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Meta-analysis reveals intraspecific variation for plant-mediated interactions in herbivores

SUMMARY

- **Plant-mediated interactions** among herbivores are important drivers of community dynamics, but we lack insight into variation among herbivores for these interactions.
- A meta-analysis of datasets investigating plant-mediated interactions between herbivorous *Tetranychus urticae* and *Tetranychus evansi* spider mites infesting *Solanum lycopersicum* tomato plants showed that *T. urticae* had negative effects on the performance of other spider mite populations, whereas *T. evansi* affected them positively.
- In both interactions effect sizes varied strongly, with 18 - 29% variation explained by the time populations had been cultured. Longer lab culturing produced smaller effect sizes.

INTRODUCTION

WHEN HERBIVORES attack a plant, they induce changes in plant traits, which affect other herbivores on the same plant. Such '**plant-mediated interactions**' among herbivores are important drivers of community dynamics (Stam *et al.* 2014).

SELECTION among herbivore populations can produce intraspecific variation for plant-mediated interactions with other herbivores. However, few studies assess this variability, which is what we did here, using plant-mediated interactions between two spider mite species on tomato host plants. We ask:

- I to what extent do the spider mites *Tetranychus evansi* and *Tetranychus urticae* affect the performance of other spider mites through plant-mediated effects?
- II what factors contribute to variation in the strength of the interaction?

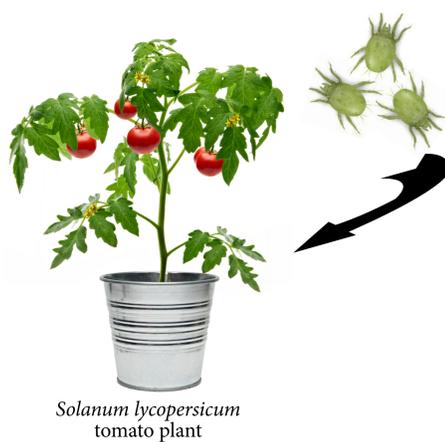
STUDY SYSTEM & EXPERIMENTS



T. urticae (left) and *T. evansi* (right) adult females

SPIDER MITES are arthropod herbivores that feed on plant parenchyma cell content. The two-spotted spider mite *Tetranychus urticae* generally induces a defense response in tomato (Kant *et al.* 2004, Martel *et al.* 2015), whereas the tomato red spider mite *Tetranychus evansi* suppresses the tomato defense response (Sarmiento *et al.* 2011, Alba *et al.* 2015).

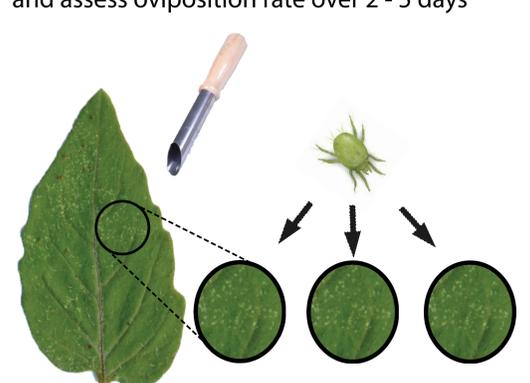
Step 1: infest with *T. evansi*, *T. urticae* or no mites for 2 - 7 days



Step 2: remove mites, eggs and web with a fine brush



Step 3: cut leaf discs from damaged tissue, place new adult females on each leaf disc individually, and assess oviposition rate over 2 - 5 days



MATERIALS & METHODS

WE FOUND 38 datasets where intact tomato plants were infested with either *T. evansi* or *T. urticae* (Step 1), and oviposition rates of other *T. evansi* or *T. urticae* populations were measured on the same leaflet (Step 3). For each dataset we calculated the standardized mean difference in oviposition rates per plant of adult females between:

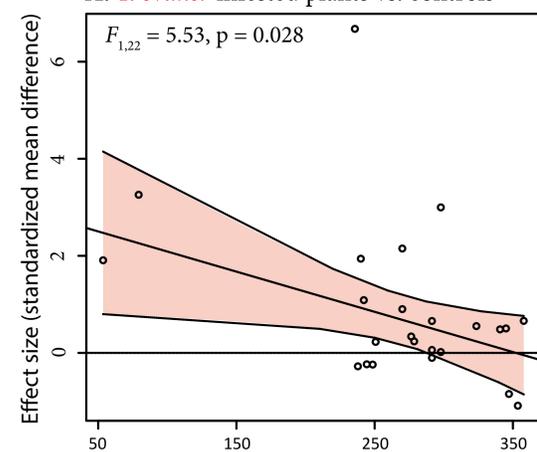
A. *T. evansi*-infested plants and clean control plants

