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

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Authorship Statement
MC, VS, OG, SM and FZ designed the experiments. MC collected data. MC and FZ performed modelling work and analysed data with advises and scripts from IF and OG. 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 reproductive interference (negative interspecific sexual interactions) have been identified as major drivers of species exclusion. Still, how these biotic interactions jointly determine competitive dominance remains largely unknown. We tackle this by coupling population models and laboratory experiments with two spider mite sibling species. Using experiments specifically designed to measure the single and combined effects of food competition and reproductive interference, we first show that the strength and symmetry of reproductive interference between species changes in presence of food competition. Next, we show that population models incorporating each type of interaction alone or their effect when combined lead to markedly different predictions, from exclusion by one species or the other, to priority effects. Moreover, accounting for the non-additive effect of these interactions led to changes in the frequency threshold determining the dominant competitor, favouring the superior competitor for food. Finally, model predictions for short-term population dynamics were corroborated with an independent population cage experiment. Altogether, our results suggest that trophic and sexual interactions have non-additive effects that strongly impact population dynamics and competitive outcomes. Hence, the joint consideration of food competition and reproductive interference is critical to accurately predict and understand species coexistence.

Introduction

How species that compete for common resources coexist is arguably one of the fundamental questions in ecology[1–3]. Modern coexistence theory posits that two competing species coexist when their niche differences, arising when intraspecific competition exceeds interspecific competition, are greater than their fitness differences (*i.e.*, differences in species' intrinsic growth rate weighted by their overall sensitivity to competition)[3,4]. A rich and vast literature addresses how different abiotic and biotic factors affect the drivers, and ultimately, the outcomes of species competition and coexistence[5–7]. In particular, competition for food often co-occurs with other types of biotic interactions, but our knowledge of their joint effects is mostly limited to trophic ones, such as predation[8–10] or parasitism[11,12], whereas the impact of other types of interactions, within the same trophic level, is to date overlooked.

Interspecific sexual interactions, owing to imperfect signal recognition, are relatively common between various assemblages of sexually reproducing species that generally also compete for food[13–16]. Such interactions, commonly referred to as 'reproductive interference', generally have negative fitness consequences on at least one of the species involved and encompass a wide range of underlying mechanisms, varying from signal jamming, heterospecific rivalry, misdirected courtship and heterospecific copulations (incl. gamete wastage), up to the production of inviable or infertile hybrids[17]. Therefore, this type of interaction includes both direct (interference) and indirect (exploitative) competition for limited shared resources associated to species reproduction (*i.e.*, breeding space, mates and/or gametes). Although historically reproductive interference has been mostly studied in speciation research due to its central role in reproductive character displacement and reinforcement[18–20], it recently attracted growing interest in ecological research[15,21–23].

Theoretical studies posit that reproductive interference can be a major driver of competitive outcomes[24–28]. Because this interaction promotes positive frequency-dependence (instead of negative-frequency dependence, as caused by food competition), it leads to priority effects in favour of the most abundant species, thereby driving faster exclusion than food competition[24,25]. These effects can thus preclude long-term coexistence between ecologically equivalent species, as evidenced by an increasing number of laboratory and field studies[29–33]. However, reproductive interference could promote coexistence at larger spatial scales if different species are numerically dominant locally (e.g., [34]). Moreover, as for other types of interactions[3,35], reproductive interference could promote coexistence via a trade-off with food competition, such that the species most affected by food competition is less affected by reproductive interference or vice-versa[26,27]. However, a limitation of prior work is the assumption that food competition and reproductive interference operate independently from one another, whereas they probably have non-additive effects instead. In fact, several empirical studies revealed that, within species, food competition can affect the reproductive success of individuals, and reciprocally, that different reproductive strategies may result in different levels of food competition[36–38]. This non-additivity is also expected to change the effect of such interactions between species, as proposed by recent theory[28]).

In sum, both reproductive interference and competition for food have strong impact on species coexistence, but their joint effect remains to be experimentally tested. This knowledge gap may be due to the fact that, unlike other abiotic or biotic factors that can easily be singled

out (e.g., temperature, salinity, competitors, parasites or predators), reproductive interference is part of the interaction between species that are simultaneously competing for food. Therefore, designing experiments that measure the impact of each of these interactions separately (which is needed as a control to evaluate their joint effect) is a true challenge. Herbivorous spider mites represent an ideal system to do so, given their amenability to experimental manipulation of both competition for food[39–41] and reproduction (incl. reproductive interference[42,43]).

