

Insecticides promote viral outbreaks by altering herbivore competition

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Abstract. While the management of biological invasions is often characterized by a series of single-species decisions, invasive species exist within larger food webs. These biotic interactions can alter the impact of control/eradication programs and may cause suppression efforts to inadvertently facilitate invasion spread and impact. We document the rapid replacement of the invasive *Bemisia* Middle East–Asia Minor I (MEAM1) cryptic biotype by the cryptic Mediterranean (MED) biotype throughout China and demonstrate that MED is more tolerant of insecticides and a better vector of tomato yellow leaf curl virus (TYLCV) than MEAM1. While MEAM1 usually excludes MED under natural conditions, insecticide application reverses the MEAM1–MED competitive hierarchy and allows MED to exclude MEAM1. The insecticide-mediated success of MED has led to TYLCV outbreaks throughout China. Our work strongly supports the hypothesis that insecticide use in China reverses the MEAM1–MED competitive hierarchy and allows MED to displace MEAM1 in managed landscapes. By promoting the dominance of a *Bemisia* species that is a competent viral vector, insecticides thus increase the spread and impact of TYLCV in heterogeneous agroecosystems.

Key words: agriculture; *Bemisia tabaci*; biological invasions; competitive displacement; insecticides; Middle East–Asia Minor I (MEAM1); Mediterranean (MED); plant virus; tomato yellow leaf curl virus (TYLCV).

INTRODUCTION

Rapid increases in the speed and volume of international trade have led to biological invasions becoming an increasingly serious problem worldwide. Invasions that bring together previously disjunct taxa have the potential to profoundly alter both natural and managed ecosystems. Despite a large body of literature on interactions between native and invasive species, there has been less attention paid to the outcome and consequences of invasive–invasive interactions (Simberloff and Von Holle 1999, Simberloff 2006). There are several reasons why understanding such interactions, and the factors affecting them, is important. First, invasive–invasive interactions should grow more common as the number and density of these species increases. Second, the rapid population growth rates of many invasive species (Sakai et al. 2001) should increase interspecific competition; a meta-analysis found that competition was stronger between invasive herbivores

than between native species (Denno et al. 1995). Even in the absence of competition, newly arrived exotic species might also alter the spread and impact of other invasive species, a phenomenon called invasional meltdown (Simberloff and Von Holle 1999, Grosholz 2005, Simberloff 2006).

Understanding the interaction between invasive species, and the factors affecting it, is especially important when the species have different impacts on a shared resource. This can happen when resource depletion is not the only (or even primary) means by which an invasive herbivore impacts its host plant. For example, the effect of herbivory on a host plant can be magnified if the herbivore acts as a disease vector (Miles 1999, Jones 2003) or facilitates the entry of secondary pathogens (Wallin and Raffa 2001). Because organisms often differ in their vector competence or feeding-related damage (Dorschner et al. 1987), interactions between exotic species with disparate impacts may alter the ecological and economic costs of invasions.

The whitefly species *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is actually a complex of genetically divergent but morphologically indistinguishable cryptic biotype (De Barro et al. 2011). The two most invasive *Bemisia* biotypes are the Middle East–

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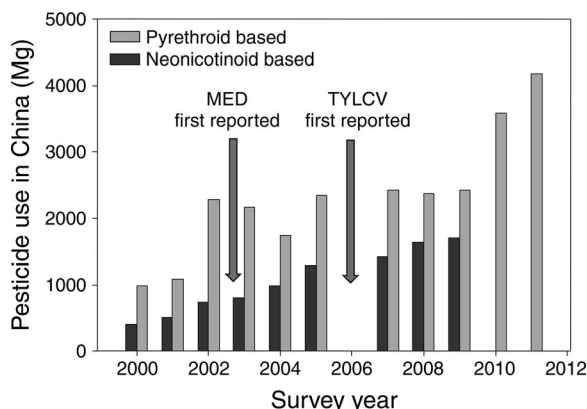


FIG. 1. Domestic use of neonicotinoid (2000–2009) and pyrethroid (2000–2011) insecticides in China. Data reflects total pesticide use summed across all crop types. The 2006 data for both insecticide classes and 2010 and 2012 data for neonicotinoids were unavailable at the time of request; all other data provided courtesy of China Pesticide Information Network (<http://www.chinapesticide.gov.cn>). Abbreviations are MED, Mediterranean *Bemisia* biotype; and TYLCV, tomato yellow leaf curl virus.

Asia Minor I (MEAM1) and the Mediterranean (MED). During the past two decades, MEAM1 and MED have invaded nearly 60 countries and caused massive agricultural losses (De Barro et al. 2011). Although their feeding itself is damaging, whiteflies also vector over 100 begomoviruses that can have catastrophic impacts on plant growth and survival (Jones 2003). The whitefly-mediated introduction of tomato yellow curl leaf virus (TYLCV) and other pathogens into agricultural ecosystems often produces outbreaks whose costs far exceed those of the whiteflies themselves (Jones 2003). Although both biotypes are viral vectors, the feeding behavior of MED makes it more likely than MEAM1 to acquire and transmit TYLCV and other viruses (Jiang et al. 2000, Pan et al. 2012); as a result, MED appears to be a more competent viral vector than MEAM1 (Pan et al. 2012).

Although MEAM1 and MED are both major pests of agricultural crops, they vary in their mating behavior and prefer different host plants (Crowder et al. 2010b, 2011, Elbaz et al. 2011, Tsueda and Tsuchida 2011). They also differ in their susceptibility to insecticides, with MED generally showing greater tolerance of neonicotinoids and other insecticides (Crowder et al. 2010a, Jones et al. 2011). The outcome of MEAM1–MED interactions can be affected by host plant and abiotic factors such as temperature and humidity (Chu et al. 2012b); in general, however, the greater ability of MEAM1 than MED to mate with conspecifics in mixed populations and greater effort devoted by MEAM1 to reproduction leads to the competitive exclusion of MED in laboratory experiments (Pascual and Callejas 2004, Pascual 2006, Crowder et al. 2010a, b, Tsueda and Tsuchida 2011).

