

Competitive exclusion of a worldwide invasive pest by a native. Quantifying competition between two phytophagous insects on two host plant species

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Summary

1. High competitive ability is believed to be an important characteristic of invasive species. Many animal studies have compared the competitive ability of invasive species with a native species that is being displaced, but few have looked at systems where an invasive species has failed to establish itself. These types of studies are important to determine if competition is relevant not only to invading species but also to the biotic resistance of a community.

2. The thrips species *F. occidentalis* is a highly invasive pest that has spread from its original range (the western states of the USA) to a worldwide distribution. Despite this, *F. occidentalis* is largely absent or occurs in low numbers in the eastern states of the USA, where the native *F. tritici* dominates. It is possible that *F. tritici* is competitively excluding *F. occidentalis* from this region.

3. Larval competition between these two thrips species was tested on two known plant hosts, *Capsicum annuum* (a crop plant), and *Raphanus raphanistrum* (an invasive weed), using a response surface design with number of larvae surviving as the response variable. The response surface design allowed competition models to be fit to data using maximum likelihood estimation, thus generating quantitative values for interspecific competition.

4. On both plant hosts, the native *F. tritici* did not experience significant interspecific competition from the invasive *F. occidentalis*. In contrast, *F. occidentalis* did experience significant interspecific competition from *F. tritici*. Competition from *F. tritici* larvae on *F. occidentalis* larvae was estimated to be 1.72 times (on *C. annuum*) and 1.76 times (on *R. raphanistrum*) the effect of intraspecific competition. The invasive *F. occidentalis* appears to be competitively excluded by the native *F. tritici*.

5. This study confirms the importance of competition in the biotic resistance of a community and is one of the few animal studies to not only test for competition in an apparently resistant ecosystem but also to quantify the level of interspecific competition between two animal species.

Key-words: competition coefficients, competitive asymmetry, competitive displacement, invasion, model fitting.

Introduction

Invading species exact both an ecological price, by the reduction in local biodiversity, and an economic price, by damage to cropping systems (Vitousek *et al.* 1996). Understanding the factors that influence a species' ability to invade is important for the prediction of future invasions and the management of present ones. One characteristic often cited as essential to the success of an invasive species is superior competitive ability (Sakai *et al.* 2001; Vila & Weiner 2004), and many researchers have demonstrated that an invading

organism is competitively superior by comparing the competitive abilities of an invasive species with those of a native species that is being displaced (e.g. Porter, Van Eimeren & Gilbert 1988; Elliott, Kieckhefer & Kauffman 1996; Levine, Adler & Yelenik 2004; Paini & Roberts 2005). However, the importance of competition in determining whether a species has the ability to invade an ecosystem is still in doubt with some researchers suggesting demographic parameters (Lodge 1993; Rejmanek & Richardson 1996), or the number and size of introductions (Kolar & Lodge 2001) being more important. Examining systems in which a species has successfully invaded presents only part of the picture. Systems in which a species has failed to invade successfully (Kolar & Lodge 2001), particularly

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those systems in which a known invasive has failed to establish despite repeated introductions is also important. Animal studies taking this approach are rare (though see O'Connor 1986; Baltz & Moyle 1993; Lounibos *et al.* 2003) yet essential as they provide an alternative test for the importance of competition for invading species and the biotic resistance of an ecosystem to invasion.

Frankliniella occidentalis (Pergande) is native to western North America and has, in the last 30 years, become a worldwide invasive pest (Kirk 2002). This species has become the dominant phytophagous thrips in many of the regions it has invaded such as Japan (Morishita 2005), Spain (Lacasa *et al.* 1995), Turkey (Atakan & Uygur 2005) and Argentina (de Borbon, Gracia & Piccolo 2006). In European greenhouses, *F. occidentalis* has replaced *Thrips tabaci* as the major thrips pest, and van Rijn, Mollena & Steehuis-Broers (1995) suggested that *F. occidentalis* is a superior competitor after finding no difference between the two species in the intrinsic rate of increase, net reproductive time, or development times. More recently, Northfield (2005) showed that *F. occidentalis* is competitively superior to *F. bispinosa*, a common thrips species of southern Florida, and argued that the greater competitive ability of *F. occidentalis* could explain its invasiveness.

Frankliniella tritici (Fitch) is native to the eastern states of the USA, where *F. occidentalis* occurs at low densities (Salguero Navas *et al.* 1991; Eckel *et al.* 1995; Felland *et al.* 1995; Reitz *et al.* 2002, 2003; Pains, unpublished data) despite multiple introductions since the 1970s (Kirk & Terry 2003). As the distribution of these two species shows an east–west trend and covers a range of climates, interspecific competition seems a likely explanation (Kirk 2002) with the native *F. tritici* competitively excluding the invasive *F. occidentalis*.

