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RESEARCH ARTICLE

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Retrospective analysis of a classical biological control programme

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Abstract

1. Classical biological control has been a key technology in the management of invasive arthropod pests globally for over 120 years, yet rigorous quantitative evaluations of programme success or failure are rare. Here, I used life table and matrix model analyses, and life table response experiments to quantitatively assess a classical biological control programme for an invasive insect pest in the western United States.
2. Life tables and matrix models were developed for populations of *Bemisia tabaci* (sweetpotato whitefly) on cotton in Arizona before (1997–1999) and after (2001–2010) the permanent establishment of two exotic aphelinid parasitoids. Analyses tested multiple hypotheses relative to the expected outcome of a successful programme.
3. Marginal rates of parasitism, rates of irreplaceable mortality from parasitism, total generational mortality and finite population growth (λ) were unchanged for *B. tabaci* populations before and after exotic parasitoid establishment. Prospective analyses showed that predation during the final nymphal stadium had the greatest influence on population growth rates regardless of parasitoid establishment. Retrospective LTREs showed that predation and unknown mortality contributed most to changes in λ after parasitoid establishment.
4. Marginal parasitism acted weakly in a direct density dependence fashion after parasitoid establishment, and for all 14 years combined. However, this did not translate into an association between pest population density and marginal rates of parasitism for the 10-year period following establishment.
5. *Synthesis and applications*. Rarely are classical biological control programme outcomes assessed rigorously. Life tables, matrix models, and life table response experiments showed that the decline in the pest status of *Bemisia tabaci* (sweetpotato whitefly) was not associated with the establishment of two exotic parasitoid species in the cotton system. Instead, native arthropod predators play a major role in pest dynamics. Further efforts to enhance conservation of the extant natural enemy community, with focus on increasing mortality in final stage nymphs and adults, may be the most efficient means of increasing biological control services.

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Analyses deployed here should be more widely applied to assessing and improving biological control generally.

KEYWORDS
Bemisia tabaci, classical biological control, elasticity, life table response experiment, matrix model, parasitism, population growth, predation

1 | INTRODUCTION

Classical biological control has been a key technology in the management of invasive arthropod pests globally for over 120 years. The goal is to provide long-lasting pest control by reestablishing upper trophic level links through the introduction of natural enemies from the pest's native region (DeBach, 1964). Recent examination of classical biological control programmes indicates about a 33% rate of success in establishing exotic agents and a 10% rate of achieving some level of satisfactory control of targeted insect pests (Cock et al., 2016). Although a risky endeavour given the low chances of success, the few economic analyses conducted for insect targets indicate a median benefit to cost ratio of around 80:1 with many programmes providing long-term pest suppression with continuing economic benefits (Naranjo, Ellsworth, & Frisvold, 2015). Classical biological control programmes are complex, with long time horizons, and with many critical steps required to achieve success (DeBach, 1964; Hokkanen, 1985; van Driesche & Hoddle, 2000). The final phase should involve evaluation of overall outcomes of the programme in ecological, sociological and economic terms, a step that is frequently overlooked due largely to the lack of personnel and financial resources during the later stages of the programme (McEvoy & Coombs, 1999; van Driesche & Hoddle, 2000).

Life tables and associated matrix models have not been widely applied in classical biological control, but they can provide important insight on the impact of introduced species on targeted pest populations. Prospective approaches have been useful for identifying life stage vulnerabilities, suggesting potential agents to exploit these vulnerabilities, and predicting the impact on pest populations by planned or ongoing biological control programmes (Barker & Addison, 2006; Davis et al., 2006; Maines, Knochel, & Seastedt, 2013; Mills, 2005; Shea & Kelly, 1998). Retrospective analyses can identify the contribution of specific vital rates and enhance our understanding of factors contributing to the success or failure of a programme (Catton, Lalonde, Buckley, & de Clerck-Floate, 2016; Dauer, McEvoy, & van Sickle, 2012; McEvoy & Coombs, 1999). Life table response experiments (LTRE) are a retrospective approach whereby changes in population growth due to an environmental variable can be decomposed into the individual contributions of the underlying vital rates (Caswell, 1996). LTREs have had broad application in investigating such areas as species conservation and ecotoxicology (Caswell, 2001) and are ideally suited to investigating pest population responses to classical biological control, where the environmental change is represented by the addition of new natural enemy species into an existing community.

Several interrelated hypotheses should be supported if introduced species have provided successful biological control. Introductions should supply new and higher levels of mortality and this mortality should be associated with declines in pest population growth. In addition, the new source of mortality might display some level of regulatory density dependence. Prospective and retrospective approaches based on life table, matrix model and LTRE analyses were used to ecologically evaluate and inform a classical biological control programme targeting *Bemisia tabaci* Gennadius (MEAM1), an insect pest of global significance.

2 | MATERIALS AND METHODS

2.1 | Study system

The invasive *B. tabaci* (sweetpotato whitefly) is a key economic pest of multiple annual crops in agricultural production regions in the southern tier of the USA, including cotton, *Gossypium hirsutum* L. (Oliveira, Henneberry, & Anderson, 2001). Classical biological control was immediately considered a viable approach for pest management due to past success with other whitefly species (Bellows, Bezark, Paine, Ball, & Gould, 1992; Onillon, 1990), and limited parasitoid diversity in affected crops (Hoelmer, 1996). In part, the programme introduced about 30 populations of *Eretmocerus* spp. and *Encarsia* spp. nymphal parasitoids into the low desert agricultural production areas of California and Arizona (Gould, Hoelmer, & Goolsby, 2008). *Eretmocerus* sp. from Ethiopia and the heteronomous hyper-parasitoid *Encarsia sophia* (Girault and Dodd) from Pakistan became permanently established in Arizona around 2001, largely displacing several native aphelinid species previously attacking the pest (Naranjo & Li, 2016).

2.2 | Study sites

Study sites were located on the ≈900 ha University of Arizona, Maricopa Agricultural Center farm in Maricopa, Arizona, USA. The farm grows a mix of crops representative of agricultural production in central Arizona, including agronomic (cotton, wheat, sorghum, alfalfa) and vegetable crops. Field-based life table data on immature *B. tabaci* were generated on insecticide-free cotton from 1997 to 2010. Cotton varieties, representative of commercial production in the area, were planted mid-April to early-May each year and grown

using regional agronomic practices. Between two and five life tables were generated each year for a total of 44 life tables over the 14-year period (see Supporting Information Table S1).

2.3 | Life table construction

Life table data were generated using an in situ observational method that took advantage of the sessile nature of the immature stages of *B. tabaci*. Briefly, for each life table, 160–240 individual newly-laid eggs (1–4 per leaf, one leaf per plant) were established from existing natural populations on cotton leaves. Separately, 160–240 individual newly-settled first instar nymphs (1–4 per leaf, one leaf per plant) were similarly established. Insects were marked by drawing a small circle around an individual with a nontoxic pen. Individual nymphs were then observed 3× per week with a hand lens to determine the developmental stage and if dead the cause of death. Observations continued until the insect died or emerged as an adult. Leaves with eggs were returned to the laboratory for observation about 10 days after setup because causes of death were too difficult to discern with a hand lens. Observable causes of death included inviability, predation and dislodgement for eggs and predation, parasitism, dislodgement and unknown for nymphs (only fourth instar nymphs show visible signs of parasitism). More detail is provided in Naranjo and Ellsworth (2005, 2017) and in Supporting Information Appendix S1.

2.3.1 | Estimation of mortality rates

Marginal mortality rates were estimated using the approach of Elkinton, Buonaccorsi, Bellows, and van Driesche (1992). Marginal rates were needed because at least three simultaneous mortality factors operated on the egg stage and each of the four nymphal stages; thus, there was no temporal sequence of mortality factors affecting any stage and mortality from one factor might mask the action of another. Based on Naranjo and Ellsworth (2005), the estimation of marginal rates simplifies to

$$M_B = d_B/(1-d_A) \quad (1)$$

where M_B is the marginal death rate from factor B, d_B is the apparent (observed) rate of mortality from factor B and d_A is the sum of apparent mortalities from all other relevant contemporaneous factors.

2.3.2 | Estimation of irreplaceable mortality rates

Irreplaceable mortality is that portion of total generational mortality that would not occur if a given mortality factor was missing. Following Carey (1989), irreplaceable mortality was estimated for each mortality factor as

$$(1-\prod_1^j[1-M_k])-(1-\prod_1^{j-1}[1-M_k]) \quad (2)$$

where M_k is the marginal mortality rate for factor k and j is the total number of mortality factors. The first product includes all mortality factors, while the second product includes all mortality factors except the one of interest. This method assumes no density-dependent compensation in mortality.