After MEAM1 entered China in the mid-1990s, it spread rapidly and caused serious crop losses while displacing native *Bemisia* spp. (Liu et al. 2007). MEAM1 dominated Chinese agricultural systems until 2003, when MED was first detected in Yunnan Province. The new biotype spread quickly and by 2007 had supplanted MEAM1 as the dominant whitefly in agricultural systems in China (Chu et al. 2010, Pan et al. 2011). The same pattern of initial invasion and dominance by MEAM1, followed by the invasion and rapid replacement of MEAM1 by MED, also occurred in Japan (MEAM1 in 1989 and MED in 2004; Ohto 1990, Ueda and Brown 2006) and South Korea (1998 and 2005, respectively; Lee and De Barro 2000, Park et al. 2012). The rapid exclusion of MEAM1 in these countries is at odds with previous laboratory studies demonstrating the competitive dominance of MEAM1 (Pascual and Callejas 2004, Pascual 2006, Crowder et al. 2010a, Tsueda and Tsuchida 2011). This apparent contradiction begs the question: what factors explain the rapid displacement of MEAM1 by MED throughout China?

We explore the factors affecting competition between invasive herbivore species and link this interaction to an increase in herbivore-vectored viral outbreaks. Specifically, we present the results of experimental work demonstrating that insecticide application reverses a naturally occurring competitive hierarchy and allows MED to exclude MEAM1. We also document a rapid increase in the domestic use of both neonicotinoid- and pyrethroid-based insecticides between 2000 and 2011 (Fig. 1) and present the results of contemporaneous landscape-level surveys documenting both the replacement of MEAM1 by MED throughout China and the tight association between TYLCV and MED. The ascent of MED, a highly competent begomovirus vector, has led to damaging outbreaks of TYLCV in China and other Pacific Rim nations. This is the first research to comprehensively address the hypothesized connection between herbivore competition, insecticide resistance, and viral outbreaks. Instead of reducing impacts, our results suggest that heavy insecticide use for whitefly suppression has exacerbated the spread of TYLCV in heterogeneous agricultural landscapes.

METHODS

Bemisia field survey

Adult whiteflies were collected from agricultural fields in 26 of 34 province-level administrative units in China during 2003 (Appendix A), 2007 (Appendix B), 2009 (Appendix C), 2011 (Appendix D), and 2012 (Appendix E). In the 2003–2011 surveys, ten adult whiteflies were collected at each site, each individual from a different individual host plant. Adult whiteflies were placed alive into 95% ethanol and stored at -20°C until DNA extraction. In the 2003–2011 surveys, genomic DNA was extracted from the ten individuals from each site; in the 2012 survey, the decreasing costs of genetic analysis allowed us to collect and determine the biotype identity

of up to 30 individuals per site (Appendices A–E). DNA was stored at -20°C until analysis of the MT-CO1 gene (Shatters et al. 2009) for biotype determination.

TYLCV-Bemisia field survey

In 2011, adult whiteflies were collected from healthy (i.e., without the leaf curls symptomatic of TYLCV infection) or TYLCV-infected (i.e., with leaf curling) fields of tomato, *Lycopersicon esculentum*. Correspondence between leaf-curling symptoms and TYLCV infection was confirmed by screening sampled whiteflies for TYLCV genes; TYLCV was always detected in whiteflies collected from leaf-curling fields but never detected in whiteflies on plants from fields where the symptomatic leaf curling was absent. A total of 48 fields from 26 province-level administrative units in China were sampled (Appendix F). At each site, at least 100 whiteflies were collected from a cluster of ten plants (at least 10 whiteflies/plant). Whiteflies were placed alive into 95% ethanol and stored at -20°C until DNA extraction. If none of the ten plants exhibited the leaf-curling symptomatic of TYLCV infection, the corresponding collections were considered to be from healthy plants; otherwise, they were classified as TYLCV-infected. For each of the 48 collections, 10–20 individual whiteflies were randomly selected for determination of biotype and TYLCV presence. DNA extraction and biotype determination were conducted as in the *Bemisia* field surveys. TYLCV presence in each whitefly was determined using two primers that amplified the AV2 gene, TYLCV-61 and TYLCV-473 (Ghanim et al. 2007).

Bemisia laboratory colonies and host plants

MEAM1 and MED laboratory populations were collected on cabbage, *Brassica oleracea* (cv. Jingfeng 1), and poinsettia, *Euphorbia pulcherrima*, in Beijing, China, in 2004 and 2009, respectively. Source populations of MEAM1 and MED were maintained in separate whitefly-proof screen cages on tomato plants (cv. Zhongza 9) in a glasshouse under natural light and controlled temperature ($26^{\circ} \pm 2^{\circ}\text{C}$) for four generations. Fifteen adults per generation were randomly selected for MT-CO1 sequencing to ensure the purity of each culture (Shatters et al. 2009).

Because MEAM1 and MED are both highly polyphagous, we explored their interactions on multiple host plants. Five crop species, each widely cultivated in China, were used as host plants in the experiments: tomato (cv. Zhongza 9), cabbage (cv. Jingfeng 1), cucumber (*Cucumis sativus*, cv. Zhongnong 12), pepper (*Capsicum annuum*, cv. Zhongjiao 6), and cotton (*Gossypium hirsutum*, cv. DP99B). Seedlings were grown to the five to seven true leaf stage in individual 1.5-L pots with potting mix (peat moss, vermiculite, organic fertilizer, and perlite; 10:10:10:1 ratio by volume). Plants were grown under natural light and controlled temperatures ($26^{\circ} \pm 2^{\circ}\text{C}$) in screen cages within a glasshouse.