Adult thrips of these two species are winged and highly vagile (Mound & Teulon 1995), and could therefore mediate competition by utilizing different plant hosts. Larvae are wingless and less mobile than adults, being limited to a particular plant or neighbouring plants. In addition, both these species are predominantly found in the flowers of host plants (Chellemi, Funderburk & Hall 1994; Hansen *et al.* 2003) and the use of such patchy, ephemeral resources may intensify competition between these two species. We therefore tested for larval competition between *F. occidentalis* and *F. tritici* using the number of larvae surviving as the response variable in a response surface design, which varies both the total density and the densities of the two competing species. This design allows competition models to be fit to the data using maximum likelihood estimation, thereby obtaining quantitative estimates of the overall value for the intensity of competition.

Competition has been shown to vary with resources for some insect assemblages (Arthur 1980a,b; Krebs, Barker & Armstrong 1992). Both *F. occidentalis* and *F. tritici* are able to reproduce on a range of host plants, which can vary in their suitability for thrips reproduction. Variation among host plants could mediate the intensity of competition between these species, and larval competition was therefore tested on two reproductive host plants, a crop host (*Capsicum annuum*) and a noncrop host (*Raphanus raphanistrum*).

Materials and methods

Both *F. occidentalis* and *F. tritici* are predominantly found in the flowers of host plants (Chellemi *et al.* 1994; Hansen *et al.* 2003). Experiments were therefore conducted using the flowers of host plant species, *R. raphanistrum* and *C. annuum* (X3R Camelot variety). All plants were grown from seeds in a greenhouse under ambient photoperiod conditions and between 18 and 23 °C. Mature flowers were cut and each was immediately transferred into a 1.5 mL centrifuge tube filled with water. Cages were constructed with the base of two Petri dishes (8.7 cm diameter) placed together and sealed with Vaseline with a screen-covered hole (4 cm diameter) in the upper lid. Trials lasted 8 days to enable larvae to develop until at least the propupa stage, at which time they cease to feed until eclosion to adult.

Larvae of *F. occidentalis* and *F. tritici* were obtained from lab colonies maintained at 24 °C and a light : dark 16 : 8 h photoperiod. At the start of a trial, a flower of either *R. raphanistrum* or *C. annuum* was placed into a cage, and first instar larvae of *F. occidentalis* and *F. tritici* were placed on to the floor of the cage. Because of flower senescence it is not possible for larvae to complete their development in one flower of either *R. raphanistrum* or *C. annuum* and larvae on these plants will disperse from a dead or dying flower to a fresh one (Pains, personal observation). This was simulated in the experiments by adding fresh flowers at regular intervals during the trial to enable larvae to disperse to them and complete development. For *R. raphanistrum* a fresh flower was added every 3 days and for *C. annuum* a fresh flower was added after 4 days.

On *R. raphanistrum* there were four densities of *F. occidentalis* and *F. tritici* larvae used (0, 10, 20 and 30 larvae). Very few published papers have recorded the natural densities of thrips larvae on this host plant. Further, these papers do not give sufficient information to determine mean or maximum larval densities (Chellemi *et al.* 1994; Buntin & Beshear 1995; Cho *et al.* 1995). However, in north Florida larval densities can be as many as 40 per flower (Reitz, unpublished data). These densities were therefore chosen so as to cover the range of densities that could occur on this plant host. Every density of *F. occidentalis* was combined with every *F. tritici* density to give a fully factorial experiment with 15 treatments. All 15 treatments were run simultaneously and repeated four times. A fifth repetition was also completed but did not include all treatments due to a shortage of *F. tritici* larvae in colonies.

On *C. annuum*, the same array of densities was used with the addition of two extra treatments. One treatment had 60 *F. occidentalis* first instar larvae with no *F. tritici* larvae, while the second extra treatment had 60 *F. tritici* first instar larvae with no *F. occidentalis* larvae. These densities were chosen as mean densities of up to 40 larvae per flower have been reported in *C. annuum* (Funderburk, Stavisky & Olson 2000) with maximum densities up to 52 larvae per flower (Funderburk, unpublished data). Each treatment was repeated between five and eight times. Experiments were conducted at 22 °C, and with a light : dark 16 : 8 h photoperiod.

At the conclusion of the experiment, flowers were destructively searched for pupae. It is not possible to distinguish between *F. occidentalis* and *F. tritici* at the pupal stage and so these pupae were placed into separate 1.5 mL centrifuge tubes until eclosion to adult. After eclosion, the species was identified under dissection microscope.