2.4 | Matrix models

Stage-structured matrix models were developed for each of the 44 life tables over the 14-year period (Caswell, 2001). The required matrix elements included (a) daily probabilities of transition from one stage, i, to the next (G_i), given as $\sigma_i\gamma_i$, where σ_i is the daily stage survival rate and γ_i the daily stage development rate; (b) the daily probability of surviving and remaining in the stage (P_i), given as $\sigma_i(1-\gamma_i)$ and (c) the mean daily rate of adult fertility (F, females per female) (Supporting Information Table S2 and Supporting Information Figure S1). The daily stage survival rate was estimated as $(1-M_i)^{\gamma}{}_i$, where M_i is the marginal mortality rate for stage i. This assumption of a constant rate over time is reasonable given the short duration of each stage. The observation interval of the life tables was too long to accurately estimate the duration of each immature stage. Thus, temperature-dependent rates of development for eggs and nymphs were estimated from Wagner (1995) using archived mean daily air temperatures from an on-site weather station (AZMET, 2016) for the short period between cohort establishment and adult emergence (Supporting Information Appendix S1). For adult survival, the constant daily rate was estimated as $1-(1/d_a)$, where d_a is adult longevity. Temperature-dependent adult fecundity and longevity were estimated indirectly for each generation using the data of Wagner (1994, T. L. Wagner, unpublished data, Supporting Information Appendix S1). Based on the summer temperatures during this study, mean daily air temperatures were calculated for the 10-day interval following adult emergence. Daily rates of fertility were estimated from the quotient of lifetime temperature-dependent fecundity and adult longevity, assuming a 50:50 sex ratio.

2.5 | Life table and matrix model analyses

The exotic aphelinid parasitoids attacking *B. tabaci* became permanently established around 2001 (Naranjo & Li, 2016). Thus, life table studies conducted from 1997 to 1999 were considered pre-establishment (control or reference treatment) and all the life table studies conducted from 2001 onward were considered post-establishment (experimental treatment); no studies were conducted in 2000.

2.5.1 | Life table analyses

Bootstrapped confidence intervals were estimated for mean marginal mortality, irreplaceable mortality, total mortality and finite population growth (λ, see below) for pre-establishment and post-establishment years (i.e. 1997–1999 and 2001–2010). Following Levin et al. (1996), individual insects with their associated histories of mortality, growth and reproduction within each life table were randomly resampled with replacement using the original sample size

of each life table. For each iteration, marginal and irreplaceable rates of mortality from each cause within each stage were reestimated as were rates of total mortality and λ for the generation. Life tables used separate cohorts of eggs and nymphs; thus, resampling was done separately within each of these stages to mimic the study design. Confidence intervals were estimated as the 2.5th and 97.5th percentiles based on 5,000 iterations. Permutation (two-sided) was used to test the null hypothesis that differences between mean pre- and post-establishment rates were zero using resampling without replacement but following the same life table resampling process above with 5,000 iterations. Given the nonrandomized nature of the treatments, tests were conducted using a before-after control-impact (BACI) approach (Wiens & Parker, 1995). The test statistic was the absolute value of the difference between treatment means. Probability levels were estimated by calculating the number of times permuted mean differences were greater than the test statistic. The error rate for multiple tests was controlled using a false discovery rate of 5% (Benjamini & Hochberg, 1995). All analyses were conducted with the resampling and Monte Carlo routines in PopTools V3.2 (Hood, 2010). The BACI approach violates the principle of randomization of treatments. Temperature is one obvious environmental variable that is likely to differ between pre- and post-establishment time periods. Thus, to test the impact of the experimental design flaw, the temperatures used in all 44 life tables for estimating rates of immature growth, adult survival and reproduction were averaged and each matrix model was then resolved using these new average rates. A permutation test estimated if λ changed between treatments with temperature effects removed and this was compared with observed differences in the original dataset.

Temporal density dependence in mortality factors was tested by regressing the *k*-value (=−ln[1−*M*], where *M* is the marginal rate) of each mortality factor within each stage (egg or nymph) on the natural log density of *B. tabaci* at the beginning of the stage. Densities of *B. tabaci* small (first and second instar) and large nymphs (third and fourth instar) per leaf disk, and adults per leaf were estimated each week from late June to late September (Naranjo & Flint, 1994, 1995). Because sampling pooled small (first and second instar) nymphs and large (third and fourth instar) nymphs, *k*-values were summed accordingly for these pooled nymphal stages. Delayed density dependence was tested by using insect densities from the beginning of the prior generation (*c.* 21 days prior). Testing for spatial density dependence was not possible due to the way in which life table cohorts were established and the lack of plant-specific sampling for *B. tabaci*. The statistical error rate for multiple simple regressions was controlled using a false discovery rate of 5%.

2.5.2 | Prospective matrix model analyses

Matrix models were developed for each life table (44 total) and were analysed to estimate λ, and the elasticity of λ with respect to vital rates. Elasticity measures the proportional change in population growth in response to a proportional change in a vital rate for a given life stage. The elasticities of λ to decomposed stage survival rates, given as the sum of the elasticities of the P_i and G_i matrix elements for a given stage, and decomposed growth rates, estimated as the product of $\sigma_i\gamma_i/\lambda$ and the difference of the G_i and P_i sensitivities (Caswell, 2001, p. 233), were estimated. Permutation tests examined effects of parasitoid introduction on elasticities of λ to P_i, G_i, σ_i and γ_i using the resampling methods detailed above. Again, error rates for multiple tests were controlled using a false discovery rate of 5% and analyses were conducted using PopTools V3.2 (Hood, 2010).

Elasticity analyses are based on looking at responses in λ to very small changes in underlying vital rates, but may not accurately predict responses to larger changes. Horovitz, Schemske, and Caswell (1997) suggested that it may be instructive to vary matrix parameters and then solve for λ directly. This approach was used to examine the contribution of specific mortality factors to population growth. The mortality associated with each factor (over all stages), each stage (over all factors) or each factor within each stage was removed and the matrix model was then resolved for λ. The per cent change in λ was used as a measure of relative contribution. Analyses were compared to traditional life table key factor analysis (Supporting Information Appendix S2).

2.5.3 | Retrospective matrix model analyses

A LTRE approach was used to assess the contribution of lower level vital rates, *x*, to changes in population growth due to parasitoid establishment. Following Caswell (1996), the effect on λ is given generally by:

$$\lambda^m - \lambda^r \approx \Sigma_{i,j}\Sigma_k (x_k^m - x_k^r)\frac{\partial\lambda}{\partial a_{i,j}}\frac{\partial a_{i,j}}{\partial x_k}|(A^m + A^r)/2 \quad (3)$$

where the superscripts *m* and *r* refer to treatment and reference (control), respectively, $a_{i,j}$ are the elements of the projection matrices, $\partial\lambda/\partial a_{ij}$ is the sensitivity of λ to a_{ij} and $\partial a_{ij}/\partial x_k$ is the sensitivity of a_{ij} to x_k, both evaluated on the mean matrix ($[A^m+A^r]/2$). Here, *x* represents lower level vital rates of growth (γ_i) and survival (σ_i), where survival, in turn, is decomposed into effects from multiple, specific mortality factors *k* such as predation, parasitism, and dislodgement (see Supporting Information Appendix S3 for detail). To control for nonadditivity, the mean matrices were estimated by averaging the individual rates of the product making up each matrix element a_{ij} (Table S2; Cooch, Rockwell, & Brault, 2001). Bootstrap confidence intervals were estimated as before for each decomposed vital rate contribution. Permutation tested if contributions differed from zero with multiple error rates controlled using a false discovery rate of 5%.

2.6 | Parasitism and host association

Pearson's correlation was used to evaluate the association between the seasonal annual abundance of large nymphs or adults of *B. tabaci* and annual mean marginal parasitism over the post-establishment period (2001–2010). These host stages were chosen because they represent the focus of current pest management strategies for this pest and best represent overall pest dynamic trajectories (Naranjo & Ellsworth, 2009).

3 | RESULTS

3.1 | Life table analyses

Rates of marginal mortality by factor pooled over all immature developmental stages varied over the 14 years of the study, but consistent patterns emerged (Figure 1). Rates of marginal predation and dislodgement were consistently the greatest sources of mortality, but these rates did not differ statistically from pre- to post-establishment of parasitoids after accounting for multiple tests ($p > 0.03$). Likewise, marginal rates of parasitism did not differ as a result of parasitoid establishment ($p = 0.45$). The highest rates of mortality were consistently observed in the fourth nymphal stage (0.69 overall years), followed by the egg stage (0.40) and then the remaining nymphal stages (0.20–0.21; data not shown).