Here, we studied the single and combined effects of reproductive interference and competition for food between two sibling species of spider mites, *Tetranychus urticae* and *T. cinnabarinus*[44] (also often referred to as the green and red forms of *T. urticae*[45]). These two species have overlapping distributions and host plant ranges[46], compete for food[41,47], and suffer from strong reproductive interference[43] due to variable reproductive incompatibilities and unfit hybridization (ranging from partial to complete hybrid sterility and hybrid breakdown[48–50]). With this experimental system, we used recent modelling advances rooted in coexistence theory[27] and its recent extensions accounting for priority effects[51], and performed a set of experiments manipulating the presence or absence of food competition and reproductive interference. This combination of theory, modelling, and experiments allowed to estimate the strength of both types of interaction, when occurring alone or together, as well as to predict their single and joint contributions to competitive outcomes. Predicted dynamics of the two mite species interacting through both food competition and reproductive interference were then validated using data from an independent population experiment.

Results

Food competition affects the strength and symmetry of reproductive interference.

We first assessed the strength of interactions by exposing females of each species to competition for food only (by using females already mated to conspecific males and sharing food on a patch; Experiment 1), reproductive interference only (by using virgin females and males, but independent food patches; Experiment 2), or both types of interactions (by allowing sexual interactions on shared food patches; Experiment 3).

Overall, these experiments revealed large asymmetries in species intrinsic growth rates and interaction coefficients. First, females of the two species grown in absence of competitors for food and heterospecific mates in all 3 experiments consistently differed in their intrinsic growth rates: *T. cinnabarinus* (Tc) females produced, on average, more offspring than *T. urticae* (Tu) females (estimated coefficients $\lambda_{Tc} > \lambda_{Tu}$; Figures 1 and 2a; Supplementary Table S1). Second, when species competed only for food (Experiment 1), both species were more sensitive to heterospecific than to conspecific competitors (estimated competition coefficients $\alpha_{TcTu} > \alpha_{TcTc}$ 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 (estimated reproductive interference coefficients $\beta_{TuTc} > \beta_{TcTu}$; Figures 1b and 2c; Table S1), suggesting that a trade-off between the two types of interaction could occur when both interactions are at play.

Finally, when both interactions occurred simultaneously (Experiment 3), we found lower intrinsic growth rates (λ) and strength of food competition (α) than in the previous experiments, but both species were equally affected, such that Tc females still produced more offspring and were more affected by food competition than Tu females (Figure 2a,b; see also Table S2 *vs.* S1). However, we found a drastic change in the strength and symmetry of reproductive interference (β): the sensitivity of Tc females to the presence of heterospecifics slightly increased and that of Tu females strongly decreased, such that Tu females switched from suffering more to suffering less than Tc females from reproductive interference ($\beta_{TcTu} > \beta_{TuTc}$; Figure 2c). Hence, when simultaneously engaged in food competition and reproductive interference, Tu suffered less than Tc from either of these interactions, and its population growth overall became higher from the second generation onwards (Figure 1c).

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

Interaction strength estimated from the small-scale 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[27].

We found that, when acting alone, food competition should promote positive density-dependent effects (denoted as negative niche differences), as both species limited their competitor's growth more than their own (*i.e.*, each species was more affected by heterospecifics than by conspecifics). This result, combined with the large fitness differences between the two species, should lead to the exclusion of Tc (but note the high variability for fitness differences among replicate populations, suggesting that priority effects[51] are also possible; Figure 3a). In absence of food competition, reproductive interference should always generate priority effects[27], such that the outcome should depend on the combination between the initial relative frequency of the two species and their relative 'fecundity differences' (*cf.* Eq. S6 in supplementary Box S3; Figure 3b). In our system (*i.e.*, with the parameter values we measured experimentally), we predicted that Tc should be favoured even when rare. Indeed, 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 predicted to lead to opposite outcomes when acting in isolation.

Then, to determine how both interactions would jointly affect long-term population dynamics, we performed simulations in which they had 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, as predicted for reproductive interference alone, we found priority effects, with the identity of the species that excludes the other depending on initial conditions (both relative frequency and absolute density in this case; Figure 3c,d). However, considering additive or non-additive effects between food competition and reproductive interference drastically changed the outcomes. When considering additive effects between the two interactions, we found that reproductive interference should

counterbalance the asymmetries in food competition, with the weaker competitor for food (Tc) excluding the stronger competitor (Tu) if this latter is initially less abundant (Figure 3c; see Figure S1 and S2 for variation among replicate populations). In contrast, when accounting for non-additive effects of the two interactions, reproductive interference had 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

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 population cage experiment (Experiment 4) in which we followed, in 5 replicate populations, the dynamics of the two species starting at equal initial densities over multiple generations[52]. 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[50]. Then, we parameterised this 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 consistent dynamics, with all Tc and hybrid females being excluded 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, whereas predictions showed much lower variance when including non-additive effects instead, with Tu always excluding Tc (Figure S4). Thus, these results confirmed the importance of incorporating non-additivity in the model to better predict population dynamics. Nevertheless, 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 (Figure S4b). 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 (Table S4). These analyses revealed that hybrid females should be at least 15 times less sensitive to food competition than purebred ones (Figure 4b) to obtain the best fit between observed and predicted dynamics (Figure 4c).

