductive interference operate independently from one another, whereas mechanisms involved in both interactions may interact or be correlated, which should result in non-additive effects when both act in combination.

Food competition and reproductive interference may directly or indirectly affect each other's intensity if the same (or correlated) traits are involved in both interactions (*e.g.*, body size[34]), or due to density-dependent behaviours affecting the strength of both interactions[27] (*e.g.*, increased dispersal and/or conspecific aggregation[35,36]). In line with this, several empirical studies revealed that food competition can affect the reproductive success of individuals[37,38], or reciprocally, that different reproductive strategies may result in different investment in food competition[39,40]. However, these studies have largely focused on intraspecific interactions, whereas trophic and sexual interactions can also simultaneously

occur between closely-related species, and jointly affect their traits[39]. In addition, while both empirical and theoretical studies investigated the impact of non-additivity between different types of trophic interactions (*e.g.*, intra- and interspecific competition[40], food competition, predation, or parasitism[41–43]) on species growth rates, potential non-additive effects between trophic and sexual interactions, such as between food competition and reproductive interference, have been considered only very recently in coexistence theory[27], and remain to be tested experimentally.

Spider mites pose an ideal system to study the single and combined effects of food competition and reproductive interference on competitive outcomes. Some herbivorous species have been shown to compete for food when sharing host plants[14,44], and some mites are closely related enough that reproductive interference can occur[32,45–48]. Here, we used two such species, *Tetranychus urticae* and *T. cinnabarinus*, also often referred to as the green and red forms of *T. urticae*[49]. These two share several host plants[50], on which they compete for food. In addition, reproductive incompatibilities between the two, owing to significant differentiation across their genomes[51], lead to variable degrees of unfit hybridization (*i.e.*, from partial to complete hybrid sterility and hybrid breakdown[52–54]). This results in strong reproductive interference[48]. With this experimental system, we used recent modelling advances rooted in coexistence theory[33] and its recent extensions[11,15,33], and parameterised them with a set of experiments manipulating the presence or absence of food competition and reproductive interference. This combination of theory, modelling, and experiments allowed to predict their single and joint contribution to competitive outcomes. Such predictions were ultimately validated with an independent large-scale cage population experiment, to distinguish which combination of food competition and reproductive interference best fit the observed population dynamics of interacting mite species.

Results

Food competition affects the strength and symmetry of reproductive interference.

Small-scale experiments, in which we assessed the strength of interactions by exposing females of each species to competition for food (Experiment 1), mates (Experiment 2), or both (Experiment 3), revealed large asymmetries between species. Indeed, females grown in absence of any competitors for food and heterospecific mates (controls) consistently differed in their intrinsic growth rates across all 3 experiments: *T. cinnabarinus* (Tc) females produced, on average, more offspring than *T. urticae* (Tu) females ($\lambda_{Tc} > \lambda_{Tu}$; Figures 1 and 2a; Supplementary Table S1). When species competed only for food (Experiment 1), both species were more sensitive to heterospecific than to conspecific competitors ($\alpha_{TcTu} > \alpha_{TcTc}$ and $\alpha_{TuTc} > \alpha_{TuTu}$), but Tc females were generally more sensitive to competition than Tu females, regardless of competitor identity ($\alpha_{TcTc}*\alpha_{TcTu} > \alpha_{TuTu}*\alpha_{TuTc}$; Figures 1a and 2b; Table S1). Conversely, when the two species were only exposed to reproductive interference (Experiment 2), Tu females suffered more from the presence of heterospecifics than Tc females ($\beta_{TuTc} > \beta_{TcTu}$; Figures 1b and 2c; Table S1). Finally, when both interactions occurred simultaneously (Experiment 3), both species had lower intrinsic growth rates (λ) and were overall less sensitive to competition (α) than in the previous experiments (Figures 2a,b; see also Table S2 *vs.* S1), but the relationship between λ and α values was conserved, with Tc females producing more offspring and being more affected by competition than Tu females (Figure 2a,b). However, we found a drastic difference in the strength and symmetry of reproductive interference, as the sensitivity of Tc females to reproductive interference slightly increased, whereas that of Tu females strongly decreased. Thus, Tu females suffered less from reproductive interference ($\beta_{TcTu} > \beta_{TuTc}$; Figure 2c), and became overall less affected by the presence of heterospecific individuals than Tc females (Figure 1c; see also Table S2 *vs* S1).

The non-additivity of food competition and reproductive interference impacts theoretical predictions for coexistence

Interaction strength estimated from the aforementioned experiments subsequently served to parameterise a population model that predicted the long-term consequences of both types of interaction. This model is a generalization of a Lotka-Volterra model that describes changes in population abundances over time as a function of species intrinsic growth rates (λ) and the negative linear effects of competition for food (α) and reproductive interference (β) due to the presence of competitors[33]. Therefore, non-additive effects between competition for food and reproductive interference can only arise from changes in the strength of the estimated parameters (rather than from an interactive term of these two effects within the population model; see Eq. 1).