A different pattern was observed for rates of irreplaceable mortality, or the mortality that would be lost if a given mortality factor was absent (Figure 2). Irreplaceable mortality from predation significantly increased after exotic parasitoid establishment ($p = 0.001$). Irreplaceable mortality from unknown causes declined significantly with establishment ($p = 0.003$, not shown). Irreplaceable mortality

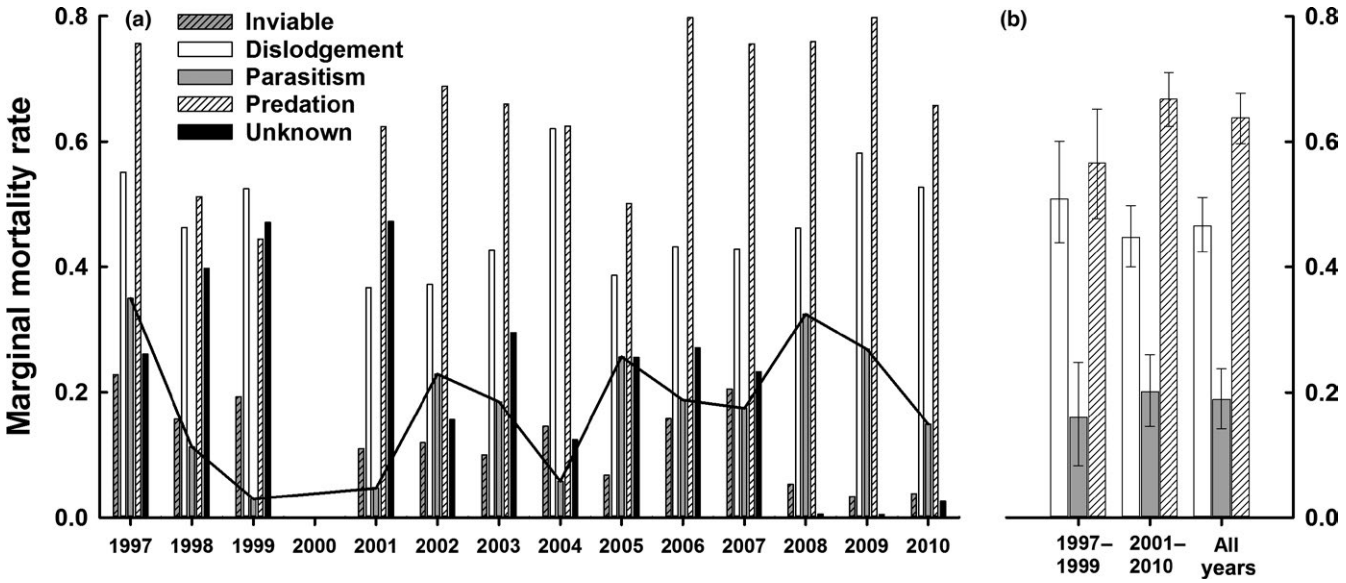

FIGURE 1 Mean marginal rates of *Bemisia tabaci* mortality by factor pooled across all immature life stages for each year (a) and averaged over time periods before (1997–1999) and after (2001–2010) the establishment of exotic parasitoids (b). The line in (a) emphasizes rates of marginal parasitism over time. Error bars are bootstrapped 95% confidence intervals

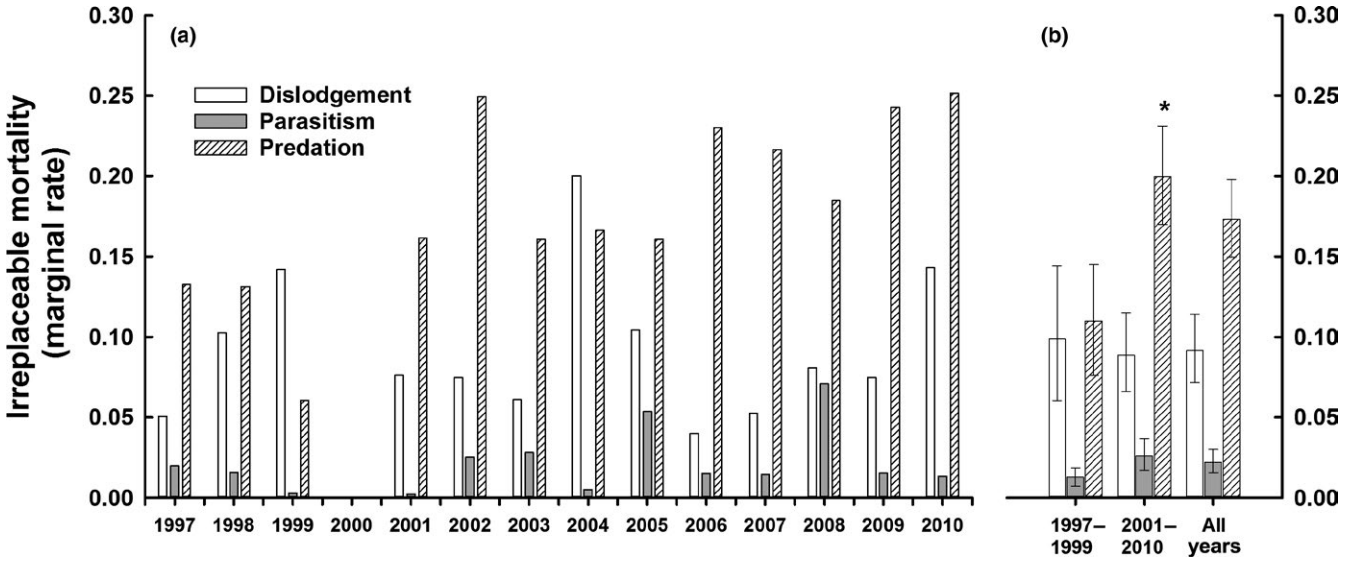

FIGURE 2 Mean marginal rates of *Bemisia tabaci* irreplaceable mortality by mortality factors pooled across all immature life stages for each year (a) and averaged over time periods before (1997–1999) and after (2001–2010) the establishment of exotic parasitoids (b). Error bars are bootstrapped 95% confidence intervals; asterisks denote significant differences based on permutation tests

from parasitism increased slightly and that from dislodgement declined slightly, but neither significantly ($p > 0.12$).

Rates of total immature mortality did not change relative to the establishment of exotic parasitoids ($p = 0.48$; Figure 3), consistent with the lack of changes in factor- or stage-specific marginal mortality rates over time.

Evidence of temporal density dependence in any stage-specific mortality associated with natural enemies was weak (Table 1). Prior to establishment there was an inverse density-dependent relationship between egg density and dislodgement and a similar inverse relationship for dislodgement of small nymphs over all 14 years. There was direct density dependence for rates of parasitism (associated with large nymphs or all nymphs) following parasitoid establishment, and for all years combined. Finally, there was delayed direct density dependence for parasitism based on all years. In all cases, the slopes of the relationships were small, suggesting weak responses to host density.