Discussion

This study provides the first empirical evidence that reproductive interference interacts in a non-additive way with competition for food, such that the combined effects of these two types of interaction on population dynamics and competitive outcomes cannot be predicted by their independent action. Specifically, we show that, in absence of reproductive interference, *T. urticae* is the stronger competitor for food and it is therefore predicted to exclude *T. cinnabarinus*. Conversely, in absence of competition for food, *T. urticae* suffers more than *T. cinnabarinus* from reproductive interference and is predicted to be excluded, except if it is at

least twice as abundant initially. Whereas such a trade-off is, in the literature, predicted to enable stable coexistence[26,27], our simulations instead show that priority effects driven by reproductive interference should remain (the identity of the species that persists hinges upon initial frequencies). Yet, assuming that both types of interactions have additive effects, food competition should balance out the advantage conferred to *T. cinnabarinus* by reproductive interference, with both species having the same likelihood to persist at an even initial frequency. However, our experiments also revealed that the strength of reproductive interference is asymmetrically affected by competition for food, with the superior competitor for food, *T. urticae*, becoming the least sensitive to reproductive interference. Our predictions when accounting for such non-additive effects indicate the exclusion of *T. cinnabarinus* in all tested scenarios, except if its competitor is initially extremely rare. Subsequently, the results obtained from an independent population cage experiment were largely compatible with this prediction, with *T. cinnabarinus* being systematically excluded when both species started at an even initial frequency. Our results therefore provide two straightforward lessons: first, food competition modulates reproductive interference, leading to non-additive effects of these interactions on species coexistence, and second, modern coexistence theory[27,28] is a suitable framework to predict their effects on the population dynamics and competitive outcomes of closely-related species.

Many studies have investigated the strength of reproductive isolation between *T. urticae* and *T. cinnabarinus*[48–50,53,54], but reproductive interference and its consequences for population dynamics have barely been considered (but see[53]). Here, in absence of competition for food, we found asymmetric reproductive interference between *T. cinnabarinus* and *T. urticae*-, a result that is congruent with previous findings on pre- and post-mating reproductive isolation between the two populations used in this study[50,54]. This is also compatible with earlier studies using Chinese populations of these species, in which *T. cinnabarinus* consistently displaces *T. urticae* when at an even initial frequency[41,47]. However, these studies also revealed that this outcome is reversed in the presence of pesticides, due to stronger pesticide resistance in *T. urticae*. In fact, any abiotic or biotic factor that affects the relative fitness of these two species, such as temperature[47], host plants[55], or natural enemies[56], should also determine their persistence. Yet, no study so far aimed at disentangling the relative role of such factors in shaping competitive outcomes, let alone the role of different intrinsic factors.

Previous theoretical work predicted that food competition and reproductive interference acting asymmetrically in opposing directions (*i.e.*, trade-off) may favour stable coexistence[26]. Although we found that competition for food balances out the advantage conferred by reproductive interference to *T. cinnabarinus* in the current study, coexistence was not predicted in any scenario. Instead, simulated population dynamics revealed that priority effects driven by reproductive interference occur even in the presence of food competition. This apparent discrepancy with previous predictions lies in the fact that we found negative niche differences in our system, a scenario yet poorly explored in the literature. Recent theoretical work suggests that changes in food competition intensity mediated by reproductive interference (*i.e.*, due to behavioural[57,58] and/or evolutionary[59] changes) could drive coexistence, by switching initially negative niche differences to positive[28]. However, our experiments were specifically designed to assess the opposite effect, that is, a change in the strength of reproductive interference in

response to food competition, a possibility that has not yet been investigated, neither theoretically nor empirically.