We found that when acting alone, food competition should promote positive density-dependent effects (denoted as negative niche differences), as each species was more affected by heterospecifics than by conspecifics. This result, combined with the fact that fitness differences between the two species were large enough (both for 3 replicate populations and for all data), should lead to the exclusion of Tc (but note that we also found high variability among replicate populations, suggesting that priority effects are also possible; Figure 3a). We also found that, in absence of food competition, reproductive interference should always generate priority effects, such that the outcome should depend on the combination between the relative 'fecundity differences' between the two species (*cf.* Eq. S6 in supplementary Box S3) and their initial relative frequency (Figure 3b). However, in our system (*i.e.*, with the parameter values we measured experimentally), we predicted that Tc should be favoured even when rare, as Tu should be excluded not only when both species are initially at equal relative frequency (as in our experimental conditions), but also when it is initially twice as abundant as Tc (predicted for all data and 3 replicate populations; Figure 3b). Thus, food competition and

reproductive interference are, overall, predicted to generate rather opposite outcomes when acting in the absence of each other.

Then, to determine how both interactions would jointly affect long-term population dynamics, we performed simulations in which they would have either additive (using parameters estimated from Experiment 1 and 2) or non-additive (using parameters estimated from Experiment 3) effects on species growth rates. In both cases, and as predicted for reproductive interference alone, we found priority effects, as the identity of the species that excludes the other depended on the initial conditions (both initial relative frequency and absolute density in this case; Figure 3c,d). However, when considering that the two interactions had additive effects, reproductive interference should counterbalance the asymmetries in food competition, with the weaker competitor for food (Tc) excluding the stronger competitor (Tu) when the former is initially more abundant (Figure 3c; see Figure S1 and S2 for variation among replicate populations). In contrast, when accounting for the non-additive effects of the two interactions, reproductive interference should have a much lower buffering effect against the effects of food competition. In this case, Tu always excluded Tc, except when extremely rare (Figures 3d; see Figures S1 and S3 for variation among replicate populations).

The model accurately predicts dynamics in cage populations

Finally, to validate our hypothesis that accounting for non-additive effects of food competition and reproductive interference improves the accuracy of model predictions, we performed a large-scale experiment in which we followed, in 5 replicate cage populations, the short-term dynamics of the two species starting at equal initial densities (Experiment 4). We also extended the population model to fit the procedure used in this experiment (*cf. Methods* and Box S4) and predict the production of sterile hybrid females along with Tu and Tc females. Then, we parameterised the model using estimates obtained either in Experiments 1 and 2 or in

Experiment 3, to predict population dynamics with additive or non-additive effects of food competition and reproductive interference, respectively. In the experiment, all replicate populations showed very consistent dynamics, with Tc and hybrids being fully excluded by Tu by the 6th and 8th generations, respectively (Figure 4a; Table S3). A similar pattern was also predicted by the model, both when accounting for additive or non-additive effects of food competition and reproductive interference. However, simulated population dynamics considering only additive effects showed extremely large variance, indicating a strong uncertainty concerning which species should exclude the other (Figure S4a). Conversely, predictions showed much lower variance when including non-additive effects instead, with Tu always excluding Tc (Figure S4b). Hence, these results further confirmed the importance of incorporating non-additivity in the model to better predict population dynamics. Still, as compared to experimental observations (Figure 4a), the model predicted lower proportions of hybrids (from generations 2 to 6), and a faster exclusion of Tc. Thus, to improve these predictions, we performed additional simulations in which we varied the sensitivity of hybrid females to food competition, as compared to purebred females, and quantitatively compared observed and predicted data with linear regressions. These analyses revealed that hybrid females should be at least 10 times less sensitive to food competition than purebred ones (Figure 4b; Table S3) to obtain the best fit between observed and predicted dynamics (Figure 4c, Table S4).

Discussion

Our study provides the first empirical evidence that reproductive interference interacts in a non-additive way with food competition, such that their combined effect on population dynamics and competitive outcomes could not be predicted by their independent action. The species that benefitted most from this non-additivity in our system was the superior competitor for food (Tu), which also became the least sensitive to interference.

Why food competition directly affected both the strength and the symmetry of reproductive interference could be explained by a positive correlation between traits involved in each of these interactions, or by the same traits being involved in both interactions[55]. One such trait that could explain our results is body size[34]. Indeed, because food availability can affect body size in spider mites[56], and Tu individuals were less sensitive than Tc to food competition, the size of Tu individuals might also be less negatively affected by food competition than that of Tc individuals. This, in turn, could reduce the sensitivity of Tu to reproductive interference while increasing that of Tc, because bigger spider mite males are generally superior competitors for mates[57,58], and bigger females preferred over smaller ones[59,60]. Another possibility could be that reduced food availability (or quality) leads to slower offspring development in spider mites as in other systems[61,62], such that under competition for food, males of the superior competitor (Tu) develop faster and secure conspecific mates, before males of the inferior competitor (Tc) became sexually mature. Moreover, although our experiments aimed at revealing whether food competition affected the strength of reproductive interference, non-additive effects may also occur in the opposite direction. For instance, male mating harassment[63] could either decrease or increase the intensity of food competition by inducing changes in female feeding behaviour (*e.g.*, reduced female feeding time to escape males[64], or increased spatial aggregation to create refuges from males[27]). Theoretically, such density-dependent phenomenological effect of reproductive interference on the intensity of

food competition can cause changes in niche differences, thereby shifting competitive outcomes from coexistence to priority effects, or the reverse[27]. However, the long-term consequences of the opposite (*i.e.*, changes in the strength of reproductive interference in response to food competition) had not yet been investigated theoretically.