DATA ANALYSIS

Because larval survival is a dichotomous response (a larva either survived or did not), data were initially analysed by multiple logistic

Table 1. Results of multiple logistic regressions to determine if larval survival of the two thrips species were dependent on intraspecific (Intra) and interspecific (Inter) competition

Focal species	Host plant species	Variable	d.f.	Parameter estimate (95% confidence intervals)	SE	Wald χ^2	<i>P</i>
<i>F. occidentalis</i>	<i>R. raphanistrum</i>	Intercept	1	-0.049 (-0.47, 0.37)	0.22	0.051	0.41
		<i>F. occidentalis</i> (Intra)	1	0.011 (-0.0050, 0.027)	0.0083	1.81	0.09
		<i>F. tritici</i> (Inter)	1	-0.023 (-0.034, -0.012)	0.0056	16.80	< 0.0001
<i>F. occidentalis</i>	<i>C. annuum</i>	Intercept	1	0.67 (0.42, 0.93)	0.13	26.84	< 0.0001
		<i>F. occidentalis</i> (Intra)	1	-0.010 (-0.016, -0.0043)	0.0029	11.70	0.0003
		<i>F. tritici</i> (Inter)	1	-0.017 (-0.025, -0.0089)	0.0040	17.08	< 0.0001
<i>F. tritici</i>	<i>R. raphanistrum</i>	Intercept	1	0.39 (-0.021, 0.81)	0.21	3.45	0.016
		<i>F. occidentalis</i> (Inter)	1	-0.0047 (-0.016, -0.0062)	0.0056	0.71	0.20
		<i>F. tritici</i> (Intra)	1	-0.014 (-0.030, 0.0022)	0.0082	2.85	0.046
<i>F. tritici</i>	<i>C. annuum</i>	Intercept	1	0.12 (-0.16, 0.40)	0.14	0.73	0.20
		<i>F. occidentalis</i> (Inter)	1	-0.0050 (-0.013, 0.0034)	0.0043	1.38	0.12
		<i>F. tritici</i> (Intra)	1	-0.0086 (-0.015, -0.0021)	0.0033	6.80	0.0046

Table 2. Maximum likelihood estimates of competition model parameters for *F. occidentalis* and *F. tritici* on two host plant species. The focal species is the species experiencing the competition. Although β for *F. occidentalis* has been estimated as a negative value on *R. raphanistrum*, because c is also negative, β is effectively positive and so are its confidence intervals

Focal species	Host plant species	Parameter estimates (95% confidence intervals)		
		λ	c	β
<i>F. occidentalis</i>	<i>R. raphanistrum</i>	0.47 (0.43, 0.51)	-0.0070 (-0.010, -0.0028)	-1.76 (-2.78, -0.95)
<i>F. occidentalis</i>	<i>C. annuum</i>	0.70 (0.66, 0.74)	0.0060 (0.0047, 0.0075)	1.72 (1.00, 2.57)
<i>F. tritici</i>	<i>R. raphanistrum</i>	0.63 (0.57, 0.68)	0.0087 (0.0052, 0.013)	0.43 (-0.21, 1.24)
<i>F. tritici</i>	<i>C. annuum</i>	0.56 (0.53, 0.60)	0.0069 (0.0048, 0.0094)	0.60 (-0.048, 1.38)

regression to determine if larval survival was dependent on conspecific larval density (intraspecific competition) and/or heterospecific larval density (interspecific competition). Analyses were conducted for each focal thrips species on each host plant. The hypotheses tested were that the probability of larval survival would decrease with increasing density, and therefore one-tailed tests were employed to determine the significance of parameter estimates. In keeping with the experimental design, the independent variables for initial densities of each thrips species were retained in the final regression models. The inclusion of interaction terms between *F. occidentalis* and *F. tritici* densities did not improve the fit of any of the four models and therefore were not retained in the final models.

Maximum likelihood estimation assuming a binomial probability distribution was then used to test five competition models (Table S1) against the data (numbers of larvae surviving) to determine which would best fit the data. Using Akaike's Information Criterion (Burnham & Anderson 1998) (Appendix S1), the most parsimonious model was:

$$\text{Species } X \text{ larval survival} = \frac{\lambda}{1 + c(X + \beta Y)} \quad (\text{Law \& Watkinson 1987})$$

where λ is larval survival of the focal species at low intraspecific densities, c is a parameter that affects the responses to competition but does not have a clear biological meaning (Inouye 2001), and β is the effect of species Y on the focal species X (interspecific competition coefficient). This interspecific competition coefficient is relative to intraspecific competition, which is set at 1. If the 95% confidence intervals of β are greater than 0 then interspecific competition is

present. If the confidence intervals are greater than 1, interspecific competition is significantly greater than intraspecific competition and species Y would be a superior competitor to species X . Maximum likelihood estimation was used to estimate the parameters, and the χ^2 approximation for the likelihood ratio test (Edwards 1992) was used to estimate the 95% confidence intervals with all other parameters fixed at their maximum likelihood values. Likelihood ratio tests were also used to estimate the probability values when testing if the competition coefficients were significantly greater than 0 or 1 (one-tailed hypothesis). SAS version 8.01 (SAS Institute 2001) was used for the multiple logistic regression analysis and R software (R Development Core Team 2005) was used for the model fitting.