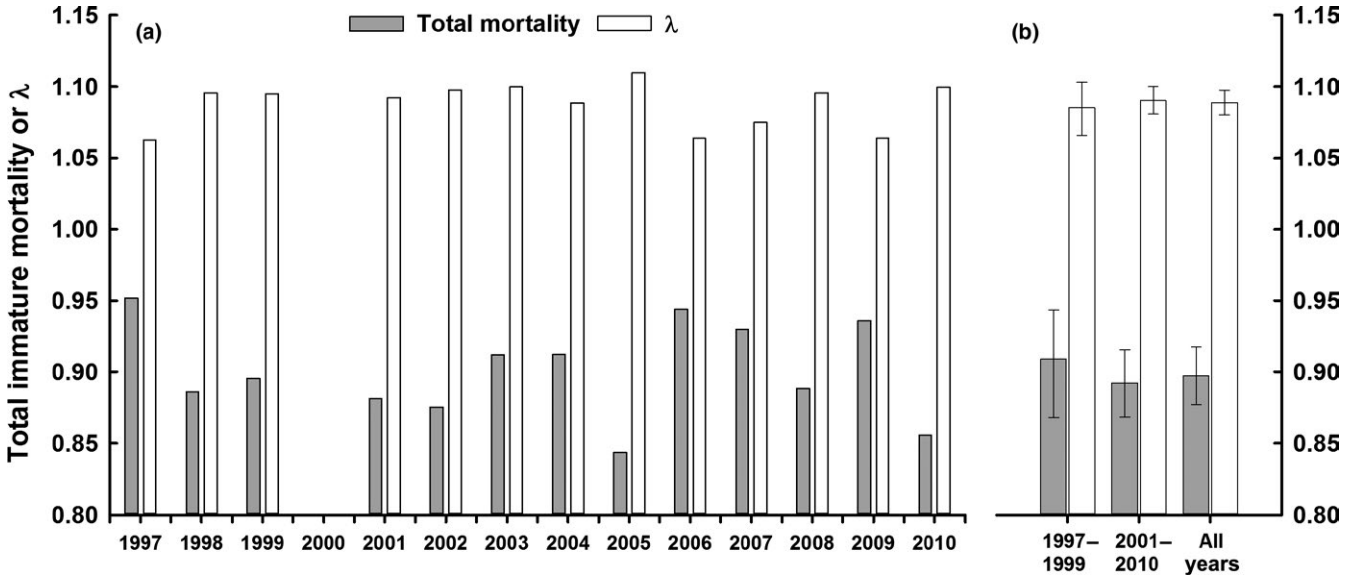

FIGURE 3 Mean rates of total immature mortality and finite rates of increase (λ) for *Bemisia tabaci* for each year (a) and averaged over time periods before (1997–1999) and after (2001–2010) the establishment of exotic parasitoids (b). Error bars are bootstrapped 95% confidence intervals

TABLE 1 Temporal density dependence of natural enemy-induced mortality of *Bemisia tabaci* on cotton before and after the establishment of exotic aphelinid parasitoids, Maricopa, Arizona, USA

	Within generation			Lag-1 generation		
Stage/Factor	1997–1999 Slope (*P*)	2001–2010 Slope (*P*)	All years Slope (*P*)	1997–1999 Slope (*P*)	2001–2010 Slope (*P*)	All years Slope (*P*)
Egg						
Predation	−0.011 (0.70)	−0.015 (0.32)	−0.017 (0.27)	0.005 (0.86)	−0.030 (0.25)	−0.014 (0.47)
Dislodgement	**−0.073 (0.01)**	−0.021 (0.49)	−0.043 (0.03)	0.007 (0.74)	−0.062 (0.16)	0.030 (0.25)
Small nymph						
Predation	0.002 (0.91)	0.003 (0.80)	0.003 (0.71)	−0.015 (0.47)	0.012 (0.48)	0.0159 (0.20)
Dislodgement	−0.084 (0.05)	−0.015 (0.31)	**−0.047 (0.006)**	−0.008 (0.59)	−0.047 (0.10)	−0.028 (0.12)
Large nymph						
Parasitism	0.009 (0.78)	**0.082 (0.002)**	**0.048 (0.01)**	0.034 (0.44)	0.106 (0.016)	**0.078 (0.01)**
Predation	0.016 (0.68)	0.008 (0.84)	0.039 (0.18)	0.090 (0.09)	−0.021 (0.73)	0.061 (0.21)
Dislodgement	0.015 (0.60)	0.012 (0.60)	0.006 (0.71)	0.028 (0.49)	0.029 (0.34)	0.021 (0.36)
All nymph						
Parasitism	0.012 (0.69)	**0.065 (0.01)**	0.041 (0.03)	0.028 (0.53)	0.102 (0.02)	0.075 (0.02)
n	14	31	45	11	23	34

Note. *k*-value of stage-specific mortality factor regressed on ln of *Bemisia tabaci* life stage density. Values in bold text indicate a slope significantly different from zero. Multiple tests corrected over observations within a time period with the false discovery rate of 5%.

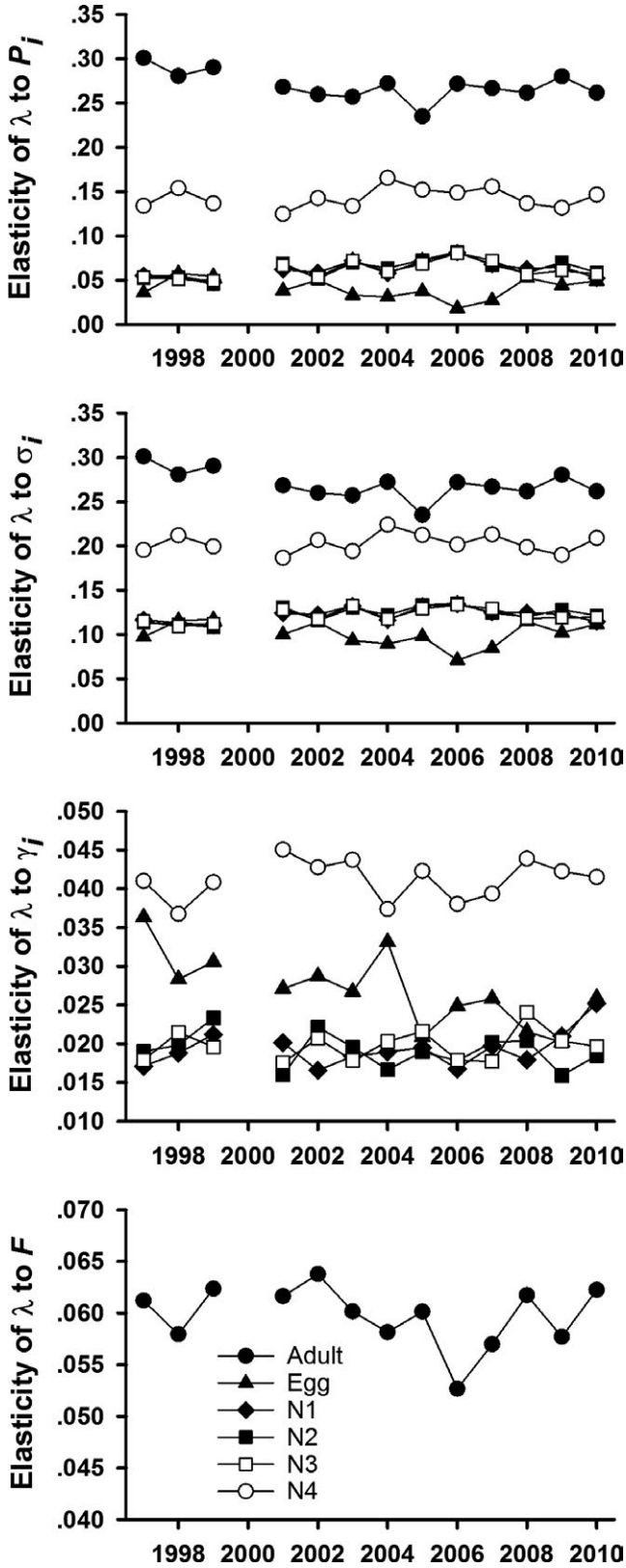

FIGURE 4 Elasticity of λ to P_i (probability of surviving and remaining in stage *i*), *F* (daily rate of females per female), σ_i (stage survival probabilities) and γ_i (stage growth probabilities) over time. Elasticity of λ to G_i (probability of transition from stage *i* to *i* + 1) was not plotted because it was small and invariable among life stages. Note scale changes in *y*-axis. N1–N4, nymphal stages 1–4

3.2 | Matrix model analyses

Finite rates of increase, λ, did not change with parasitoid establishment ($p = 0.70$; Figure 3). Finite population growth averaged 1.085 before establishment, 1.090 after and 1.089 over all 14 years, indicating growing populations. There were no differences in λ pre- and post-establishment when using the same mean temperatures for estimating immature growth, and adult survival and fecundity in all matrices ($p = 0.16$).

3.2.1 | Prospective matrix model analyses

Elasticities of λ to matrix elements P_i and G_i and decomposed survival (σ_i) and growth (γ_i) rates were strongest for the fourth nymphal stage (Figure 4). Elasticities remained largely unchanged with the establishment of exotic parasitoids ($p > 0.14$), but some small elasticities associated with 1st–3rd nymphal survival did vary between treatments ($p < 0.008$). Elasticity of λ to adult survival, was comparatively high but adult longevity was estimated from laboratory data and may not accurately reflect the mortality dynamics of this life stage in the field (Figure 4).