Our ability to inform population models with such detailed experiments allowed us to predict the long-term consequences of the interaction between food competition and reproductive interference. Following principles from modern coexistence theory, we observed that food competition promoted a combination of reduced niche differences and fitness differences favouring Tu. Thus, predicted ecological outcomes based on the effect of food competition alone showed that Tc should overall be excluded, although in some replicate populations, Tc could exclude Tu when initially present at a higher frequency. Reproductive interference was instead found to promote priority effects[26,65] that should favour Tc over Tu. Indeed, we predicted that Tc should exclude Tu except when the latter was initially much more abundant. Our findings are thus in line with several studies reporting reproductive interference as a mechanism of exclusion, whether based on theory[26,32,66], or on empirical data for a variety of systems[21,24,25,31,67]. However, although food competition and reproductive interference acting asymmetrically in opposing directions is a condition previously predicted to favour stable coexistence[26], this was not the case in our system.

In this study, we provided the first experiment-based predictions of modern coexistence theory incorporating both food competition and reproductive interference. Our simulated population dynamics revealed that priority effects driven by reproductive interference remained even in the presence of food competition. Hence, reproductive interference is a key determinant of population dynamics in this system, whereas food competition determined which species was dominant by reducing the threshold frequency at which the superior competitor for food (Tu) was able to invade. Moreover, we showed that non-additive effects of

the two interactions increased the importance of food competition relative to that of reproductive interference in determining competitive outcomes in this system, as the lower sensitivity of the superior competitor (Tu) to reproductive interference served as a buffer against priority effects. This was evidenced by an even greater reduction of the threshold frequency required for Tu to exclude Tc. The apparent discrepancy between this result and previous theoretical predictions, whereby coexistence should be possible via a trade-off between reproductive interference and food competition[26], lies in the fact that we found negative niche differences in our system, a scenario yet unexplored until very recently. Indeed, recent theoretical work showed that only a shift towards positive niche differences, due to changes in food competition intensity mediated by reproductive interference, could drive coexistence in systems in which niche differences are initially negative[27].

Finally, using independent data for model parameterisation and validation, we demonstrated, for the first time, the importance of accounting for non-additive effects between trophic and sexual interactions to accurately predict coexistence outcomes between closely-related species. These findings further showed that it is possible to generate very accurate predictions for population dynamics using a simple model that incorporates all possible mechanisms of reproductive interference[18,19], without explicitly modelling each individual mechanism (*i.e.*, the concept of 'demographic reproductive interference'[25]). Interestingly, we also show that including the ecological impact of hybrids by adjusting their sensitivity to food competition further improved our ability to predict the system's dynamics. Indeed, since hybrid females are mostly sterile in our system[54], they may require much less resources than purebred females. A direct consequence of this, predicted by our model and observed experimentally, is an increased relative frequency of hybrid females in the populations. This, in turn, may generate cascading density-dependent effects, potentially affecting both reproductive interference and food competition's intensities. Thus, while studies of speciation mainly focus on the ecological

impact of hybrids in the context of adaptation[68,69], our results highlight how even hybrids that do not contribute genetically to the following generations may have a significant ecological impact through competitive interactions.

In conclusion, our results highlight that food competition and reproductive interference interact in a non-additive way. Such results, which were overlooked by ecological theory, have significant consequences for understanding the short-term population dynamics of interacting species as well as their long-term competitive outcomes. We believe these non-additive effects are not specific to spider mites, but can rather be a general feature of many other ecological systems, as has recently been proposed[27]. In fact, this can be expected in any system where the same (or correlated) traits are involved in both sexual and trophic interactions (*cf.* above), and even more particularly in systems where the two types of interactions are intertwined, such as in species with sexual cannibalism[70]. The potential ubiquity of such non-additive effects should be considered in future work for two main reasons. From a theoretical perspective, it indicates that studies accounting for several types of interactions, such as the combination of trophic and sexual interactions[33], or exploitative and apparent competition[71], must more systematically explore theory beyond assuming simple additive effects[72]. From an empirical perspective, it highlights the necessity to consider several types of interactions in isolation and together to better understand the magnitude of non-additive effects. In sum, species interactions have been intensively studied for more than a century as a major determinant of species distribution and competitive outcomes. Yet, our results collectively show that we are still in the infancy of understanding how different mechanisms interact to determine the population dynamics of interacting species. Combining theoretical and empirical progress is still needed to obtain a more holistic view of the causes and consequences of species interactions.