An experimental test of the combined effects of reproductive interference and competition for food revealed that these interactions are not additive. Whereas the intrinsic growth rate of both species and their sensitivity to competition were overall consistently lower in the presence of reproductive interference, the intensity of the latter was stronger for *T. urticae* than for *T. cinnabarinus* in absence of food competition and similar for both species in its presence. This could be explained by a positive correlation between traits involved in each of these interactions, or by the same traits being involved in (and affected by) both interactions[60] (e.g., body size[61], development time, locomotor activity, etc.). For instance, food competition may affect trait values more severely in the offspring of the lower competitor, which in turn become more affected by reproductive interference (e.g., because they produce mating signals of lower quality, become less competitive for mates, produce fewer/smaller/less mobile gametes, etc.). Alternatively, non-additive effects may result from density-dependent feedbacks between the effects of food competition and the intensity of reproductive interference, such that the strength of reproductive interference (the beta values) would vary depending on total population density (as proposed to tackle changes in alpha values due to reproductive interference[28]). However, this hypothesis would also require species-specific responses to density to explain our results. Although future work is necessary to unravel the mechanisms underlying non-additivity between trophic and sexual interactions, our simulations revealed important consequences for the predictions of our model, with a strong increase in the threshold initial frequency under which the lower competitor for food (*T. cinnabarinus*) cannot persist. This latter result thus further highlights the importance of understanding the magnitude and direction of non-additive effects in a particular system.

Finally, using independent data for model parameterisation and validation, we demonstrated the importance of accounting for non-additive effects of trophic and sexual interactions to accurately predict population dynamics. In particular, we show that a simple model capturing the demographic effects of reproductive interference with only two parameters (β and θ; *cf.* Methods), hence not explicitly modelling each of its underlying mechanisms (or 'fitness components'[16]), can generate very accurate predictions for the dynamics of two species in experimental cage populations. Moreover, this ability to predict the system dynamics was further improved with an adaptation of the model to account for the production of hybrid females that are less sensitive to food competition. While the ecological impact of hybrids is widely studied in the context of adaptation[62,63], the demographic impact of 'unfit' hybrids on parental species has been largely overlooked. Yet, an increased frequency of hybrids in parental populations (as predicted and observed here) could generate unpredicted changes in population dynamics, especially if they strongly compete for food. However, our analyses instead revealed that hybrid females in our system may require much less resources than purebred females, possibly because most of them do not produce eggs[50].

In conclusion, our study reveals that food competition and reproductive interference affect the dynamics of competing species in a non-additive way. Given that reproductive interference is expected to often occur between species that compete for food[14], these non-additive effects are likely a general feature of many ecological systems involving taxa that incidentally engage in sexual interactions[15], and may have major consequences for the study of

ecological coexistence. Indeed, our results show that such non-additive effects can change the shape of the trade-off between reproductive interference and competition for food, unbalancing the priority of one species over another in systems with negative niche differences (while potentially hampering coexistence in systems with positive niche differences). Understanding these effects is also crucial for speciation research, as the likelihood and duration of coexistence between closely-related species will determine the opportunities for reinforcement. Our findings may thus have far-reaching consequences for a recently growing field at the interface between speciation and coexistence theory[64–67]. Finally, despite species interactions being intensively studied for more than a century as a major determinant of species distribution and competitive outcomes, 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 approaches is key to unveil how different types of interactions non-additively impact species coexistence or exclusion.

Methods

Spider mite populations

We used one population of *T. urticae* ('Tu') and one of *T. cinnabarinus* ('Tc'), both free of any known endosymbiont (see details in Supplementary Box S1). Due to incomplete pre-zygotic isolation[54] and strong post-zygotic isolation[50] between these two populations, strong reproductive interference is expected when they share the same environment[43]. Indeed, females do not display any mate preference (non-assortative mating), whereas males of both species prefer to mate with Tc females[54]. Moreover, sex ratio distortion occurs in heterospecific crosses between Tu females and Tc males (with an overproduction of haploid sons instead of hybrid daughters probably due to fertilization failure[50]), and both directions of heterospecific cross result in fully sterile hybrids (most hybrid females do not lay eggs and the few eggs laid do not hatch)[50]. Finally, although the two species can be easily distinguished based on their body colouration (Figure S5), we ensured, prior to performing experiments, that they were fully homozygous for the presence (Tu) or absence (Tc) of a recessive nonsynonymous mutation that can be additionally used to differentiate populations of each species (*cf.* 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. First, to quantify how food competition affected the growth of both species in absence of reproductive interference (Experiment 1), focal females that had mated with conspecific males were exposed to increasing densities of conspecific and heterospecific competitors[68], and their number of descendants was counted (Figure 5a). Spider mites have first-male sperm precedence[69], hence females that have mated with conspecifics will drastically reduce their receptivity and not produce offspring from subsequent mates[54]. Second, to quantify the strength of reproductive interference while restricting competition for food (Experiment 2), we counted the number of offspring produced by females isolated on individual food patches after they interacted sexually with conspecific males only (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 (Experiment 3), we assessed the per capita production of daughters by females of each species 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. The detailed procedure for each of the three different experiments is provided in Box S2.