Results

The logistic regressions showed that *F. occidentalis* larval survival was significantly reduced by interspecific competition from *F. tritici* on both *R. raphanistrum* and *C. annuum*, while intraspecific competition was only significant on *C. annuum* (Table 1). On both host plant species, *F. tritici* larval survival was significantly reduced by intraspecific competition, but not by interspecific competition from *F. occidentalis* (Table 1).

Fitting the competition model to the data revealed no significant difference in the model estimates of larval survival at low densities (λ) for *F. tritici* on the plant host species (Table 2). However, there was a reversal in the rankings when comparing the two thrips species on the two host plant species. On *C. annuum*, larval survival at low densities (λ) for

F. occidentalis was significantly higher than for *F. tritici*, while on *R. raphanistrum*, it was significantly lower than for *F. tritici*.

On *R. raphanistrum*, the interspecific competition coefficient (β) value for *F. occidentalis* was negative (Table 2). However, the c parameter was also negative, so the value of β was effectively positive and is subsequently referred to as a positive. On *R. raphanistrum* and *C. annuum* the interspecific competition coefficients (β) for *F. occidentalis* were 1.76 and 1.72, respectively. These values indicate that the effect of interspecific competition from *F. tritici* larvae on *F. occidentalis* larval survival is 1.76 and 1.72 times the effect of intraspecific competition. The 95% confidence intervals for both these values did not encompass 0 and *F. occidentalis* larvae were therefore experiencing significant interspecific competition from *F. tritici* larvae on both *R. raphanistrum* ($P < 0.00001$) and *C. annuum* ($P < 0.00001$).

These interspecific competition coefficients also indicate if the competing species is competitively superior to the focal species. For *F. occidentalis* as the focal species on *C. annuum*, the competition coefficient was significantly greater than 1 ($P = 0.05$), and so *F. tritici* was competitively superior to *F. occidentalis*. On *R. raphanistrum*, the competition coefficient was not significantly greater than 1 ($P = 0.07$).

The interspecific competition coefficients (β) for *F. occidentalis* as a competitor of *F. tritici* on *R. raphanistrum* and *C. annuum* were 0.43 and 0.60, respectively. The 95% confidence intervals for both these values encompassed 0 (Table 2), and *F. tritici* larvae were therefore not experiencing interspecific competition from *F. occidentalis* larvae on either of these two host plant species.

Discussion

There has been significant historical debate regarding the factors affecting thrips population growth. Davidson & Andrewartha (1948a,b) first suggested that populations of *Thrips imaginis* were density independent. While various authors have since argued both for and against density-dependent regulation of thrips populations (for a summary see Funderburk *et al.* 2000), it is now largely accepted that predation is a significant density-dependent factor in thrips populations. In addition, competitive interactions have also been speculated to occur among thrips species, and in particular, that interspecific competition may be a factor in the distinct ranges of *F. occidentalis* and *F. tritici* (van Rijn *et al.* 1995; Kirk & Terry 2003; Deligeorgidis *et al.* 2006). This question, however, of thrips competition, has rarely been empirically tested (though see Northfield 2005). Interspecific competition on two different host resources was therefore tested to determine, first, if interspecific competition was occurring and, secondly, if it could be altered by the plant host resource.

The multiple logistic regressions and the parameter estimates generated from the competition model indicated that on both host plants, the invasive *F. occidentalis* experienced significant interspecific competition from the native *F. tritici*, while *F. tritici* did not experience interspecific competition

from *F. occidentalis*. The competition model generates a value for interspecific competition relative to intraspecific competition, which is set at 1, with the assumption that intraspecific competition is present. The multiple regression analyses confirmed that intraspecific competition occurred within *F. occidentalis* on *C. annuum*, though not on *R. raphanistrum*. While the coefficient value generated on *C. annuum* (1.72) is therefore reliable, the value on *R. raphanistrum*, though a similar quantity (1.76), may not be. Despite this, the logistic regression clearly showed that on *R. raphanistrum*, as well as *C. annuum*, *F. occidentalis* was experiencing significant interspecific competition from *F. tritici*.