Analyses examining the effect of removing mortalities associated with specific life stages or factors on population growth showed that mortality during the fourth stadium, predation over all stages and predation during the fourth nymphal stadium were associated with the largest reductions in population growth (Table 2). These results were consistent with more traditional key factor analyses (Supporting Information Table S4). The establishment of exotic parasitoids did not alter these patterns.

3.2.2 | Retrospective matrix model analyses

Population growth rate increased slightly in the years following exotic parasitoid establishment, as noted above, and LTRE analyses enabled assessment of the contributions of each decomposed vital rate to this change (Figure 5). Consistent with an increase in λ, the contributions of many of the individual sources of mortality were positive, albeit only the contribution from unknown causes during the third nymphal stadium was significantly greater than zero ($p = 0.001$; Figure 5a). In contrast, predation during the fourth stadium contributed negatively ($p = 0.001$), consistent with the higher level of irreplaceable mortality supplied by this factor over all stages (see Figure 2). The patterns of positive contributions to the change in λ are further demonstrated when the differences are summed over factor or stage (Figure 5c,d). Compared with the actual change in λ between treatments, the LTRE analysis accounted for 99.33% of the difference.

3.3 | Changing host density and parasitism

A common approach to assessing the impact of biological control introductions is to examine the longer term trends in pest density in relation to the activity of the introduced agent(s). Population densities of *B. tabaci* large nymphs and adults, and marginal rates

TABLE 2 Contribution of mortality by stage and factor to finite population growth (λ) for *Bemisia tabaci* in cotton before and after the establishment of exotic parasitoids, Maricopa, Arizona, USA. The most influential stages or factors are noted in bold type

		Matrix model analysis[a]		
	Factor/stage	Pre (97–99)	Post (01–10)	All years
Stage	Egg	3.291	2.319	2.643
	N1	1.276	1.121	1.167
	N2	1.507	0.992	1.144
	N3	1.354	1.167	1.223
	N4	**3.415**	**3.683**	**3.567**
Factor	Inviable	0.857	0.484	0.594
	Dislodgement	3.208	2.669	2.828
	Parasitism	0.379	0.586	0.524
	Predation	**3.394**	**4.076**	**3.874**
	Unknown	1.812	0.883	1.157
N4 factor	Dislodgement	0.458	0.385	0.406
	Parasitism	0.379	0.586	0.524
	Predation	**0.955**	**1.720**	**1.494**
	Unknown	0.739	0.576	0.624

Note. [a]Mean per cent change in λ when mortality from the indicated stage or factor was removed from the matrix model; n = 13 pre-establishment, 31 post-establishment.

of parasitism, varied considerably over the 10 years since establishment of the exotics (Figure 6). However, there was no relationship between host density and marginal parasitism rate (large nymphs, Spearman's = 0.03, p = 0.93, n = 10; adults, Spearman's = 0.14, p = 0.70, n = 10) since establishment.

4 | DISCUSSION

Life table response experiments, and analyses of the associated underlying life tables and matrix models, represent a robust approach for quantifying how changes in factors affecting vital rates ultimately contribute to population growth or decline. The addition of an exotic natural enemy to an ecosystem represents a clear change, the impacts of which should be measurable in terms of altered vital rates and an associated decline in the target pest population (Catton et al., 2016; Dauer et al., 2012; McEvoy & Coombs, 1999). While observations showing correlation between increased apparent parasitism and decline of pest density may support a conclusion of potentially successful biological control (e.g. Bellows et al., 1992; De Barro & Coombs, 2009; Pickett, Keaveny, & Rose, 2013;), matrix models and LTREs provide for a more robust quantitative and mechanistic assessment. Such an approach enables an understanding of the factors contributing to pest population decline and strengthens our ability to build on such successes (or failures) in the future. Recently, Cock et al. (2016) noted that just over 600 classical biological control programmes for insect pests have resulted in at least satisfactory control of the target, but Greathead and Greathead (1992) suggested that reporting is not always accurate and it is unclear how many of these have received careful quantitative assessment. While not simple or inexpensive, life table, matrix model and LTRE analyses should be more broadly applied to the assessment of classical and other approaches to biological pest control.

The classical biological control programme for *B. tabaci* resulted in the successful establishment of two exotic parasitoids that largely or entirely replaced their native parasitoid counterparts in the cotton system by 2004 (Naranjo & Li, 2016), but did not appear to change any of the factors contributing to pest population suppression. Specifically, analyses showed that introductions (a) did not result in increased marginal rates of parasitism, (b) did not supply novel sources of mortality absent before introductions and (c) ultimately did not result in lower rates of pest population growth. Additionally, mortality during the fourth nymphal stadium, especially that provided by predation, contributed the most to reductions in population growth, and this pattern was not altered by parasitoid establishment. There was evidence of temporal direct density dependence in parasitism rates following introductions and delayed density dependence over all 14 years, but it is unclear what role this played in pest population dynamics as it did not translate into a relationship between increasing parasitism and declining pest density at the study site. Generally, the prevalence and impact of density dependence in insect populations has been debated (Hassell, Latto, & May, 1989; Stiling, 1988). Overall, the outcome here supports the hypothesis that classical biological is unsuccessful if maximum parasitism rates fail to exceed 33%–36% (Hawkins & Cornell, 1994). Parasitism exceeded this threshold in only a single year in each of the pre- and post-establishment periods with parasitism averaging 20% since establishment and 18.9% over the 14-year study.

Population growth was positive both before and after parasitoid establishment. Even so, regional population of *B. tabaci* have greatly declined from the initial invasion as have the associated application of insecticides (Naranjo & Ellsworth, 2009). I show here that these

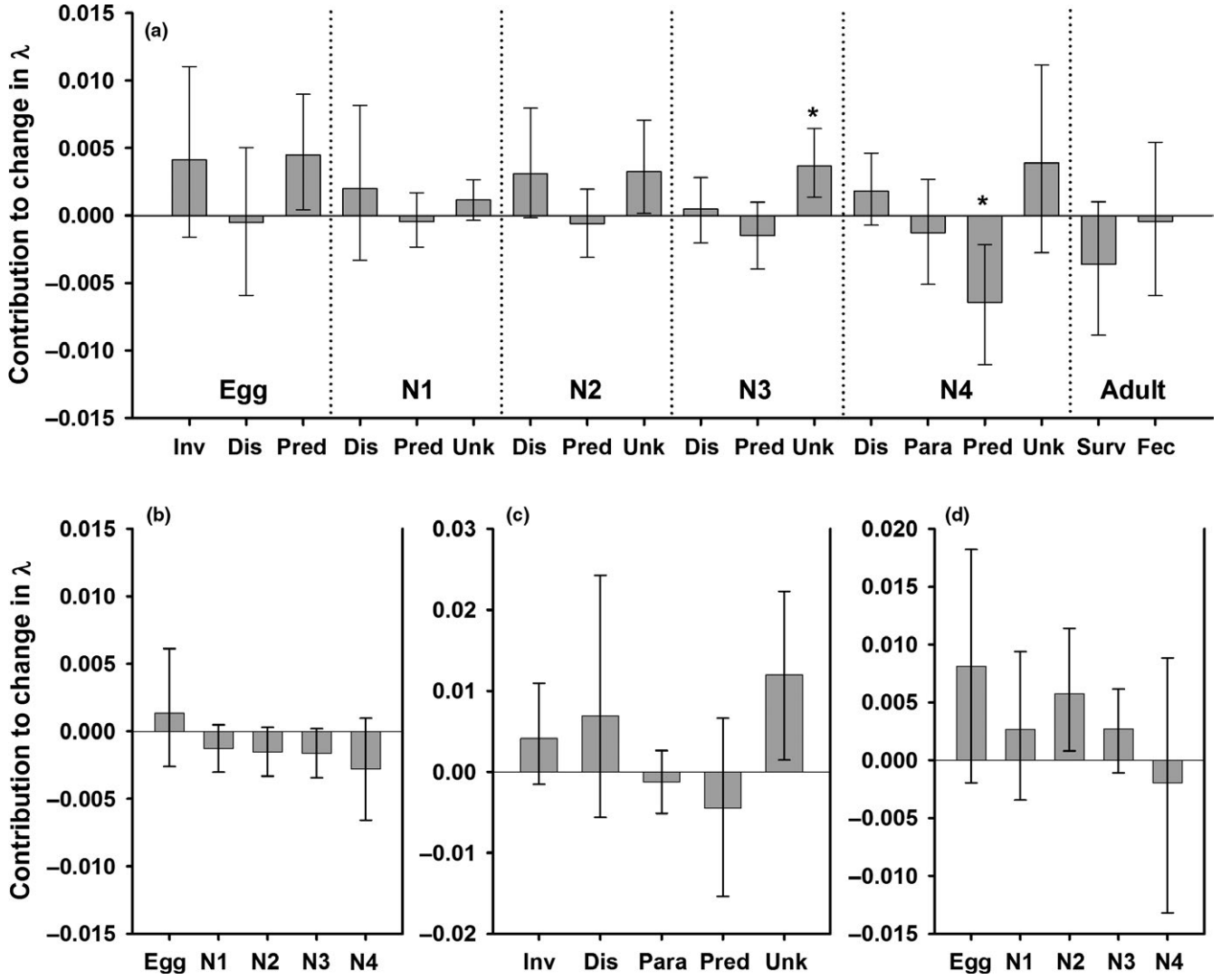

FIGURE 5 Contribution of decomposed vital rates to changes in λ relative to the establishment of exotic parasitoids. (a) All stages and mortality factors, (b) stage growth rates, (c) mortality contributions summed over all stages and (d) stage contributions summed over all mortality factors. Asterisks denote significant contributions based on permutation tests. N1–N4, nymphal stages 1–4; Inv = inviable, Dis = dislodgement, Pred = predation, Para = parasitism, Unk = unknown, Surv = adult longevity, Fec = fecundity