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.[27], in which a reproductive interference term was added to the Beverton-Holt function used to predict population dynamics under food competition[70]. 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:

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

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 interaction. The middle term represents the effect of food competition. The α_{ii} and α_{ij} are, respectively, the per capita effects of food competition with $N_{i,t}$ - 1 competitors of species *i* and $N_{j,t}$ competitors of species *j* (*i.e.*, intraspecific and interspecific competition, respectively) at generation *t*. We excluded the focal individual (*i.e.*, we used $N_{i,t}$ - 1 rather than $N_{i,t}$ in the food competition term of the equation) because the quantity of food provided to single individuals is not limiting: we assume its growth to be limited only by the presence of competitors. The rightmost term represents the per capita effect of reproductive interference, where β_{ij} is the per capita effect of interspecific sexual interactions with $N_{j,t}$ individuals of species *j* on the growth rate of species *i*. Detailed procedures to estimate parameter values (and their 95% confidence intervals) in each of the experiments 1, 2 and 3 are provided in the Supplementary Box S3.

Estimated parameter values were then used to compute three 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 refer 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[3]; 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[27]. Equations used to compute these key metrics, as well as analytical solutions and numerical analyses to predict the long-term outcome of interactions between species 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 the 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[50]), by using an additional parameter θ (*cf.* Eq. S8 in Box S4). 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 parameterising the model with estimates from Experiments 1 and 2, or from Experiment 3, respectively; parameter values in Table S1 vs. S2); and (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 parameterisation leads to the best fit between predicted and observed dynamics (*cf.* detailed procedure in Box S4).

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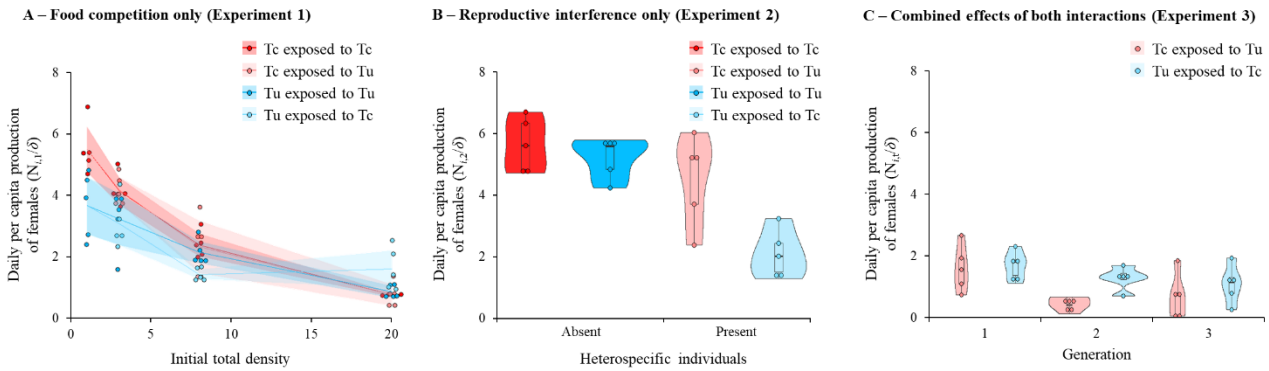

Figure 1. Three experiments teasing apart the single and combined effects of food competition and reproductive interference on the per capita growth rate of each species. In (A), lines represent the average number of females produced daily under increasing densities of either conspecific or heterospecific competitors (dark and light colours, respectively) on a common food patch, but in absence of reproductive interference. Shaded areas represent the 95% confidence intervals. In (B) and (C), violin plots show the distribution of mean number of females produced daily in (B) absence or presence of heterospecific individuals (dark and light colours, respectively) on a common mating patch, but in absence of food competition; or (C) when individuals shared the same food and 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, and *T. cinnabarinus* (Tc) and *T. urticae* (Tu) are displayed in red and blue, respectively.