Insecticides

We tested the impact of three insecticides on MEAM1 and MED: Thiamethoxam (Syngenta China, Beijing, China), Spirotetramat (trade name Movento; Bayer CropScience China, Hangzhou, Zhejiang Province, China), and Bifenthrin (Ruidefeng Pesticide, Shenzhen, Guangdong Province, China). Thiamethoxam, a neonicotinoid insecticide, was introduced in China in 2000 for the control of *Bemisia* on field and greenhouse crops (Wu et al. 2003). Spirotetramat, a spirotetramic acid derivative, is a systemic insecticide that targets whiteflies and other phloem-feeding insects (Cheng et al. 2013); it was introduced in China in 2008. Bifenthrin is a pyrethroid insecticide that has been widely used against *Bemisia* and other crop pests in China since the mid-1990s (Ma et al. 2007).

Insecticidal bioassays

The effect of Thiamethoxam, Bifenthrin, and Spirotetramat on *Bemisia* eggs was assessed using a slightly modified version of the standard bioassay protocol (Cahill et al. 1996). Fifteen mating pairs of MEAM1 or MED whiteflies were transferred to separate cotton seedlings (first true leaf stage, ~ 11.4 cm in height) for egg laying, then removed after 24 h. After determining egg density on each leaf, seedlings were dipped in different serial dilutions of insecticide for 20 s and dried naturally for 2 h. Because MEAM1 and MED differ in their susceptibility to insecticides (Crowder et al. 2010a, Jones et al. 2011), we used one set of serial dilutions for MEAM1 (water only; 6.25, 12.5, 25, 50, 100, and 200 mg/L) and another for MED (water only; 100, 200, 400, 800, and 1600 mg/L). Seedlings were maintained in water-filled 50-mL beakers and the number of nymphs recorded. Hatching rate was calculated by dividing the number of nymphs by the number of eggs. There were four replicates for each species \times insecticide concentration combination; water-only treatments were controls. Bioassays were conducted in an incubator at $26^{\circ} \pm 2^{\circ}\text{C}$ and a 16 h light:8 h dark photoperiod.

Nymphal bioassays were conducted using standard procedures (Li et al. 2012). After determining the per-seedling density of late second-instar nymphs, seedlings were sprayed with different insecticide concentrations. MEAM1 nymphs were exposed to water only at 0.225, 0.45, 0.9, 1.8, 3.6, and 7.8 mg/L; MED nymphs were exposed to water only at 3.6, 7.8, 15.6, and 31.2 mg/L. After 6 days, the per-seedling density of fourth-instar nymphs was determined and used to calculate the mortality rate of third-instar nymphs. Replication and control treatment were as in the egg bioassays.

Adult bioassays were conducted using standard procedures (Feng et al. 2009). Twenty adult whiteflies (~ 5 days posteclosion) in a glass tube were sprayed with different insecticide concentrations. MEAM1 adults were exposed to water only at 0.5, 1.5, 6, 24, and 96 mg/L; MED adults were exposed to water only at 1.5, 6, 24, 96, 384, 1536, and 6144 mg/L. Mortality was

assessed after 48 h. There were four replicates for each species \times insecticide concentration combination; water-only treatments were used as controls.

Host plant effects on MEAM1–MED competition

We conducted a laboratory experiment assessing MEAM1–MED competition on five plant species: cabbage, cotton, cucumber, pepper, and tomato. Each $0.6 \times 0.4 \times 0.8$ m screened cage (or one replicate) contained two plants of the same species. Each replicate was inoculated with 20 male-female pairs of newly emerged MEAM1 adults and 20 male-female pairs of MED adults (80 total whiteflies). There were three replicates per plant host for cabbage, cotton, pepper, and tomato, and five replicates for cucumber. Briefly, the sampling protocol and timing was as follows: two days after the progeny of each *Bemisia* generation began emerging, we collected 100 whiteflies per replicate, identified each of them as either MEAM1 or MED, and expressed the results as the proportion of MED present in the 100-*Bemisia* sample.

Insecticide effects on MEAM1–MED competition

We conducted a laboratory experiment examining how insecticides affect MEAM1–MED competition on cucumber and tomato. Cage design was as in the host plant experiment, with two plants per cage (or one replicate). In the cucumber experiment, 20 male-female pairs of newly emerged MEAM1 adults and 20 male-female pairs of newly emerged MED adults (80 total whiteflies) were added per replicate. We added whiteflies to each replicate 7 d before applying the control and insecticide treatments to allow them to establish populations on the host plants. At the beginning of the second whitefly generation, each replicate was randomly assigned to one of the following four treatments: water spray (control), Thiamethoxam spray, Spirotetramat spray, or Bifenthrin spray (applied at concentrations of 31.3, 20, and 96 mg/L, respectively). These concentrations reflect recommended spraying rates for *B. tabaci* management on cucumber and tomato (*available online*).¹ Insecticides and water were applied by spraying each plant to run-off; each treatment was replicated five times. The tomato experiment was identical except that it contained only two treatments, water spray and Thiamethoxam spray (31.3 mg/L), with four replicates per treatment. Insecticides and water were reapplied every 7 d after the initial spraying. Briefly, the sampling protocol and timing was as follows: two days after the progeny of each *Bemisia* generation began emerging, we collected 100 whiteflies per replicate, identified each of them as either MEAM1 or MED, and expressed the results as the proportion of MED present in the 100-*Bemisia* sample.