Methods

Spider mite populations

We used one population of *T. urticae* ('Tu') and one of *T. cinnabarinus* ('Tc'), for which pre- and post-zygotic isolation were previously assessed: heterospecific crosses result in fully sterile hybrids (most hybrid females do not lay eggs and the few eggs laid do not hatch[54]), but males of both colour forms prefer to mate with red females (*i.e.*, red males mate assortatively, while green males mate disassortative; Cruz et al. *in prep.*). Such incomplete pre-zygotic isolation, coupled with strong post-zygotic isolation, is expected to result in strong reproductive interference when populations of these two species share the same environment[19,48]. Prior to performing experiments, we ensured that both populations were free of endosymbionts, and either fully homozygous for the presence (Tu) or absence (Tc) of a recessive nonsynonymous mutation that can be used to differentiate populations of each species (see detailed procedure in Supplementary Box S1).

Measuring food competition, reproductive interference, and their combined effects

To determine whether food competition and reproductive interference have additive or non-additive effects on the growth of interacting species, we derived 5 replicate populations from each of the Tu and Tc populations, and performed a set of three different experiments (*cf.* detailed procedure in Box S2). First, to quantify how food competition affected the growth of both species in absence of reproductive interference, focal females that had already mated with conspecific males were exposed to increasing densities of conspecific and heterospecific competitors[73], and their number of descendants was counted (Figure 5a). Second, to quantify the strength of reproductive interference while restricting competition for food, we counted the number of offspring produced by females isolated on individual food patches after they interacted sexually with only conspecific males (control), or with both conspecific and

heterospecific males. This was done over 2 generations to encompass the costs resulting from the production of sterile F1 hybrids (Figure 5b). Third, to quantify the combined effect of food competition and reproductive interference on the growth rate of each species, we assessed their per capita production of daughters when they interacted sexually and shared a common resource over 3 generations (Figure 5c). In all three experiments, controls with no competitors for food (nor heterospecific mates) were also used to estimate the individual growth rate of each species in absence of any interactions.

Theoretical approach for parameter estimations and to predict the outcome of interactions between populations

To estimate key interaction coefficients from data obtained in each of the experiments described above, we adapted a discrete-time population model developed by Schreiber et al[33], in which a reproductive interference term was added to the Beverton-Holt function used to predict population dynamics under food competition[12]. In this model, the number of individuals of a species i (N_i) is predicted at each generation t, accounting for interactions with individuals of a species j (N_j), with the following equation:

$$N_{i,\,t+1} = N_{i,t}\,\delta\,\lambda_i \cdot \frac{1}{1+\alpha_{ii}\,(N_{i,t}-1)+\alpha_{ij}\,N_{j,t}} \cdot \frac{N_{i,t}}{N_{i,t}+\beta_{ij}\,N_{j,t}} \qquad \text{(Eq. 1)}$$

In this equation, the leftmost term represents population growth in absence of limiting interactions for species i. The δ, corresponds to the oviposition period in days, and λ_i is the per-capita daily intrinsic growth rate of species i in absence of any type of interactions. The middle term represents the effect of food competition. α_{ii} and α_{ij} are, respectively, the per capita effects of food competition with N_i - 1 competitors of species i (we excluded the focal individual here as the quantity of food provided to single individuals in our experiments is not limiting: we assume its growth to be limited only by the presence of competitors), and N_j competitors of species j (i.e., intraspecific and interspecific competition, respectively). The rightmost term

represents the per capita effect of reproductive interference, where β_{ij} is the per capita effect of interspecific sexual interactions with N_j individuals of species j on the growth rate of species i. Detailed procedure used for estimations of parameter values (and their 95% confidence interval) in each of the experiments 1, 2 and 3, is provided in the Supplementary Box S3.

Estimated parameter values were then used to compute three different key metrics allowing to infer the impact of food competition and reproductive interference in the long-term: the average fitness differences (k_j/k_i computed using the λ and α parameters), which refers to the competitive advantage of one species over the other; the niche overlap (ρ computed using the α parameters), which represents the degree to which each species limits its own growth as compared to how it limits the growth of the competitor species[10]; and the relative strength of reproductive interference (γ computed using the β parameters), which corresponds to the degree to which one species is more sensitive to reproductive interference than the other[33]. Equations used to compute these key metrics, as well as analytical solutions and numerical analyses used to predict the long-term outcome of interactions between species (when food competition and reproductive interference act alone or simultaneously, respectively), are fully described in the Supplementary Box S3.

Empirical test of model predictions: Dynamics in cage populations

To determine whether our estimated interaction coefficients enable accurate predictions of short-term population dynamics, we performed a larger-scale experiment (Experiment 4) in which we followed the relative frequencies of Tu and Tc female mites, as well as that of hybrid females, in cage populations over eight discrete generations (Figure 6 and detailed procedure in Box S4). We also adapted our mathematical model to fit the procedure used in the population cage experiment (*cf.* details and equations in Box S4). In short, the model was extended to account for random sampling of the females used to start each new generation, and for the

asymmetrical production of sterile hybrid females in our system (due to sex-ratio distortion in crosses between Tu females and Tc males[54]). Then, we compared the proportion of Tu, Tc, and hybrid females observed in the cage populations every two generations, with those predicted under different scenarios: (1) assuming additive vs. non-additive effects of food competition and reproductive interference (by parametrizing the model with estimates from Experiments 1 and 2, or from Experiment 3, respectively; parameter values in Table S1 vs. S2); (2) assuming different sensitivity of the hybrids to food competition by evaluating a range of scale factors of the α parameters in the equation used to predict hybrid production. We then used linear regressions to determine which model parameterization leads to the best fit between predicted and observed dynamics (*cf.* detailed procedure in Box S4).