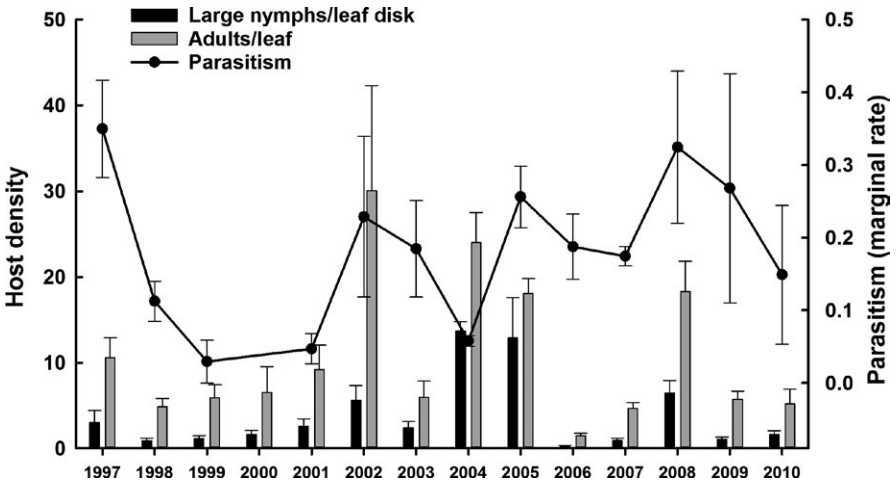

FIGURE 6 Association between seasonal mean *Bemisia tabaci* densities and mean marginal rates of parasitism in cotton 1997–2010. Error bars are SEM; n = 2–5 life tables per year, n = 7–15 dates per year for host density

patterns were not the result of improved biological control from the two introduced parasitoids. Instead, multiple tactics associated with improved integrated pest management strategies for all pests in major host crops such as cotton and various vegetables (Naranjo & Ellsworth, 2009; Palumbo, Horowitz, & Prabhaker, 2001) have affected this outcome. In cotton, one key tactic has been conservation and use of generalist arthropod predators through adherence to economic thresholds, and use of selective insecticides. The generally increasing levels of predation, even after the establishment of exotic parasitoids, point to the critical role of predation in the population dynamics of *B. tabaci*. These patterns also suggest that the overall agroecosystem has become more favourable to ecosystem services like biological control.

Greathead and Greathead (1992) suggested that many classical biological control failures go unreported and many factors can influence success or failure (Hokkanen, 1985; van Driesche & Hoddle, 2000). Several elements may have contributed to the lack of efficacy of this classical biological control programme, including poor parasitoid dispersal (Hagler, Jackson, Henneberry, & Gould, 2002) coupled with the ephemeral nature of annual crops that require recolonization each season, and the polyphagous biology of the pest (Kennedy & Storer, 2000). The relatively poor record of success of classical biological control in annual compared with perennial crops further supports this challenge (DeBach, 1964; Hawkins, Mills, Jervis, & Price, 1999). In contrast, the generalist predator community appears well adapted to exploiting ephemeral prey resources (Naranjo, Ellsworth, & Cańas, 2009). The introduction of the autoparasitoid (*E. sophia*) also may have played a role, but this species became dominant only by 2006 (Naranjo & Li, 2016), and there is no clear change in levels of parasitism from before this time. Life tables may not have adequately quantified host-feeding, and thus additional mortality imposed by either the native or exotic parasitoids. This behaviour is common in aphelinid parasitoids attacking a wide range of insect species, including those here (Ardeh, de Jong, & van Lenteren, 2005; Zang & Liu, 2008). Life table observations failed to detect any obvious evidence of host-feeding on *B. tabaci* nymphs (Naranjo & Ellsworth, 2017), although this mortality could have, on occasion, been incorrectly captured in the unknown category. Nonetheless, even if exotic parasitoids engaged more readily in host-feeding than their native counterparts, this did not translate into reduced population growth rates. Finally, studies here were intensively focused over a long duration in a single crop in a single region, but were not extensive in terms of examining other key host crops and/or other geographic regions for this polyphagous pest. Stronger biological control in other crops could have cascaded into better control in cotton by reducing immigration (see Supporting Information Appendix S4 for further discussion).

Prospective matrix model analyses point to potential avenues of exploration for improving biological control of *B. tabaci* in this system. For example, elasticity was greatest for survival during the fourth nymphal instar and the adult stage. This former vulnerability is already being exploited by native generalist arthropod predators (Naranjo & Ellsworth, 2005), and could perhaps be enhanced beyond selective insecticides by active habitat management to encourage even higher populations of predators. Interestingly, although prospective analyses were never applied before the launch of the *B. tabaci* classical biological control programme, *a priori* application of my analyses would likely have pointed to aphelinid parasitoids as useful agents. They may attack earlier instar nymphs but affect their mortality during the fourth stadium. Unfortunately, the mortality caused by the exotic species simply replaced that of the native species. The adult stage represents another vulnerability that has not been explicitly exploited. Arthropod predators and entomopathogens can affect adults (Faria & Wraight, 2001; Hagler, Jackson, Isaacs, & Machtley, 2004) and further examination and enhancement of these mortality forces later in the life cycle appear warranted.

Parasitoids are most often the key factor in introductions for control of exotic pests on native or exotic crops (Hawkins et al., 1999). However, in this system predators remained the "key" factor even after parasitoid establishment, based on both life table and matrix model analyses. Traditional key factor analysis (Varley, Gradwell, & Hassell, 1973) has been criticized as not being reflective of the patterns of population change and the underlying causes (Royama, 1996). Elasticity analysis, removal of mortality forces in matrix model analyses and key factor analysis all pointed to mortality during the fourth nymphal stadium (specifically predation) as most influential to the rate of population growth. This suggests that traditional key factor analysis may be revealing in some situations.

Ideally, deployment of life tables and matrix models for classical biological control should be considered in advance so that proper before and after treatments can be established. In some instances, it may be possible to implement treatments spatially before the exotic natural enemies become widely established. With only temporal separation between treatments, another limitation was the nature of the statistical analyses that are possible. In this study, there were no randomized replicates of each treatment (before or after establishment). This limitation is common in the assessment of classical biological control (van Driesche & Hoddle, 2000) and in other ecological processes that have changed or been disturbed by disasters (Wiens & Parker, 1995). The BACI approach cannot provide unbiased statistical tests of effects. However, if the breadth of the metrics examined is large and/or the effect sizes are either very small or very large, then the statistical tests are less important relative to the obvious ecological effects.

In conclusion, life tables, matrix models and LRTEs enable robust quantitative assessment of biological control programmes and provide important insight into pest demographics within the context of existing mortality forces. Their application confirms and extends previous work in showing that immature stages of *B. tabaci* are consistently subject to high levels of natural mortality in cotton (Naranjo & Ellsworth, 2005), with much of it due to the activity of generalist arthropod predators. Biological control plays a key role in the management of this pest but the classical biological control programme did not appear to improve these ecosystem services. These analytical approaches should be more broadly applied in biological control both prospectively, to better match agents with pest demographics, and retrospectively, to delineate mechanisms responsible for programme success or failure.