¹ <http://www.chinapesticide.gov.cn>

Sampling and identification of whiteflies in biotype exclusion experiments

Whitefly samples for biotype determination were taken 2 d after the progeny of each generation began emerging. Each sample consisted of 100 randomly selected whiteflies per cage, each of which was identified as MEAM1 or MED via MT-CO1 analysis (Shatters et al. 2009). After sampling, we removed one of the two plants in each cage (and the whiteflies on it) and replaced it with a whitefly-free plant to prevent overcrowding. In the experiment evaluating the impact of insecticides, each plant was sprayed with the appropriate treatment (water or insecticide) before being placed in the cage. Sampling ended when only one biotype was detected in the sample; the experiment ended when all treatments consisted of a single biotype.

Statistical analysis

For the TYLCV-*Bemisia* survey, a Fisher's exact test was used to compare the percentage of MEAM1 and MED at sites with and without TYLCV-infected plants, and the percentage of TYLCV-infected MEAM1 and MED. We used logistic regression for binary data to assess the effects of sample month, percentage of MED individuals, and the percentage of TYLCV-infected MEAM1 or MED individuals on the odds of tomato plant infection by TYLCV. Because there was evidence of a tight fit when the percentage of TYLCV-infected MED was included in the model, regression parameters were estimated using a Firth-adjusted maximum likelihood method. As there was no evidence that month or the percentage of MED individuals was significantly associated with the odds of plant infection (drop-in-deviance test, $df = 4$, $\chi^2 = 3.92$, $P = 0.42$), we removed these two factors in a reduced logistic regression model that investigated the effect of the percentage of TYLCV-infected MEAM1 and MED individuals.

Bioassay data, including LC_{50} values (lethal concentration; i.e., the pesticide concentration necessary to kill 50% of the population) and their 95% fiducial limits, were calculated from probit regressions using POLO-PC (LeOra Software, Berkeley, California, USA). Mortality was corrected using Abbott's formula for individual probit analyses. Resistance to an insecticide was considered significantly different between biotypes if the 95% fiducial limits associated with the LC_{50} values of each biotype did not overlap. JMP v.9 (SAS, Cary, North Carolina, USA) was used for all statistical analyses.

RESULTS

Changes in Bemisia species composition in China, 2003–2012

At the start of our surveys in 2003, MED was absent from 17 provinces and occurred sporadically in or around the flower markets of Yunnan, Henan, and Beijing (Fig. 2A). By 2007, MED was present in 11/24 sampled provinces (46%; Fig. 2B); by 2009, MED was