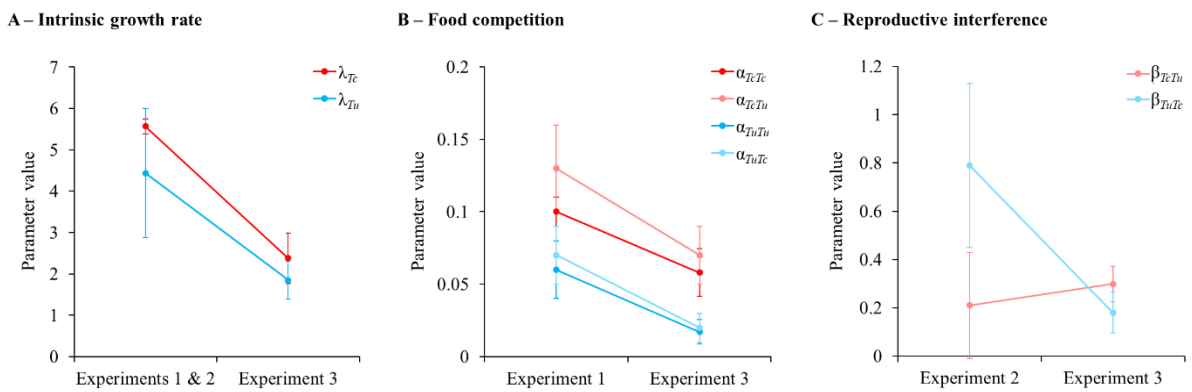

Figure 2. The strength and symmetry of reproductive interference change in the presence of food competition. (A) Intrinsic growth rate (λ) estimated as the mean number of daughters produced daily by single isolated females, averaged for Experiments 1 and 2, or measured in Experiment 3. (B) Per capita 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 *T. cinnabarinus* (Tc) and *T. urticae* (Tu) are displayed in red and blue, respectively.