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DATA ACCESSIBILITY

Data available via the Ag Data Commons (USDA National Agricultural Library) https://doi.org/10.15482/usda.adc/1373297 (Naranjo, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Appendix S1. Life table set-up, identification of mortality factors, and temperature-dependent development and reproduction.

LIFE TABLE SET-UP

Life table data were generated using an *in situ* observational method that took advantage of the sessile nature of the immature stages of *B. tabaci*. This approach avoided practical issues associated with the broadly overlapping generations of this multivoltine insect. Groups of newly-laid eggs were established from existing natural populations on the undersides of cotton leaves. These eggs were characterized by their creamy-white color and their location on leaves near the terminal growth of the cotton plant. With the aid of an 8X Peak® loupe (Adorama, New York, New York, USA), a non-toxic, ultra-fine-point black permanent marker (Sanford, Illinois, USA) was used to draw a small circle around individual eggs or small clusters of no more than 4–5 eggs. A small numbered tag was then placed around the petiole of the leaf and flagging tape was tied around the mainstem of the plant to facilitate relocation. No more than 5–7 eggs were marked on a single leaf, and the main leaf sectors defined by the major leaf veins were used to help track each egg in the study cohort. Only a single leaf was used per plant and plants were evenly spaced along the central 2–3 rows of each study plot. The total number of plants used per plot varied depending on insect density and ranged from 20–40. Forty to sixty eggs were marked in each plot for a total of 160–240 eggs on 80-160 plants per life table over four replicate plots.

A similar procedure was used to locate and mark the position of newly settled 1st instar nymphs with the exception that marked circles never contained more than one nymph. Crawlers were readily distinguished from settled 1st instars as the latter have a more translucent color and are flush with the leaf surface. Typically, crawlers settle in a few minutes to 1-2 h after eclosion. To verify that settled nymphs and not mobile crawlers were marked, leaves were re-examined 1-2 h later and re-marked as needed. Forty to sixty nymphs were marked per plot on 20-40 plants (total of 160–240 nymphs on 80-160 plants per cohort). Cohorts were established on a single day during morning hours and eggs and 1st instar nymphs were marked on different plants. Between 2–6 individual life tables were established each year of the study and generally between late-June and late September. These dates cover the breadth of the insect's occurrence on cotton in central Arizona (Naranjo & Ellsworth 2009). Using this *in situ* observational approach each life table represented a single generation of this multivoltine insect, which facilitated direct estimation of mortality rates due to various causes.

IDENTIFICATION OF MORTALITY FACTORS

After establishing cohorts each nymph was examined every 2–3 days (three times per week) in the field with the aid of a 15X Peak® loupe (Adorama, New York, New York, USA) until that individual died or emerged as an adult. Eggs were too difficult to examine in the field and so all leaves containing eggs were collected after 8-10 days and returned to the laboratory for examination under a dissecting microscope. Under typical summer conditions in central Arizona eggs complete development in about 5 days and so any relevant field mortality would have already occurred by the time they were collected. During each observation, the instar of each live nymph and the instar and cause of death of each dead nymph were recorded. Mortality was categorized into one of five causes; dislodgment, predation, parasitism, inviability (eggs only), and unknown. Dislodgement was the result of abiotic factors such as wind and rain, and chewing predation. The stage of dislodged nymphs was estimated by the average stage of other dead

nymphs on the same observation date. Predation was mortality primarily due to sucking predators that had evacuated the contents of the whitefly body leaving a deflated and transparent nymphal cuticle or egg chorion on the leaf (see Naranjo & Ellsworth 2017). Very infrequently, chewing predation could be seen in partially intact cadavers. Aphelinid parasitoids can successfully attack all nymphal stages of *B. tabaci* (Foltyn & Gerling 1985; Headrick, Bellows & Perring 1995, Liu & Stansly 1996), but parasitism is only visible in 4th instar nymphs. Parasitoid presence was characterized by the displacement of the whitefly's bacteriosomes or by live parasitoid larvae or pupae within the host. There are no known egg parasitoids of *B. tabaci*. Inviable eggs were simply those that failed to eclose after 10 days. When all marked individuals on a leaf either had died or emerged, the leaf was collected and returned to the laboratory to verify the cause of death (with a dissecting microscope) for those cadavers remaining on the leaf. Mortality during the brief period between crawler emergence and settling was not explicitly measured. The duration between eclosion and settling averages only a few hours (Price & Taborsky 1992; Simmons 2002), and field studies have shown that crawler mortality on cotton is negligible (Naranjo 2007).

TEMPERATURE-DEPENDENT DEVELOPMENT AND REPRODUCTION

The temperature-dependent rates of development for eggs and nymphs were estimated from Wagner (1995). He used the 6 and 4 parameter Sharpe and DeMichele (1977) models for eggs and nymphs (1st instar to adult), respectively, given as

$$\frac{RHO25\frac{T}{298.15}e^{[HA/R(0.0034-1/T)]}}{1+e^{[HL/R(1/TL-1/T)]}+e^{[HH/R(1/TH-1/T)]}} \quad \text{eqn. S1}$$

$$\frac{RHO25\frac{T}{298.15}e^{[HA/R(0.0034-1/T)]}}{1+e^{[HH/R(1/TH-1/T)]}} \quad \text{eqn. S2}$$

where temperature, *T*, is measured in degrees Kelvin, *R* is the university gas constant (1.987), and *RHO25, HA, HL, TL, HH*, and *TH* are fitted biophysical parameters. The duration of each nymphal stadium was then estimated from the proportion of time spent in each of the four nymphal stages (Bethke, Paine & Nuessly 1991; Powell & Bellows 1992). Temperatures were estimated from archived mean daily air temperatures from an on-site weather station (AZMET 2016) for the short period (2-3 week) between cohort establishment and adult emergence for each life table.

Parameter	Egg	Nymph
RHO25	0.2043	0.0977
HA	21,176	25,232
HL	-84,284	
TL	286.2	
HH	42,173	61,409
TH	304.2	301.7
R^2	0.99	0.98

Temperature-dependent lifetime fecundity (eggs per female) and adult longevity was derived from published and unpublished data by Wagner (1994). A bounded (15 – 40˚C) 3rd degree polynomial regression predicted lifetime fecundity as a function of temperature, t in ˚C (fecundity = $95.99t - 3.62t^2 + 0.04t^3 - 655.2$, $R^2 = 0.36$). Adult longevity was predicted by regressing ln longevity on

temperature (ln[longevity] = 4.41 – 0.073t, $R^2 = 0.68$). Mean daily air temperatures were calculated for the 10-day interval following adult emergence using the archived weather data noted above for each life table.

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Table S1. Summary of cotton life table study sites, 1997–2010, Maricopa, Arizona, USA

Year	Cultivar	Study area (ha)	Total exp. area (ha)	No. generations	Associated study
1997	DP NuCOTN33B	0.24	1.9	4	†
1998	DP NuCOTN33B	0.26	2.1	5	†
1999	DP NuCOTN33B	0.26	2.1	4	†
2001	DP NuCOTN33B/5415*	0.68	1.4	4	‡
2002	DP NuCOTN33B/5415*	0.68	1.4	4	‡
2003	DP NuCOTN33B/5415*	0.68	1.4	4	‡
2004	DP 449BR	0.38	0.8	2	Current study
2005	DP 449BR	0.30 – 0.52	5.3	4	Current study
2006	DP 449BR	0.52	5.4	2	Current study
2007	DP 164B2RF	0.52	3.7	2	Current study
2008	DP 164B2RF	0.72	3.8	3	¶
2009	DP 164B2RF	0.72	2.6	3	¶
2010	DP 1044B2RF	0.60	2.2	3	¶

* Deltapine 5415 is the non-Bt isoline of NuCOTN33B

† Naranjo, S.E. & Ellsworth, P.C. (2005) Mortality dynamics and population regulation in *Bemisia tabaci*. *Entomologia Experimentalis et Applicata* **116,** 93-108.

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Table S2. General projection matrix for the stage-structured *B. tabaci* population model, where σ_i is daily stage-specific survival rate, γ_i is daily stage-specific rate of growth to the next stage, and F is the mean daily rate of adult fertility (females per female).