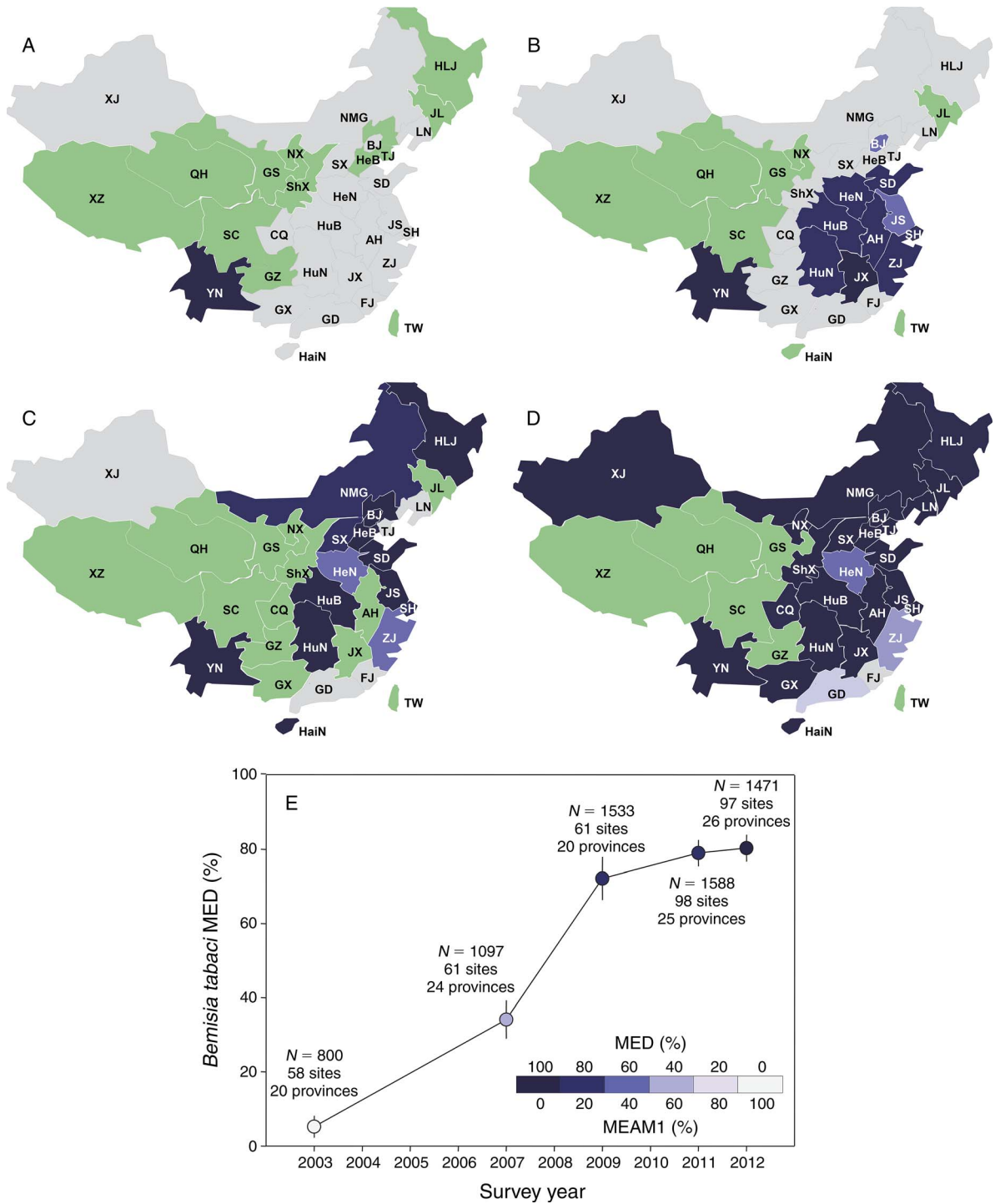


FIG. 2. Replacement of Middle East-Asia Minor I *Bemisia* biotype (MEAM1) by MED in China. Field surveys were carried out in (A) 2003, (B) 2007, (C) 2009, 2011 (not shown), and (D) 2012. See *Methods: Bemisia field survey* for survey details. Values are means \pm SE. In panels (A–D), green denotes unsurveyed regions; colors of sampled provinces denote differing percentages of MED (as indicated by the index in panel E). (E) Summary data indicating the mean province-level proportion of MED in sampled populations over time. The number of *Bemisia* adults, sites, and provinces sampled per survey is listed above each point.

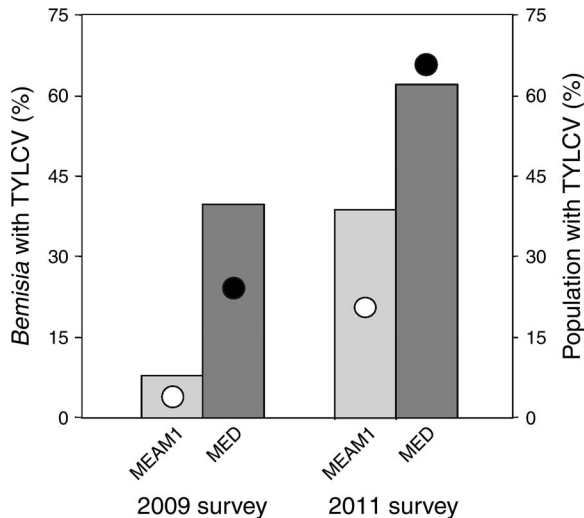


FIG. 3. Observed frequencies of tomato yellow leaf curl virus (TYLCV) infection in MEAM1 and MED in China in 2009 and 2011. See *Methods: TTLCV-Bemisia field survey* for survey details; the 2009 data was previously published in Pan et al. (2012) and is provided solely for the purpose of comparison. The left axis shows the percentage of sampled MEAM1 (open circles) and MED (solid circles) per population infected with TYLCV. The right axis (bars on the graph) shows the percentage of MEAM1 and MED populations infected with TYLCV.

present in 14 of 19 sampled provinces (74%; Fig. 2C). At the time of the 2012 survey (Fig. 2D), MED occurred in 25/26 provinces (96%) and had completely excluded MEAM1 from 13 of them. At the province level, the mean proportion of MED in sampled *Bemisia* populations increased from <5% in 2003 to >80% in 2012 (Fig. 2E)

TYLCV-Bemisia field survey

Of the 48 *Bemisia* populations sampled in 2011, 25 collections from 11 provinces contained only MED, three collections from three provinces contained only MEAM1, and 20 collections contained both MEAM1 and MED (Appendix F). MED was dominant (>50% of sampled individuals) in 14 of 20 mixed-biotype samples. Across all collections, TYLCV was more commonly detected in MED than MEAM1 (Fig. 3; Fisher's exact test, $P < 0.001$). MED was also more abundant at sites with TYLCV-infected tomato plants (85% MED) than at sites with healthy tomato plants (70% MED; Fisher's exact test, $P < 0.001$). Of 45 populations with MED in 2011, 28 of them (62%; also see Fig. 3) had at least one TYLCV-positive MED individual; of 23 populations of MEAM1 in 2011, nine of them had at least one TYLCV-positive MEAM1 individual (39%; again, see Fig. 3).

The logistic regression model that included the effects of month, percentage of MED individuals, and percentages of TYLCV-infected MEAM1 and MED adequately described the variation in tomato plant infection (goodness of fit $\chi^2 = 3.09$, $df = 13$, $P = 0.99$; Akaike's

information criterion corrected for sample sizes, $AIC_c = 29.0$). Of the four factors, only the percentage of TYLCV-infected MED was positively and significantly associated with tomato plant infection (slope = 3.42, SE = 1.66, $\chi^2 = 6.81$, $P = 0.009$). The reduced logistic regression model that only included the percentage of TYLCV-infected MEAM1 and MED also had a good fit but lower AIC_c (goodness of fit $\chi^2 = 1.38$, $df = 17$, $P = 1$; $AIC_c = 10.3$). This reduced model produced similar results: plant infection was associated with TYLCV infection of MED (slope = 5.25, SE = 2.14, $\chi^2 = 12.96$, $P = 0.003$) but not with infection of MEAM1 (slope = 2.55, SE = 2.60, $\chi^2 = 0$, $P = 1$).

Insecticidal bioassays

The LC_{50} of MEAM1 eggs exposed to Thiamethoxam was 6.6 times lower than of MED eggs. Nymphs of both biotypes were far more susceptible than eggs to Thiamethoxam; again, however, the LC_{50} of MEAM1 nymphs was 4.9 times lower than in MED. Resistance increased in both MEAM1 and MED adults, but the LC_{50} of MEAM1 remained substantially (3.1 times) lower than it was for MED adults.

The same pattern occurred when both biotypes were exposed to Spirotetramat and Bifenthrin. Eggs of MEAM1 were ~25 times less resistant to Spirotetramat than those of MED, while MEAM1 nymphs and adults were 6.5 times and 7 times less resistant, respectively. Bifenthrin, a contact insecticide used primarily against adult whiteflies, was not toxic to MEAM1 or MED eggs, and was similarly toxic to MEAM1 and MED nymphs; MEAM1 adults were, however, 3.7 times less resistant than MED adults.