The competition model also indicated that *F. tritici* was competitively superior to *F. occidentalis* on *C. annuum*. Although the competition model indicated that *F. tritici* was not competitively superior on *R. raphanistrum*, the P -value was marginal ($P = 0.07$), and the logistic regression analysis confirmed that *F. tritici* is superior as the confidence intervals for the *F. occidentalis* and *F. tritici* coefficients did not overlap and were therefore significantly different (Table 1). Finally, there was no evidence of altered interspecific competition by the host, as the interspecific competition coefficients for these two host plants were similar and their confidence intervals overlapped. In addition, the confidence intervals generated from the regression analyses also showed that the *F. tritici* variables were not significantly different on the two host plant species.

Because the invasive species *F. occidentalis* was an inferior competitor to the native *F. tritici* on both the cultivated and uncultivated host plants tested, this competitive asymmetry may be leading to the exclusion of *F. occidentalis* from the eastern states of the USA where *F. tritici* is endemic. Although the superior competitive ability of *F. tritici* confers a degree of biotic resistance in agricultural and uncultivated ecosystems to invasion by *F. occidentalis*, there is little evidence that biotic resistance alone can cause the complete repulsion of an invader (Levine *et al.* 2004), and it is therefore not surprising that *F. occidentalis* is still present in this community, though at low densities.

These two thrips species utilize a large range of reproductive host species (Paini, unpublished data) and phytophagous insects will forage and oviposit on inferior host plants if the effects of predation (Gotthard *et al.* 2005), parasitism (Singer *et al.* 2004) or competition (Ekbom 1998) are reduced. However, in the southern end of *F. tritici*'s range, there is considerable overlap in the reproductive host ranges of these species with *F. tritici* having a broader host range than *F. occidentalis* (Paini, unpublished data). This apparent inability of *F. occidentalis* to avoid competition from *F. tritici* by exploiting alternative hosts may explain the low densities of this invasive species within the geographical range of *F. tritici*.

The likely mechanism of competition between the two species was interference rather than exploitative competition. Thrips feed in the flowers by piercing and sucking plant tissue as well as pollen grains, and it did not appear that either of these resources was significantly depleted at the conclusion of our trials. Thrips are thigmotactic (Kirk 1997), preferring the small crevices found in flowers probably for the protection

they provide from predators and also the more favourable microclimate. It is possible that *F. tritici* displaced *F. occidentalis* from these areas thereby decreasing *F. occidentalis* survival, but thrips behaviour during the trials was not observed and so this cannot be confirmed.

Considering that *F. occidentalis* is a highly invasive and competitive pest, which has spread to all continents except Antarctica (Kirk & Terry 2003), it is somewhat surprising that it is an inferior competitor to *F. tritici*. However, there are other factors that can lead to an organism being a successful invader, including high intrinsic growth rate, rapid development, good dispersal mechanisms (either natural or human), multiple introductions, and release from predators or parasites (Sakai *et al.* 2001). Some of these factors are believed to have contributed to the successful invasion of *F. occidentalis* throughout the world (Kirk & Terry 2003; Morse & Hoddle 2006). While high intrinsic growth rate and rapid development clearly contribute significantly to the success of this insect, the factor that has probably contributed the greatest to its success is its dispersal via infected plant material transported around the world (Kirk & Terry 2003).

These factors, however, may not be operating in the eastern USA where *F. tritici* is present. For example, *F. occidentalis* does not have an intrinsic reproductive advantage over *F. tritici* (Reitz *et al.* 2002) and *F. occidentalis* is not released from natural enemies in the eastern USA (Funderburk *et al.* 2000).

Given its broad reproductive host range and its superior competitive ability, *F. tritici* has the potential to also be invasive. Why it has not remains unclear, but *F. occidentalis* has been spread mainly via the infestation and passive transportation of plant material, and this may not as yet have occurred in *F. tritici*. In addition, plant material is typically treated with pesticides before shipment, and *F. occidentalis* has shown rapid development of resistance to many insecticides (Immaraju *et al.* 1992; Broadbent & Pree 1997), while such resistance has not been reported in *F. tritici*.

Survival at low densities (λ) for *F. tritici* was not different between *C. annuum* and *R. raphanistrum*. In contrast, survival of *F. occidentalis* at low densities was significantly higher on *C. annuum* than on *R. raphanistrum*. Adult *F. occidentalis* will respond to plant defensive compounds produced by *R. raphanistrum* by altering feeding behaviour (Agrawal, Kobayashi & Thaler 1999) and *F. occidentalis* larval survival may also be affected by these defensive compounds, as this has been shown with other insects (Inbar *et al.* 1999; Zalucki, Brower & Alonso 2001). Crop plants, such as *C. annuum* are bred for yield, with resistance to insect attack a lower priority (Brown 2002), thereby reducing defensive compounds in breeding lines. *Frankliniella occidentalis* may have a higher larval survival rate on crop plants with low amounts of defensive chemicals. This intolerance to defensive compounds could also influence the competitive interactions between *F. tritici* and *F. occidentalis*, accentuating the competitive superiority of *F. tritici* on those host plants that employ defensive mechanisms.