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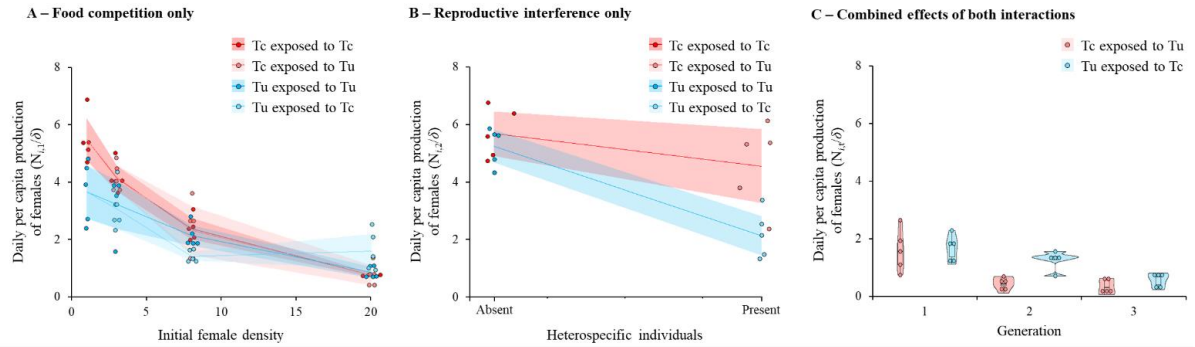

Figure 1. Single and combined effects of food competition and reproductive interference on the daily per capita production of daughters by *Tetranychus urticae* (Tu) and *T. cinnabarinus* (Tc) populations. In (A), lines represent the average number of females produced under increasing densities of either conspecific or heterospecific competitors (dark and light colours, respectively) on a common food patch, but in absence of reproductive interference. In (B), lines represent the average number of females produced in absence or presence of heterospecific individuals (dark and light colours, respectively) on a common mating patch, in absence of food competition. In (C), violin plots show the distribution of mean number of females produced when individuals competed for the same food and shared their mating patches over 3 generations. In all panels, individual points show the mean number of females produced daily by a single female (per capita) for each of 5 different replicate populations. Red: Tc females; Blue: Tu females.

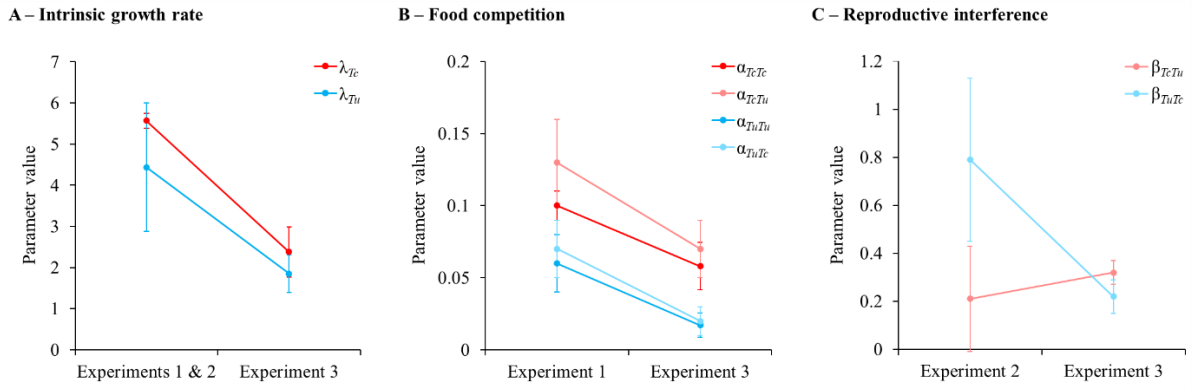

Figure 2. Comparison of parameter values estimated across experiments for both *Tetranychus urticae* (Tu) and *T. cinnabarinus* (Tc) populations. (A) Intrinsic growth rate (λ) estimated as the mean number of daughters produced daily by single isolated females, averaged for Experiments 1 and 2, or measured in Experiment 3. (B) Per capita effect of food competition (α) estimated from Experiments 1 and 3. (C) Per capita effect of reproductive interference (β) estimated from Experiments 2 and 3. In all panels, dots show parameter values (± 95% confidence intervals) estimated across 5 replicate populations, dark and light colours represent within- and between-species effects, respectively, and parameter values for Tc and Tu are displayed in red and blue, respectively.