Host plant effects on MEAM1-MED competition

MEAM1 competitively excluded MED from four of five host plants, taking between four (on cabbage) and nine (on cucumber) generations to eliminate MED (Fig. 4). The only exception to this occurred on pepper, where MED excluded MEAM1 in two generations.

Insecticide effects on MEAM1-MED competition

In the absence of insecticide, MEAM1 excluded MED by the ninth generation on cucumber plants. Insecticide application reversed this outcome, allowing MED to exclude MEAM1 within five generations (Fig. 5A). This result held true on tomato, where MEAM1 excluded MED within six generations in the absence of Thiamethoxam but MED excluded MEAM1 when the insecticide was used (Fig. 5B).

DISCUSSION

Our research provides strong support for the hypothesis that insecticide use in China (Fig. 1) reverses the competitive hierarchy between MEAM1 and MED, allowing highly resistant MED to displace moderately resistant MEAM1 in managed landscapes throughout the country (Fig. 2). By promoting the dominance of a

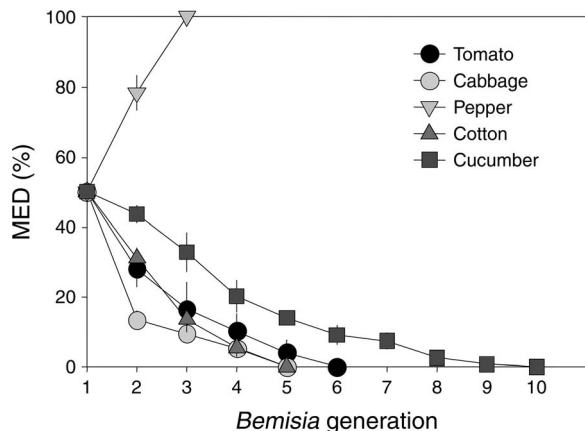


FIG. 4. Changes in the proportion of MEAM1 and MED (as measured by percentage of MED in the population) on five different host plants over time. Mixed cultures were reared on cotton (*Gossypium hirsutum*), cucumber (*Cucumis sativus*), cabbage (*Brassica oleracea*), tomato (*Lycopersicon esculentum*), and pepper (*Capsicum annuum*). See *Methods: Host plant effects on MEAM1–MED competition* for treatment details. Values are mean \pm SE from three replicates (five replicates for *C. sativus*).

Bemisia biotype that is a superior viral vector (Fig. 3), insecticide use facilitated the spread of TYLCV in heterogeneous agricultural landscapes. Increased chemical control of *Bemisia* and other pests (i.e., the use of pyrethroid insecticides rose 72% between 2009 and 2011; Fig. 1) thus appears to enhance rather than reduce the likelihood and severity of future *Bemisia*-mediated viral outbreaks.

The application of three different insecticides (neonicotinoid, pyrethroid, and tetracycline) reversed the normal competitive hierarchy (Fig. 4) and allowed MED to exclude MEAM1 on both tomato (Fig. 5A) and cucumber (Fig. 5B). All MED life-history stages were more resistant than MEAM1 to these insecticides (Table 1). Other researchers working with Chinese MEAM1 and MED have found similar differences in resistance: one study found that a Jiangsu MED population was 1900 times more resistant to imidacloprid and 1200 times more resistant to Thiamethoxam than MEAM1 (Wang et al. 2010).

Our finding that MED is replacing MEAM1, and that this switch is related to pesticide application, is consistent with observations from other parts of the world. In Israel, for example, MED became dominant in mixed-field populations treated with pyriproxyfen and neonicotinoids (Horowitz et al. 2005). The ability of insecticides to mediate the MEAM1–MED interaction was initially described by Crowder et al. (2010a), who used modeling and an experimental manipulation of North American *Bemisia* to demonstrate the potential for MED to competitively exclude MEAM1. The present work, for the first time, provides empirical evidences from both a 10-year field survey and laboratory experiments to establish this framework, identifies the unexpected consequences of this reversal,

and confirms that three insecticides, each recommended for control of *Bemisia* and other plant sucking pests, produce the same outcome.

The replacement of MEAM1 by MED in China (Fig. 2) and neighboring countries has been repeatedly linked to TYLCV outbreaks. In China, for instance, MEAM1 was first detected in 1990, followed by MED in 2003, and TYLCV in 2006 (Fig. 1; Hu et al. 2011, Pan et al. 2011). Our survey (Fig. 3) demonstrates the association between TYLCV and MED in China. In addition, we found a positive relationship between TYLCV infection in tomato and the percentage of TYLCV-infected MED; in contrast, there was no relationship between plant health and the percentage of TYLCV-infected MEAM1. In sum, our findings are in accord with previous surveys (Pan et al. 2012, Park et al. 2012) and experimental work (Jiang et al. 2000, Liu et al. 2013a) indicating that vector-plant transmission of TYLCV in Asia is predominantly associated with MED.