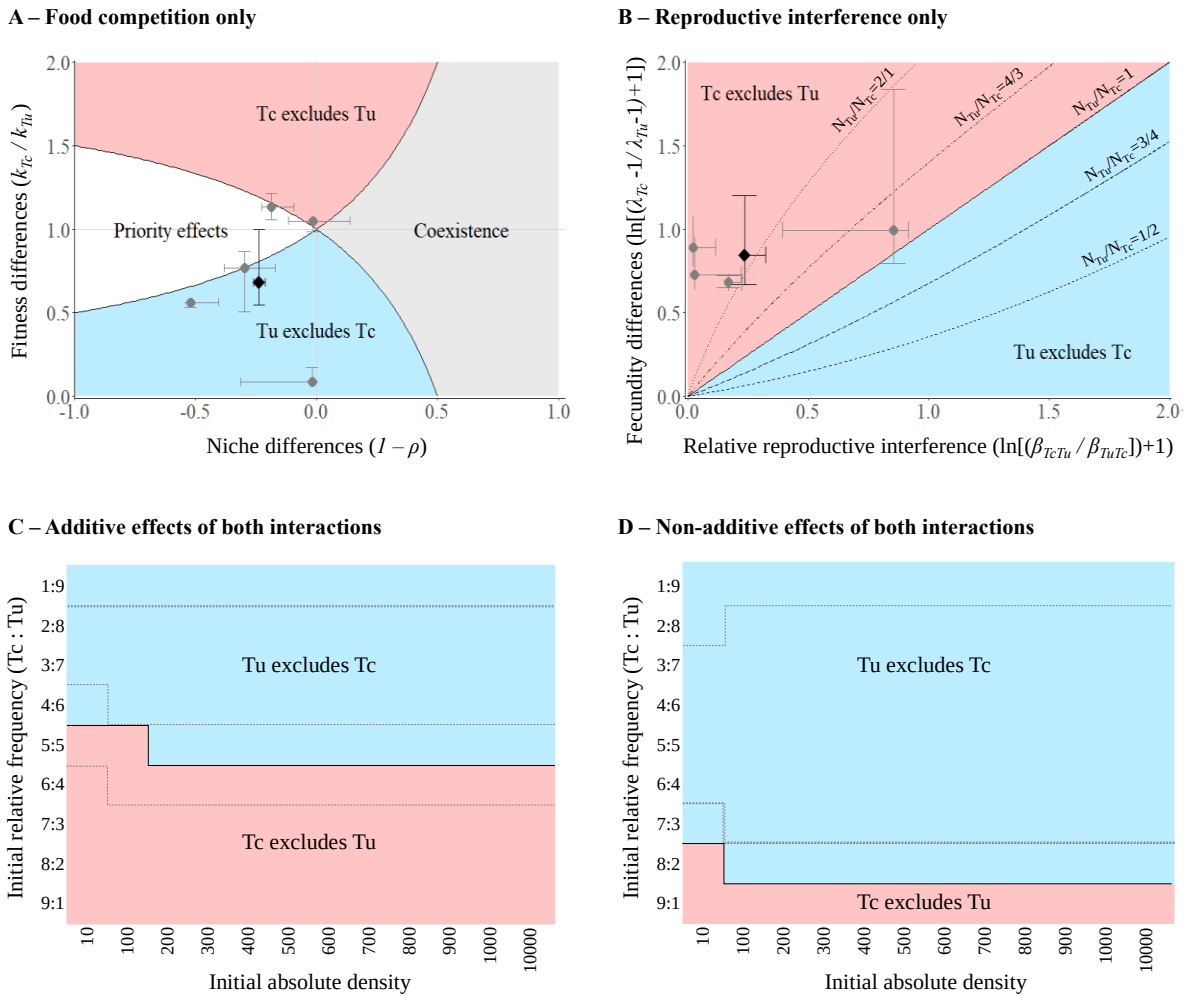

Figure 3. The non-additive effects of food competition and reproductive interference change the predicted competitive outcomes. (A) Predicted outcomes depending on the niche and fitness differences between species when populations only compete for food. The two solid black lines define the space in which species can coexist (grey area) or enter alternative stable states (priority effects; white area). Otherwise, the species with higher fitness will exclude the other. (B) Predicted outcomes depending on the relative strength of reproductive interference and fecundity differences when populations only interact during reproduction. 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). (C) and (D) Predicted outcomes for different initial absolute densities and relative frequencies of the two species when both types of competition have 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. In all panels (but only for equal initial frequency of the two species in panel B, and for all data in panels C and D), the red area defines the space in which *T. cinnabarinus* (Tc) excludes *T. urticae* (Tu), and the blue area defines the space in which Tu excludes Tc. In (A) and (B), grey circles and black diamonds are means (± 95% confidence intervals) for each replicate population and for all data, respectively. In (C) and (D), dashed grey lines and solid black lines delimit the space in which each species excludes the other, using parameters estimated with each replicate population and with all data, respectively (but note that negative parameter values and confidence intervals are not displayed).

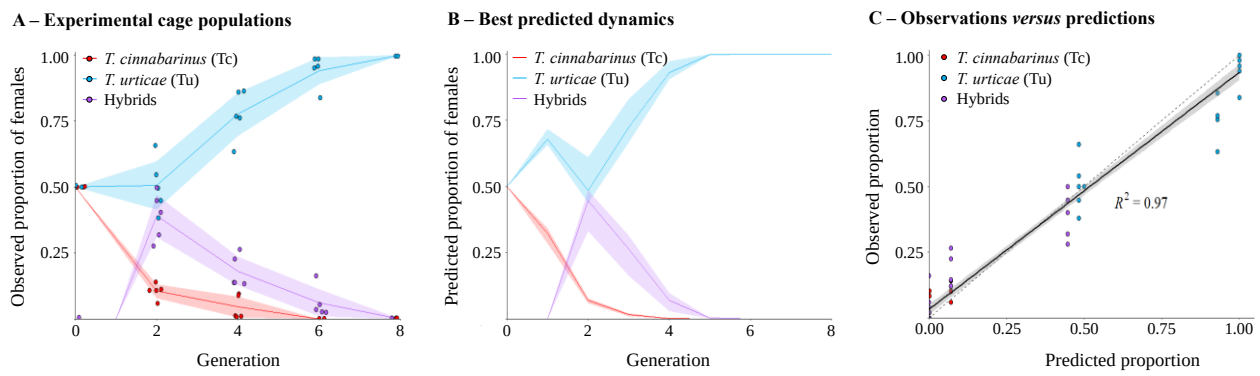

Figure 4. The model predictions accurately fit the dynamics observed in cage populations. (A) Observed proportions of *Tetranychus urticae* (Tu), *T. cinnabarinus* (Tc), and hybrid females in experimental cage populations over 8 generations. Dots show the observed proportions in each replicate population, 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 across all replicate populations), and hybrid females 15 times less affected by food competition than purebred females. Coloured lines and shaded areas show predicted proportions and associated upper and lower limits that could be obtained given all possible combinations between the 95% confidence intervals of each parameter of the model. (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.