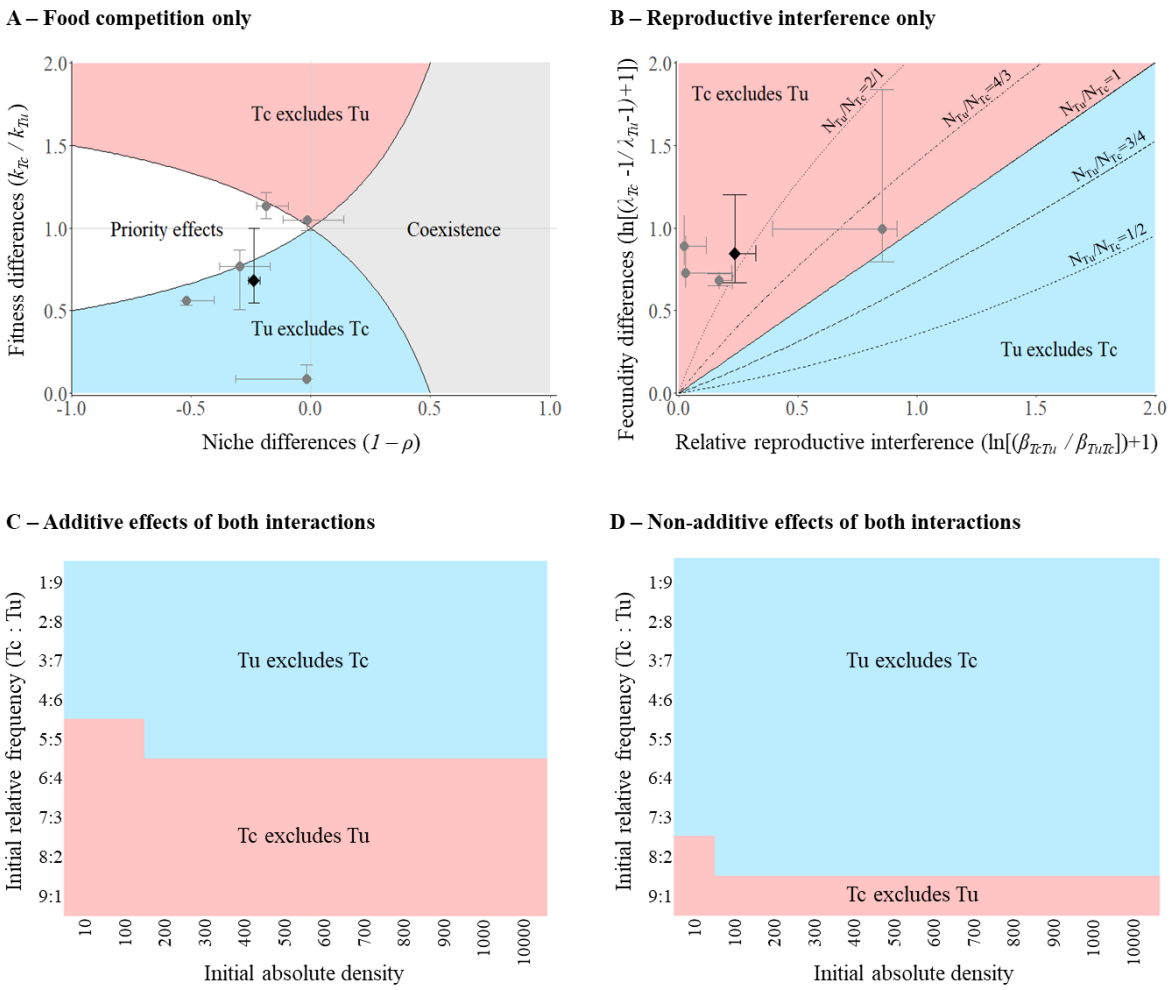

Figure 3. Theoretical predictions for the outcome of competition between *Tetranychus urticae* (Tu) and *T. cinnabarinus* (Tc) populations. (A) and (B) show predicted outcomes depending on the niche and fitness differences between species when populations only compete for food or depending on the relative strength of reproductive interference and fecundity differences when populations only interact during reproduction, respectively. In (A), the two solid black lines define the space in which species can coexist (grey area) or enter alternative stable states (priority effects; white area). Otherwise, the species with higher fitness will exclude the other. In (B), due to priority effects, coexistence is possible if reproductive interference equalises the fecundity differences between populations at equal initial frequency of both species (solid line: N_{Tu}/N_{Tc} = 1), or if the initial frequency of the inferior competitor is sufficiently high to compensate for the combined effects of its fecundity disadvantage and/or higher sensitivity to reproductive interference (dotted lines from left to right: N_{Tu}/N_{Tc} = 2/1, 4/3, 3/4, and 1/2). In (A) and (B), grey circles and black diamonds are means (± 95% confidence intervals) for each replicate population and for all data, respectively. Note that negative parameter values and confidence intervals are not displayed. (C) and (D) show predicted outcomes for different initial absolute densities and relative frequencies of the two species, obtained from simulations using parameters estimated with all data (*cf.* Figure S1 for each replicate population) when both types of competition had additive or non-additive effects, respectively. In both panels, heat maps show that the identity of the remaining species after 20 generations depends on the initial conditions due to priority effects (see also Figures S2 and S3 for the full population dynamics). Red area: Tc excludes Tu; Blue area: Tu excludes Tc (only for equal initial frequency of the two species in panel B).