While the displacement of an established exotic species by another invader has been previously documented (Reitz and Trumble 2002), the unintended economic consequences of this insecticide-driven dis-

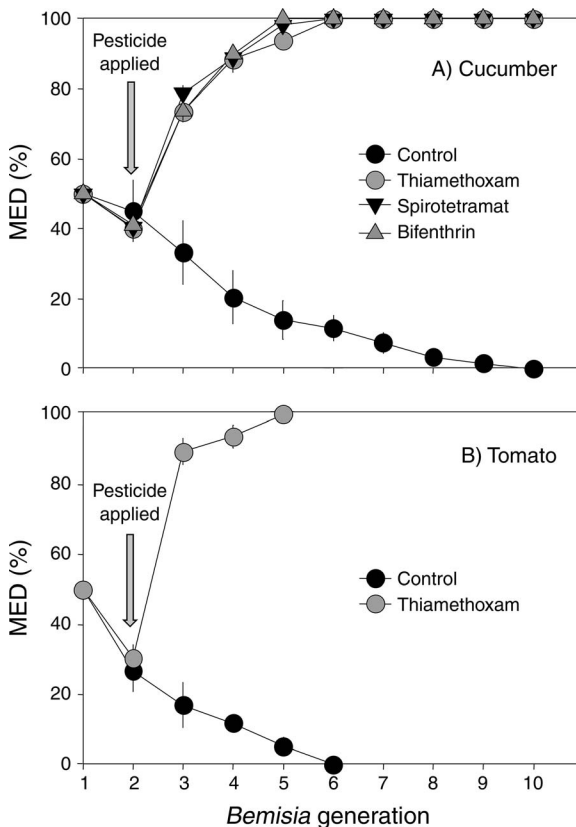


FIG. 5. Effect of insecticides on the proportion of MEAM1 and MED (as measured by percentage of MED in the population) on (A) cucumber and (B) tomato. See *Methods: Insecticide effects on MEAM1–MED competition* for treatment details. Values are mean \pm SE from (A) four replicates and (B) five replicates.

TABLE 1. Bioassay results of MEAM1 and MED to insecticides commonly used for *Bemisia* control in China.

Insecticide, stage, and biotype	Slope	LC ₅₀ (mg/L)	95% FL	RR
Thiomethoxam				
Egg				
MEAM1	0.54 (0.073)	130 ^a	73.2–230	6.6
MED	1.58 (0.125)	860 ^b	670–1105	6.6
Nymph				
MEAM1	1.19 (0.105)	1.0 ^a	0.8–1.4	4.9
MED	1.89 (0.201)	5.2 ^b	3.1–8.3	4.9
Adult				
MEAM1	1.06 (0.112)	17.8	9.8–32.5	3.1
MED	0.60 (0.084)	54.9	19.2–157	3.1
Spirotetramat				
Egg				
MEAM1	1.63 (0.101)	0.18 ^a	0.15–0.22	24.2
MED	0.47 (0.038)	4.34 ^b	2.26–8.33	24.2
Nymph				
MEAM1	0.73 (0.048)	0.00107 ^a	0.000610–0.00186	7.0
MED	1.88 (0.101)	0.00751 ^b	0.00620–0.00911	7.0
Adult				
MEAM1	1.51 (0.209)	2450 ^a	1628–3687	>6.5
MED	...	>16000 ^b	...	>6.5
Bifenthrin				
Egg				
MEAM1	...	no effect	...	na
MED	...	no effect	...	na
Nymph				
MEAM1	1.37 (0.080)	39.5	29.0–53.7	1.5
MED	1.59 (0.129)	58.2	46.7–72.6	1.5
Adult				
MEAM1	1.89 (0.149)	63.2 ^a	50.9–78.4	3.7
MED	1.88 (0.144)	233 ^b	187–293	3.7

Notes: Slope is mean increase in mortality as chemical concentration increases (with SE in parentheses); LC₅₀ is concentration of chemical sufficient to cause 50% mortality in the target population; 95% FL is 95% fiducial limit around the LC₅₀; RR is resistance ratio (the ratio of the LC₅₀ of MED and MEAM1; na, not applicable). Within a stage, biotype LC₅₀ values with different lowercase letters are significantly different at $P < 0.05$. Ellipses indicate no data available.

placement for agriculture in China and other Pacific Rim nations make this system unusual and perhaps unique. Although information on the economic impact of TYLCV in China is not publicly accessible, data from other countries can provide a perspective on the possible costs. Outbreaks of TYLCV in India, a country whose farming infrastructure is similar to that of China, cause yield losses ranging from 50–100% (Reddy et al. 2010). By way of comparison, TYLCV outbreaks in the early 2000s that reduced tomato yields by 20% in North America and Europe had a cost of more than US\$300 million (Glick et al. 2009). Given the polyphagous nature of *Bemisia tabaci*, the hundreds of viruses it can vector, and the extensive agricultural sector in China, the total economic cost of TYLCV and other viral pathogens are likely higher, perhaps dramatically so. Such impacts amply justify *B. tabaci*'s selection as one of the world's 100 worst invasive species.

Our results provide strong support for the hypothesis that the insecticide-mediated competitive replacement of

MEAM1 by MED is linked to the spread of TYLCV. In other countries, however, different outcomes have occurred. In Israel, for instance, the MEAM1–MED competitive hierarchy fluctuates, with MEAM1 being relatively more abundant than MED in field crops and MED more abundant than MEAM1 in glasshouses and other protected environments where insecticides are intensively used (Kontsedalov et al. 2012). A similar but more extreme situation is observed in the United States, where MED is only found in greenhouses in 23 states, while MEAM1 is present in both field crops and greenhouses (McKenzie et al. 2012). Why has the MEAM1–MED interaction played out so differently in China?

The most likely explanation for these divergent outcomes involves the infrastructure and incentives in place for pest management. Chinese farming is dominated by the household responsibility system of small family farms whose owners are often uneducated and lack access to agricultural extension personnel. As a

result, the vast majority of farmers rely on high-dose chemical treatments for pest and weed management (Xu et al. 2008). Although effective in controlling pest species, many of these insecticides also alter local food webs. Alarm at the impact of neonicotinoid insecticides on pollinators, for instance, has led the European Commission to approve a two-year ban on their widespread use. These concerns notwithstanding, Chinese farmers continue to increase use of neonicotinoids and other synthetic insecticides, with unknown consequences for the surrounding ecosystems. This reliance has been exacerbated by China's investment in chemical production facilities in the early 2000s; the global recession decreased exports and flooded the domestic market with insecticides (Fig. 1; CCM 2012). The low cost and high efficacy of these products further encourages small farmers in China to spray their way out of pest problems (Xu et al. 2008).