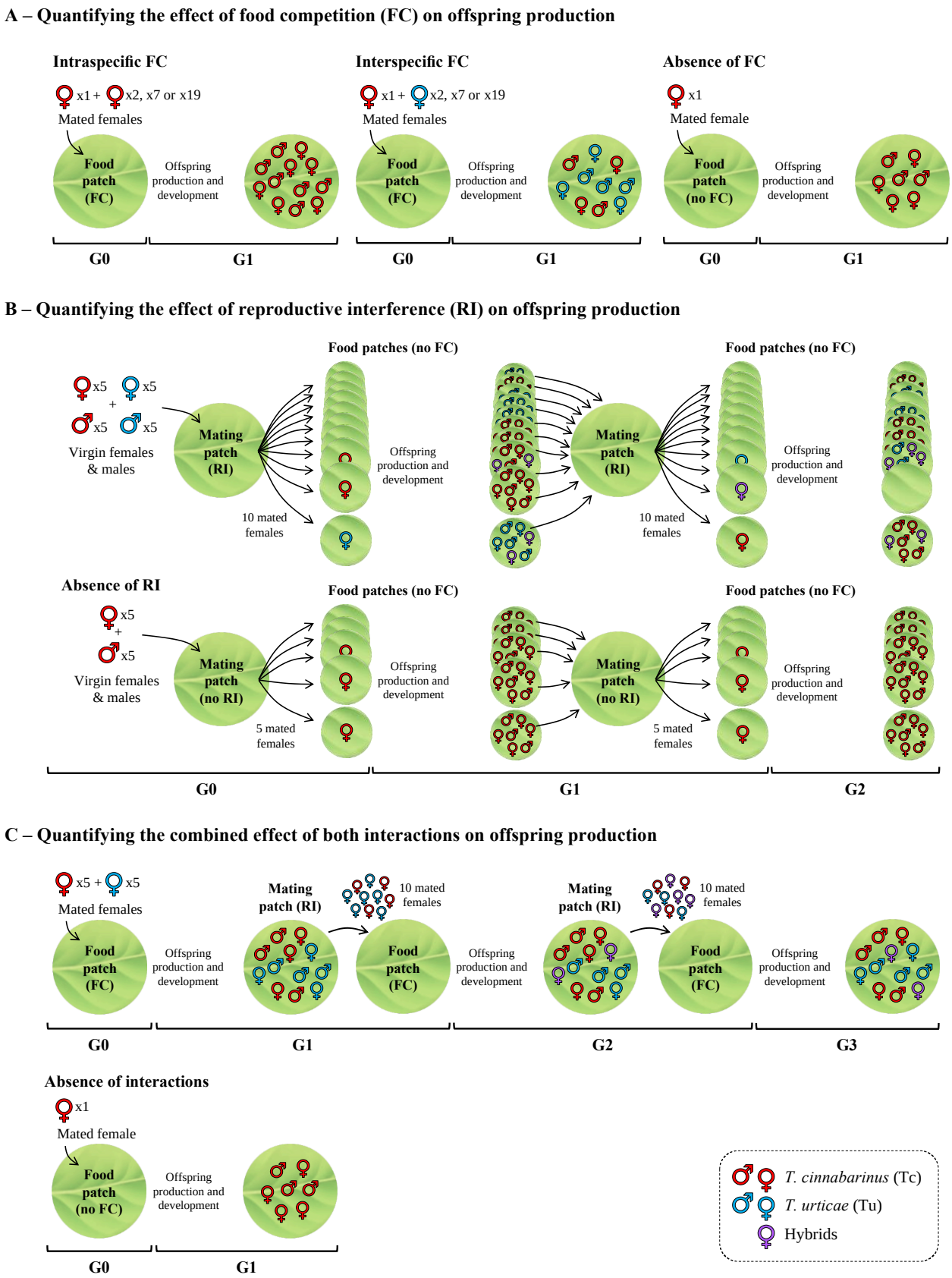

Figure 5. Experimental procedures used to quantify the effects of food competition and/or reproductive interference on offspring production. (A) Food competition in absence of reproductive interference was measured by placing females mated with conspecific males on food patches where their juveniles 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: *T. cinnabarinus* (Tc) females; Blue: *T. urticae* (Tu) females; Purple: hybrid females.

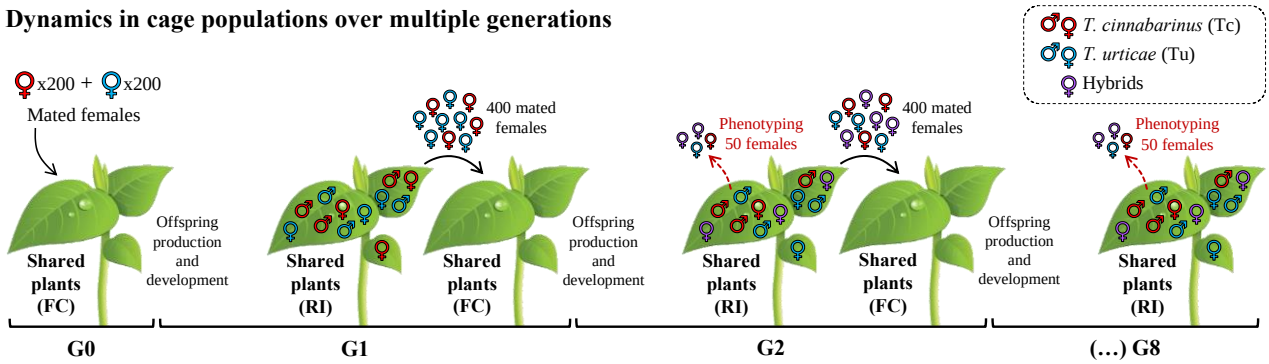

Figure 6. Experimental procedure used to follow the dynamics of both species and their hybrids in cage populations. Common plants were used for the entire life cycle of individuals of both species. This procedure enabled food competition between females and developing juveniles, as well as reproductive 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: *T. cinnabarinus* (Tc) females; Blue: *T. urticae* (Tu) females; Purple: hybrid females.