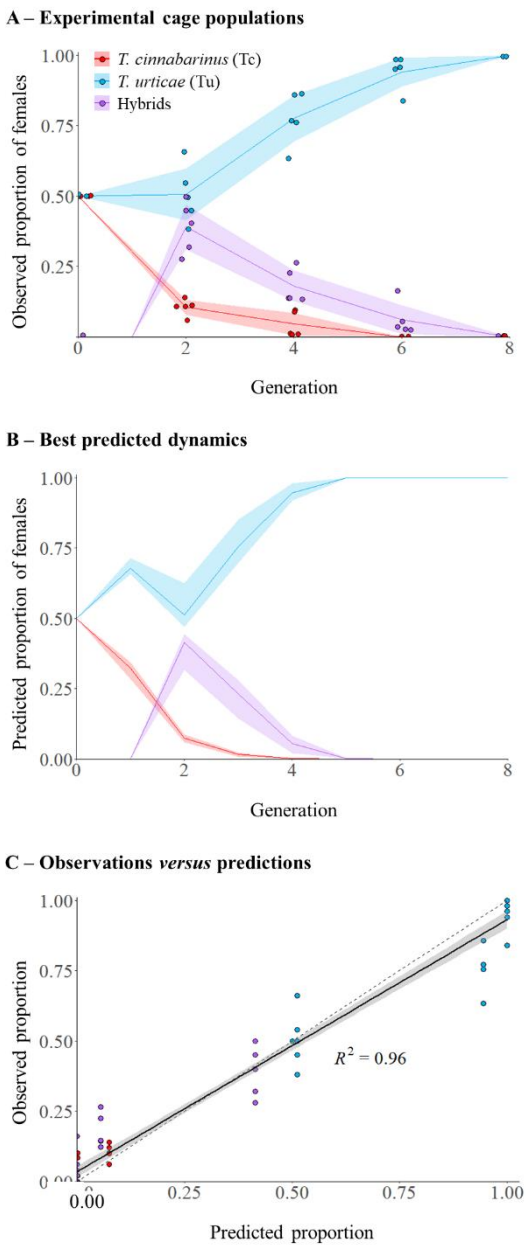

Figure 4. Observed and predicted dynamics of *Tetranychus urticae* (Tu), *T. cinnabarinus* (Tc), and of their hybrids, in cage populations over 8 generations. (A) Observed proportions of females in experimental cage populations. Dots show the observed proportions in each replicate population, and coloured lines and shaded areas show the averages and associated 95% confidence intervals across all replicate populations. (B) Predicted proportions of females assuming non-additive effects of food competition and reproductive interference (parameters estimated from Experiment 3), and hybrid females 10 times less affected by food competition than purebred females. Coloured lines and shaded areas show predicted proportions and associated 95% confidence intervals using parameters estimated across all replicate populations. (C) Linear regression between observed and predicted proportions. Dots show each replicate population, the solid line shows the linear regression between observed and predicted proportions, and the dashed line shows the 1:1 relationship between values in the two axes. Blue: Tu females; Red: Tc females; Purple: hybrid females.