Using a response surface design and fitting a competition model allowed us to generate competition coefficients and

quantify the levels of competition between larvae of these two thrips species. Of the hundreds of animal competition studies published to date, few have attempted to estimate competition coefficients (though see Park 1948; Shorrocks *et al.* 1984; Inouye 1999; Northfield 2005). The need for large numbers of density combinations in a response surface design (Goldberg & Scheiner 2001) and the more complicated analysis necessary for analysing data may explain the lack of studies (Inouye 2001). Despite this, researchers should be encouraged to pursue this methodology as studies such as this not only make an important link between empirical and theoretical work (Damgaard 1998), they also provide a quantitative estimate of competition rather than the qualitative conclusions (presence or absence of competition) drawn from additive and substitutive designs (Inouye 2001).

The results reported here provide evidence that the native *F. tritici* is competitively superior to the invasive *F. occidentalis* and may be causing the competitive exclusion of *F. occidentalis* from the range of *F. tritici*. Many researchers have attempted to determine the reasons certain pests are able to invade an ecosystem and what gives an ecosystem biotic resistance. While demographic parameters and propagule pressure are no doubt of importance, in this system it appears the factor of significant influence is that of competitive ability.

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References

- Agrawal, A.A., Kobayashi, C. & Thaler, J.S. (1999) Influence of prey availability and induced host-plant resistance on omnivory by western flower thrips. *Ecology*, **80**, 518–523.
- Arthur, W. (1980a) Interspecific competition in *Drosophila* I. Reversal of competitive superiority due to varying concentration of ethanol. *Biological Journal of the Linnean Society*, **13**, 109–118.
- Arthur, W. (1980b) Interspecific competition in *Drosophila* II. Competitive outcome in some 2-resource environments. *Biological Journal of the Linnean Society*, **13**, 119–128.
- Atakan, E. & Uygur, S. (2005) Winter and spring abundance of *Frankliniella* spp. & *Thrips tabaci* Lindeman (Thysan., Thripidae) on weed host plants in Turkey. *Journal of Applied Entomology*, **129**, 17–26.
- Baltz, D.M. & Moyle, P.B. (1993) Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications*, **3**, 246–255.
- de Borbon, C.M., Gracia, O. & Piccolo, R. (2006) Relationship between tospovirus incidence and thrips populations on tomato in Mendoza, Argentina. *Journal of Phytopathology*, **154**, 93–99.
- Broadbent, A.B. & Pree, D.J. (1997) Resistance to insecticides in populations of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) from greenhouses in the Niagara region of Ontario. *Canadian Entomologist*, **129**, 907–913.
- Brown, J.K.M. (2002) Yield penalties of disease resistance in crops. *Current Opinion in Plant Biology*, **5**, 339–344.
- Buntin, G.D. & Beshear, R.J. (1995) Seasonal abundance of thrips (Thysanoptera) on winter small grains in Georgia. *Environmental Entomology*, **24**, 1216–1223.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference. A Practical Information-Theoretic Approach*. Springer, New York.
- Chellemi, D.O., Funderburk, J.E. & Hall, D.W. (1994) Seasonal abundance of flower-inhabiting *Frankliniella* species (Thysanoptera: Thripidae) in wild plant species. *Population Ecology*, **23**, 335–342.