In contrast, crop production in the United States is dominated by large-scale agricultural concerns acutely aware of the danger posed by insecticide-resistant *Bemisia* (Osborne 2013). The integrated pest management strategy for *Bemisia* control in the United States emphasizes nonchemical approaches and strict action thresholds for chemical treatments in field crops (Ellsworth and Martinez-Carrillo 2001). Organized and sustained grower education facilitated the deployment and adoption of this plan, which has lowered both *Bemisia*-targeted insecticide use and whitefly problems (Ellsworth and Martinez-Carrillo 2001). The emphasis on managing for reduced insecticide resistance may have favored MEAM1 in field crops in the United States, keeping MED relatively rare and confined to high-pesticide areas like greenhouses (McKenzie et al. 2012). These disparate approaches to pest management likely explain why TYLCV has become a greater problem in China than in the United States.

While we consider insecticide use to be the most likely explanation of the rapid spread of MED and TYLCV in China, other factors could influence success of this species. For example, temporal changes in diversity of agricultural landscape could have affected coexistence of MEAM1 and MED. In Israel, MEAM1 and MED dominated on different agricultural plant families, although MED was the most abundant on a broader range of host plants (Crowder et al. 2011). This wider resource niche of MED could foster coexistence by providing a refuge against MEAM1, which is superior at reproductive interference competition (Crowder et al. 2011). By contrast, our host-plant experiment confirmed previous research finding that MEAM1 was dominant over MED on most, but not all, plant species (Fig. 4; Iida et al. 2009, Tsueda and Tsuchida 2011, Liu et al. 2013b). Specifically, our results agree with work (Tsueda and Tsuchida 2011) that found MEAM1 could not develop on pepper but did better than MED on tomato, cabbage, and cucumber. Reasons for the differences in host-plant mediated competition between Israel and

China is currently unknown, but could be related to geographical changes in the haplotypes of one or more species (De Barro et al. 2011). Nevertheless, our results indicate that a shift towards MED-preferred host plants could favor this species (and TYLCV) over MEAM1, although we are unaware of any such large-scale change in cropping systems occurring during the last 10 years in China.

Although MED has spread through agricultural systems in China, it is unlikely to extirpate MEAM1. Our competition experiments (Figs. 4 and 5), for example, were carried out under warm ($26^{\circ} \pm 2^{\circ}\text{C}$) conditions with no climatic variation. MEAM1 and MED respond differently to temperature variation, however, with MED being more tolerant than MEAM1 of temperature extremes (Elbaz et al. 2011, Chu et al. 2012b). Although MED now dominates agricultural systems, China contains a heterogeneous mix of landscapes that vary in their abiotic, biotic, and anthropogenic (i.e., insecticide use) conditions. Prior to the entry of MED, MEAM1 displaced native whiteflies from agricultural systems; these species persisted in natural landscapes (Liu et al. 2007, Hu et al. 2011). MEAM1 may persist in a similar manner in low-insecticide systems or on vegetation growing near high-pesticide fields; adopting IPM strategies to reduce chemical use and favor susceptible organisms might favor the resurgence of MEAM1 and increase their likelihood of excluding MED (and, perhaps, their viruses) from systems.

While our work provides a cogent explanation for the recent upsurge of whitefly-vectored diseases in heterogeneous agricultural systems, other questions remain to be answered. While TYLCV and MED are tightly linked in China and other Pacific Rim nations (Pan et al. 2012, Park et al. 2012), TYLCV in Israel is primarily associated with MEAM1 (Gottlieb et al. 2010). These differences are driven by the geographic differences in the composition of *Bemisia* endosymbiont communities (Gottlieb et al. 2010), and insecticide-driven shifts in community structure may also alter vector competence. Recent research has also identified five well-defined MED haplotypes (Chu et al. 2012a) whose endosymbiont communities may well differ. Exploring the interaction between insecticide resistance and endosymbiont communities may help develop management programs aimed at reducing viral outbreaks.

One drawback of our work is that the comprehensive nature of our approach (combining multiple surveys, experiments, and assays) precluded a completely factorial design. In other words, we did not have sufficient resources to rear both *Bemisia* biotypes on all five host plants prior to the experiment, repeat the insecticide bioassays using whiteflies reared on all five host plants, carry out the insecticide-mediated competition experiment on all five host plants, etc. While we would have preferred to test all host plants in all experiments, there is no indication that any of these five plant species are,

for instance, capable of altering the response of *Bemisia* to insecticides. We thus believe it to be highly unlikely that our results confound the effects of host plant and insecticides in a way that invalidates our conclusion, an interpretation supported by the fact that our laboratory results are substantially consistent with data emerging from our field surveys.

Our research demonstrates that insecticide use alters the competitive interaction between two invasive whiteflies and is the likely driver of MED's displacement of MEAM1 throughout China. The ascent of MED, an effective viral vector, has in turn been linked to economically damaging agricultural disease outbreaks. Our experiments and surveys strongly suggest that the overuse of insecticides has, through food web interactions, inadvertently exacerbated the problem it sought to solve. This result is especially important since a substantial fraction of agricultural land worldwide is managed by small landholders rather than by large-scale producers. As a consequence, phenomena observed in a heterogeneous agricultural system like China may also occur in several Asian states (e.g., Japan and Korea) and other countries worldwide. Given the larger context of increasing biological invasions worldwide and the importance of species interactions in determining community structure, policies of single-species management that do not account for the larger food web may produce similarly counterintuitive outcomes that pose a major challenge to natural and managed systems alike.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–F are available online: <http://dx.doi.org/10.1890/14-0752.1.sm>

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.334n3>