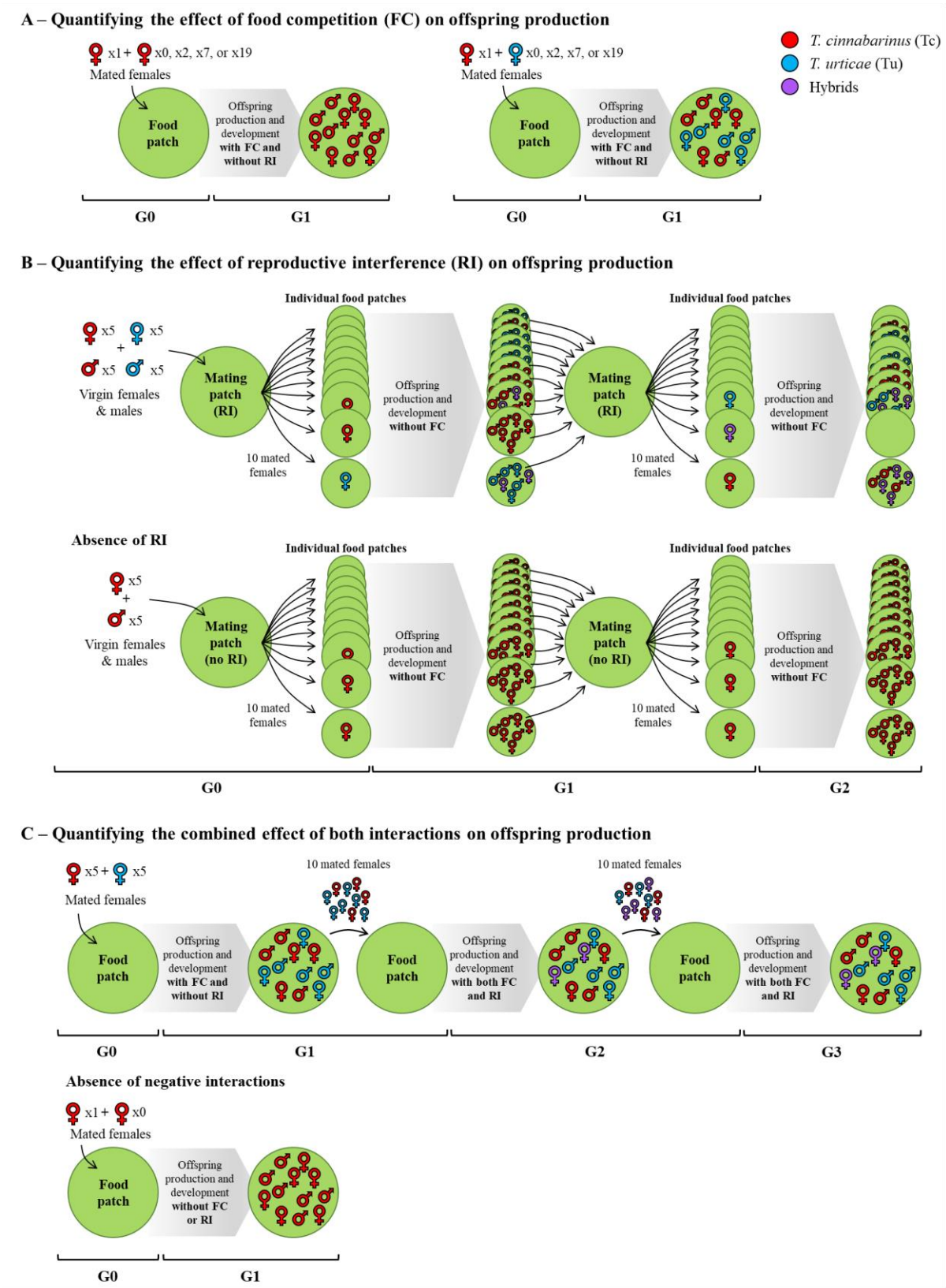

Figure 5. Experimental procedures used to quantify the effects of food competition and/or reproductive interference on *Tetranychus urticae* (Tu) and *T. cinnabarinus* (Tc) offspring production. (A) Food competition in absence of reproductive interference was measured by placing females mated with conspecific males on food patches where their juveniles would develop. The two different types of competition, intraspecific

(left) and interspecific (right), are shown, with Tc focal females as an example. (B) Reproductive interference in absence of food competition was measured across two consecutive generations (G0 to G2) to account for the costs resulting from the production of sterile F1 hybrids. Common mating patches were used for virgin females and males of the two species, but individual food patches were used for ovipositing females and developing juveniles. (C) The combined effect of food competition and reproductive interference were measured across three consecutives generations (G1 to G3) by using common (food and mating) patches for the entire life cycle of the individuals. As females mated with males from their own population were used at the onset of the experiment, the first generation (G0 to G1) allowed re-estimating food competition in absence of reproductive interference (to correct for testing time). The next generations of offspring (G2 to G3) allowed re-estimating reproductive interference in the presence of food competition. Red: Tc females; Blue: Tu females; Purple: hybrid females.

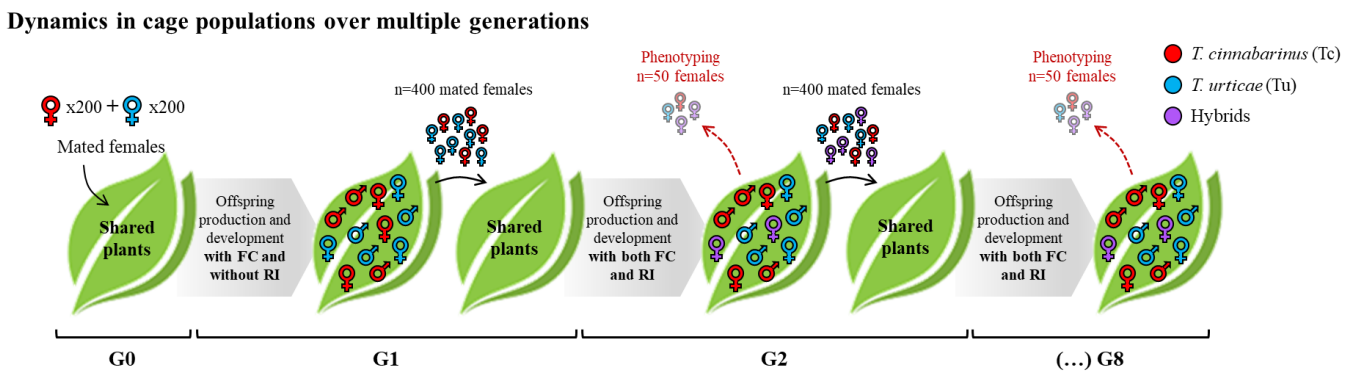

Figure 6. Experimental procedure used to follow the dynamics of *Tetranychus urticae* (Tu) and *T. cinnabarinus* (Tc) populations simultaneously interacting through food competition and reproductive interference. Common plants were used for the entire life cycle of individuals of both species. This procedure enabled food competition between females and developing juveniles, as well as reproductive interference between virgin adult individuals of both species. The figure depicts the initial installation of mated females (G0), the transfer of 400 randomly sampled mated females to start each subsequent discrete generation (G1 onward), as well as random sampling and phenotyping of 50 virgin females every two generations. Red: Tc females; Blue: Tu females; Purple: hybrid females.