- Cho, K.J., Eckel, C.S., Walgenbach, J.F. & Kennedy, G.G. (1995) Overwintering of thrips (Thysanoptera: Thripidae) in North Carolina. *Environmental Entomology*, **24**, 58–67.
- Damgaard, C. (1998) Plant competition experiments: testing hypotheses and estimating the probability of coexistence. *Ecology*, **79**, 1760–1767.
- Davidson, J. & Andrewartha, H.G. (1948a) Annual trends in a natural population of *Thrips imaginis* (Thysanoptera). *Journal of Animal Ecology*, **17**, 193–199.
- Davidson, J. & Andrewartha, H.G. (1948b) The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). *Journal of Animal Ecology*, **17**, 200–222.
- Deligeorgidis, P.N., Ipsilandis, C.G., Kaltsoudas, G., Giakalis, L., Petkou, D., Deligeorgidis, N.P., Stavridis, D.G. & Sidiropoulos, G. (2006) The competitive relation between *Frankliniella occidentalis* and *Thrips tabaci*: the impact on life-cycle and longevity. *Journal of Entomology*, **3**, 124–129.
- Eckel, C.S., Cho, K., Walgenbach, J.F. & Kennedy, G.G. (1995) Thrips fauna in north Carolina agroecosystems. *Thrips Biology and Management* (eds B.L. Parker, M. Skinner & T. Lewis), p. 479. Plenum Press, New York.
- Edwards, A.W.F. (1992) *Likelihood* (expanded edition). Johns Hopkins University Press, Baltimore, MD.
- Ekbom, B. (1998) Clutch size and larval performance of pollen beetles in different host plants. *Oikos*, **83**, 56–64.
- Elliott, N., Kieckhefer, R. & Kauffman, W. (1996) Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia*, **105**, 537–544.
- Felland, C.M., Teulon, D.A.J., Hull, L.A. & Polk, D.F. (1995) Distribution and management of thrips (Thysanoptera: Thripidae) on nectarine in the mid-Atlantic region. *Journal of Economic Entomology*, **88**, 1004–1011.
- Funderburk, J.E., Stavisky, J. & Olson, S.M. (2000) Predation of *Frankliniella occidentalis* (Thysanoptera: Thripidae) in field peppers by *Orius insidiosus* (Hemiptera: Anthracoridae). *Environmental Entomology*, **29**, 376–382.
- Goldberg, D.E. & Scheiner, S.M. (2001) ANOVA and ANCOVA: Field competition experiments. *Design and Analysis of Ecological Experiments* (eds S.M. Scheiner & J. Gurevitch), pp. 77–98. Oxford University Press, New York.
- Gotthard, K., Margraf, N., Rasmann, S. & Rahier, M. (2005) The evolution of larval foraging behaviour in response to host plant variation in a leaf beetle. *Oikos*, **109**, 503–512.
- Hansen, E.A., Funderburk, J.E., Reitz, S.R., Ramachandran, S., Eger, J.E. & McAuslane, H. (2003) Within-plant distribution of *Frankliniella* species (Thysanoptera: Thripidae) and *Orius insidiosus* (Heteroptera: Anthracoridae) in field pepper. *Environmental Entomology*, **32**, 1035–1044.
- Immaraju, J.A., Paine, T.D., Bethke, J.A., Robb, K.L. & Newman, J.P. (1992) Western flower thrips (Thysanoptera: Thripidae) resistance to insecticides in coastal California greenhouses. *Journal of Economic Entomology*, **85**, 9–14.
- Inbar, M., Doostdar, H., Leibe, G.L. & Mayer, R.T. (1999) The role of plant rapidly induced responses in asymmetric interspecific interactions among insect herbivores. *Journal of Chemical Ecology*, **25**, 1961–1979.
- Inouye, B.D. (1999) Estimating competition coefficients: strong competition among three species of frugivorous flies. *Oecologia*, **120**, 588–594.
- Inouye, B.D. (2001) Response surface experimental designs for investigating interspecific competition. *Ecology*, **82**, 2696–2706.
- Kirk, W.D.J. (1997) Distribution, abundance and population dynamics. *Thrips as Crop Pests* (ed. T. Lewis), pp. 217–258. CAB International, Wallingford.
- Kirk, W.D.J. (2002) The pest and vector from the West: *Frankliniella occidentalis*. *Thrips and Tospoviruses: Proceedings of the 7th International Symposium on Thysanoptera* (eds R. Marullo & L. Mound), pp. 33–42. Australian National Insect Collection, Canberra, Australia.
- Kirk, W.D.J. & Terry, L.I. (2003) The spread of the western flower thrips *Frankliniella occidentalis* (Pergande). *Agricultural and Forest Entomology*, **5**, 301–310.
- Kolar, C.S. & Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, **16**, 199–204.
- Krebs, R.A., Barker, J.S.F. & Armstrong, T.P. (1992) Coexistence of ecologically similar colonizing species III. *Drosophila aldrichi* and *D. buzzatii*: larval performance on, and adult preference for, three *Opuntia* cactus species. *Oecologia*, **92**, 362–372.
- Lacasa, A., Esteban, J.R., Beitia, F.J. & Contreras, J. (1995) Distribution of western flower thrips in Spain. *Thrips Biology and Management* (eds B.L. Parker, M. Skinner & T. Lewis), pp. 465–468. Plenum Press, New York.
- Law, R. & Watkinson, A.R. (1987) Response-surface analysis of two-species competition: an experiment on *Phleum arenarium* and *Vulpia fasciculata*. *Journal of Ecology*, **75**, 871–886.
- Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975–989.
- Lodge, D.M. (1993) Biological invasions—lessons for ecology. *Trends in Ecology and Evolution*, **8**, 133–137.
- Lounibos, L.P., O'Meara, G.F., Nishimura, N. & Escher, R.L. (2003) Interactions with native mosquito larvae regulate the production of *Aedes albopictus* from bromeliads in Florida. *Ecological Entomology*, **28**, 551–558.
- Morishita, M. (2005) Seasonal abundance of the western flower thrips, *Frankliniella occidentalis* (Pergande), and onion thrips, *Thrips tabaci* (Lindeman) (Thysanoptera: Thripidae), on weeds in persimmon and mandarin orange orchards. *Japanese Journal of Applied Entomology and Zoology*, **49**, 195–203.
- Morse, J.G. & Hoddle, M.S. (2006) Invasion biology of thrips. *Annual Review of Entomology*, **51**, 67–89.
- Mound, L.A. & Teulon, D.A.J. (1995) Thysanoptera as phytophagous opportunists. *Thrips Biology and Management* (eds B.L. Parker, M. Skinner & T. Lewis), pp. 3–19. Plenum Press, New York.
- Northfield, T.D. (2005) *Thrips competition and spatiotemporal dynamics on reproductive hosts*. Masters Thesis, University of Florida, Gainesville.
- O'Connor, R.J. (1986) Biological characteristics of invaders among bird species in Britain. *Philosophical Transactions of the Royal Society of London, Series B*, **314**, 583–598.
- Paini, D.R. & Roberts, J.D. (2005) Commercial honey bees (*Apis mellifera*) reduce the fecundity of an Australian native bee (*Hylaeus alycaeus*). *Biological Conservation*, **123**, 103–112.
- Park, T. (1948) Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. *Ecological Monographs*, **18**, 265–307.
- Porter, D., Van Eimeren, B. & Gilbert, L.E. (1988) Invasion of red imported fire ants (Hymenoptera: Formicidae): microgeography and competitive displacement. *Annals of the Entomological Society of America*, **81**, 913–918.
- R Development Core Team (2005) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, <http://www.R-project.org/>.
- Reitz, S.R., Funderburk, J.E., Hansen, E.A., Baez, I., Waring, S. & Ramachandran, S. (2002) Interspecific variation in behavior and its role in thrips ecology. *Thrips and Tospoviruses: Proceedings of the 7th International Symposium on Thysanoptera* (eds R. Marullo & L. Mound), pp. 133–140. Australian National Insect Collection, Canberra, Australia.
- Reitz, S.R., Yearby, E.L., Funderburk, J.E., Stavisky, J., Momol, M.T. & Olson, S.M. (2003) Integrated management tactics for *Frankliniella* thrips (Thysanoptera: Thripidae) in field-grown pepper. *Journal of Economic Entomology*, **96**, 1201–1214.
- Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1661.
- van Rijn, P.C.J., Mollema, C. & Steenhuis-Broers, G.M. (1995) Comparative life history studies of *Frankliniella occidentalis* and *Thrips tabaci* (Thysanoptera: Thripidae) on cucumber. *Bulletin of Entomological Research*, **85**, 285–297.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. & Weller, S.G. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–332.
- Salguero Navas, V.E., Funderburk, J.E., Beshear, R.J., Olson, S.M. & Mack, T.P. (1991) Seasonal patterns of *Frankliniella* spp. (Thysanoptera: Thripidae) in tomato flowers. *Journal of Economic Entomology*, **84**, 1818–1822.
- SAS Institute (2001) *PROC User's Manual*, Version, 8th edn. SAS Institute, Cary, NC.
- Shorrocks, B., Rosewell, J., Edwards, K. & Atkinson, W. (1984) Interspecific competition is not a major organizing force in many insect communities. *Nature*, **310**, 310–311.
- Singer, M.S., Carriere, Y., Theuring, C. & Hartman, T. (2004) Disentangling food quality from resistance against parasitoids: diet choice by a generalist caterpillar. *American Naturalist*, **164**, 423–429.
- Vila, M. & Weiner, J. (2004) Are invasive plant species better competitors than native plant species? Evidence from pairwise experiments. *Oikos*, **105**, 229–238.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L. & Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist*, **84**, 468–478.
- Zalucki, M.P., Brower, L.P. & Alonso, A. (2001) Detrimental effects of latex and cardiac glycosides on survival and growth of first-instar monarch butterfly larvae *Danaus plexippus* feeding on sandhill milkweed *Asclepias humistrata*. *Ecological Entomology*, **26**, 212–224.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Testing of five commonly used competition models against the data to determine which would be the best fit

Table S1. Five competition models fit to the data using MLE

Table S2. AIC results of the model fitting

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