B. *T. urticae*-infested plants and clean control plants

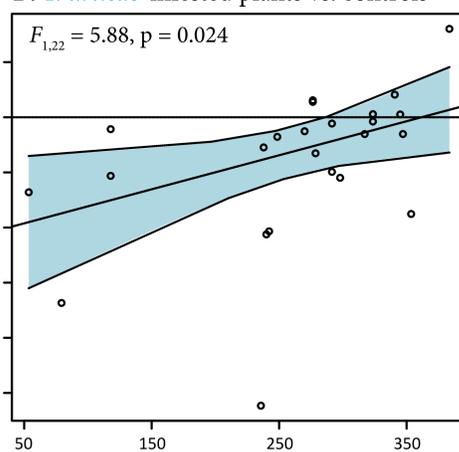
We used these effect sizes (std mean difference) as input for random-effects meta-analysis.

- II Effect size decreased as populations had been cultured in the lab for longer periods, explaining 18 - 29% of the variation among datasets. The remaining variation was not explained.

A. *T. evansi*-infested plants vs. controls



B. *T. urticae*-infested plants vs. controls



Solid lines indicate model predictions, shaded areas delineate 95% confidence intervals, and circles indicate observed effect size estimates.

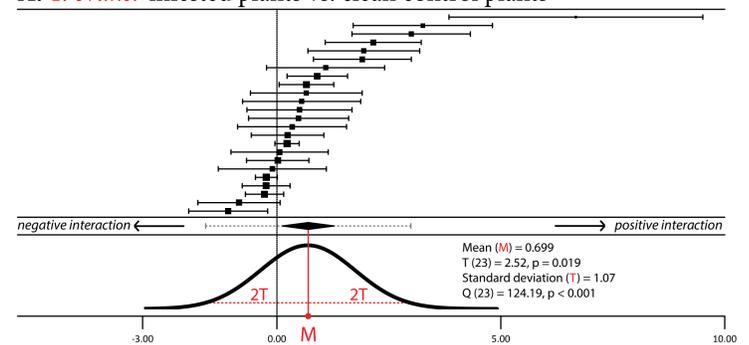
DISCUSSION

- The reduction in effect size over time can be explained by loss of function due to selection against plant defense induction and suppression in lab cultures, or due to mutation accumulation as a result of random genetic processes.
- This case of 'inadvertent selection' in lab cultures demonstrates intraspecific variation in herbivores for plant-mediated effects on other herbivores, and suggests a change in heritable variation for these interactions over time.

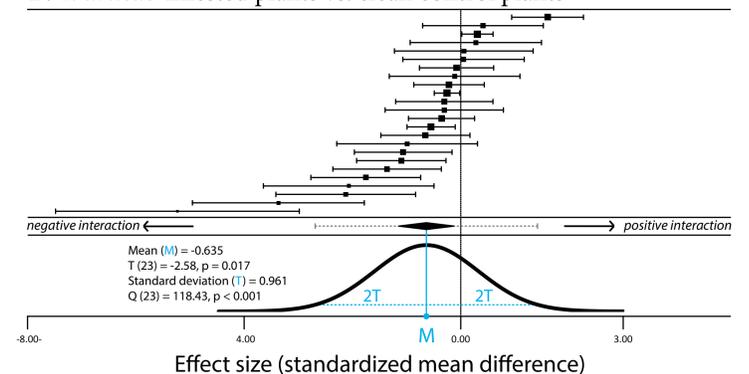
RESULTS

- I *T. evansi* had positive effects on the performance of other mites, and *T. urticae* affected them negatively. Both interactions showed strong variability.

A. *T. evansi*-infested plants vs. clean control plants



B. *T. urticae*-infested plants vs. clean control plants



Effect sizes are indicated by filled squares, and error bars represent their 95% confidence intervals. The estimated summary effect is represented by a diamond, of which the vertical extremes indicate the summary effect size and the horizontal extremes the 95% confidence interval. The error bars next to the diamond indicate the 95% prediction interval.

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