	Egg	**N1**	**N2**	**N3**	**N4**	**Adult**
Egg	$\sigma_e(1-\gamma_e)$	0	0	0	0	F
N1	$\sigma_e(\gamma_e)$	$\sigma_{N1}(1-\gamma_1)$	0	0	0	0
N2	0	$\sigma_{N1}(\gamma_1)$	$\sigma_{N2}(1-\gamma_2)$	0	0	0
N3	0	0	$\sigma_{N2}(\gamma_2)$	$\sigma_{N3}(1-\gamma_3)$	0	0
N4	0	0	0	$\sigma_{N3}(\gamma_3)$	$\sigma_{N4}(1-\gamma_4)$	0
Adult	0	0	0	0	$\sigma_{N4}(\gamma_4)$	σ_a

Where N1-N4 are nymphal instars 1-4 and,

$\sigma_e = \sigma_{inviable(e)}\sigma_{dislodged(e)}\sigma_{predation(e)}$

$\sigma_{N1} = \sigma_{dislodged(N1)}\sigma_{predation(N1)}\sigma_{unknown(N1)}$

$\sigma_{N2} = \sigma_{dislodged(N2)}\sigma_{predation(N2)}\sigma_{unknown(N2)}$

$\sigma_{N3} = \sigma_{dislodged(N3)}\sigma_{predation(N3)}\sigma_{unknown(N3)}$

$\sigma_{N4} = \sigma_{dislodged(N4)}\sigma_{parasitism(N4)}\sigma_{predation(N4)}\sigma_{unknown(N4)}$

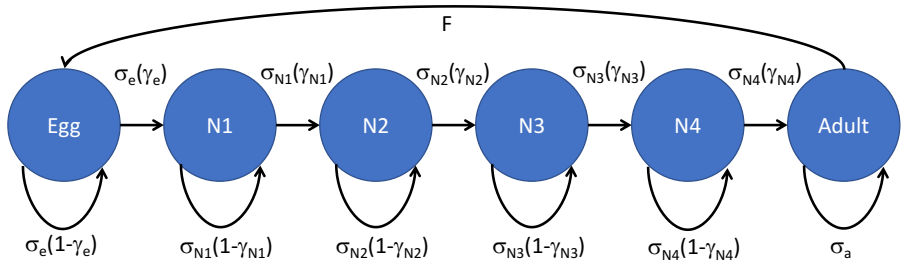

Figure S1. Life cycle diagram for projection matrix depicted in Table S2.

Appendix S2. Key factor analysis

Introduction

Key factor analysis (Varley, Gradwell & Hassell 1973) is frequently applied in life table studies as a means of understanding what mortality factor and/or stage contribute the most to variability in total population survival. The approach has been criticized because it is thought to lack the ability to reflect patterns of population change and the underlying causes of this change (Royama 1996; Sibly and Smith 1998). A key factor analysis was conducted here to compare patterns with elasticity analysis and with matrix manipulations where mortality associated with particular factors and life stages were removed from the model.

Materials and Methods

Key factor analysis was conducted using the regression approach of Podoler & Rogers (1975), where individual stage or factor mortality k-values (k=-ln[1-M], where M is marginal mortality) are regressed on total K (generational mortality). The largest positive regression coefficient (slope) identifies the key factor. Analyses identified the key stage across all factors, the key factor across all stages and the key factor within the 4^{th} nymphal stage. Additional focus on mortality within the 4^{th} stage was indicated from the elasticity and matrix model analyses, and prior research (Naranjo & Ellsworth 2005; Asiimwe, Ellsworth & Naranjo 2016).

Results

Key factor analysis indicated that mortality during the 4^{th} nymphal stadium was most closely associated with changes in generational mortality both before and after the establishment of exotic aphelinid parasitoids (Table S3). Looking at mortality factors over all stages, predation emerged as the key factor and this pattern was again no changed with exotic parasitoid establishment. Parasitism was the third to fourth most important factor associated with changes in generational mortality. Given the apparent importance of mortality during the 4^{th} nymphal stadium, further focus was placed on mortality factors within this stage. Again, predation was the key factor with parasitism being the least important factor during pre-establishment but the second most important factor after establishment.

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Table S3. Analyses for identifying which life stage mortality and which mortality factors contribute to changes in generational mortality (key factor) of *Bemisia tabaci* in cotton before and after the establishment of exotic aphelinid parasitoids, Maricopa, Arizona, USA. The most influential stages or factors are depicted in bold type.

	Factor/Stage*	**Key factor analysis†**		
		Pre (97-99)	Post (01-10)	All years
Stage¶	Egg	0.342	0.088	0.182
	N1	-0.008	0.113	0.076
	N2	0.069	0.016	0.038
	N3	0.001	0.058	0.041
	N4	**0.597**	**0.725**	**0.661**
Factor	Inviable	0.191	0.026	0.117
	Dislodgement	0.311	0.235	0.256
	Parasitism	0.154	0.166	0.139
	Predation	**0.333**	**0.519**	**0.378**
	Unknown	0.009	0.037	0.101
N4 Factor	Dislodgement	0.149	0.043	0.088
	Parasitism	0.132	0.166	0.139
	Predation	**0.222**	**0.363**	**0.233**
	Unknown	0.163	0.065	0.123

n = 13 generations for pre-establishment, 31 for post-establishment.
* Stage, each life stage over all factors (N1 = 1st instar nymph, etc.); Factors, each factor over all life stages; N4 factor, mortality factors during 4th stadium only and so slopes shown do not sum to unity for key factor analyses.
†Values are the slopes of k-values for stages or factors regressed on total K for the generation.

Appendix S3. Details of LTRE analyses

Retrospective matrix model analyses. A LTRE approach was used to assess the contribution of vital rates to changes in population growth due to parasitoid establishment. Following Caswell (1996) the effect on λ is given generally by:

$$\lambda^m - \lambda^r \approx \sum_{i,j}(a_{i,j}^m - a_{i,j}^r)\frac{\partial\lambda}{\partial a_{i,j}}\Big|_{(A^m+A^r)/2} \quad \text{eqn. S1}$$

where the superscripts *m* and *r* refer to treatment and control (or reference), respectively, $a_{i,j}$ are the elements of the projection matrices and $\partial\lambda/\partial a_{i,j}$ is the sensitivity of λ to changes in the matrix elements evaluated on the mean of the treatment and control matrices ($[A^m+A^r]/2$). The matrix elements alone are of little interest here because they are composed of vital rates representing both growth (γ_i) and survival (σ_i). Survival, in turn, is composed of effects from multiple, specific mortality factors (e.g., predation, parasitism, dislodgement, etc.). Caswell (1996) showed that in general the sensitivity of λ to changes in any lower-level vital rate *x* is given by:

$$\frac{\partial\lambda}{\partial x} = \sum_{i,j}\frac{\partial\lambda}{\partial a_{i,j}}\frac{\partial a_{i,j}}{\partial x} \quad \text{eqn. S2}$$

Thus, for decomposed lower level vital rates, eqn. S1 can be expanded to:

$$\lambda^m - \lambda^r \approx \sum_i(\sigma_i^m - \sigma_i^r)\frac{\partial\lambda}{\partial\sigma_i} + \sum_i(\gamma_i^m - \gamma_i^r)\frac{\partial\lambda}{\partial\gamma_i} + (F^m - F^r)\frac{\partial y}{\partial F} \quad \text{eqn. S3}$$

where

$$\frac{\partial\lambda}{\partial\sigma_i} = \frac{\partial\lambda}{\partial P_i}(1-\gamma_i) + \frac{\partial\lambda}{\partial G_i}\gamma_i \quad \text{eqn. S4}$$

$$\frac{\partial\lambda}{\partial\gamma_i} = \frac{\partial\lambda}{\partial P_i}(-\sigma_i) + \frac{\partial\lambda}{\partial G_i}\sigma_i \quad \text{eqn. S5}$$

Given that survival for any single immature stage is the product of the individual survival values s_k from each cause of mortality *k,*

$$\sigma_i = \prod_k s_k \quad \text{eqn. S6}$$

eqn. S3 can be further decomposed into specific causes of death by substituting for σ_i:

$$\lambda^m - \lambda^r \approx \sum_i\sum_k(s_k^m - s_k^r)\frac{\partial\lambda}{\partial s_{i,k}} + \sum_i(\gamma_i^m - \gamma_i^r)\frac{\partial\lambda}{\partial\gamma_i} + (F^m - F^r)\frac{\partial\lambda}{\partial F} + (\sigma_a^m - \sigma_a^r)\frac{\partial\lambda}{\partial\sigma_a} \quad \text{eqn. S7}$$

where σ_a is adult survival and

$$\frac{\partial\lambda}{\partial s_{i,k}} = \frac{\partial\lambda}{\partial P_i}(1-\gamma_i)(\prod_k s_{i,k})/s_{i,k} + \frac{\partial\lambda}{\partial G_i}\gamma_i(\prod_k s_{i,k})/s_{i,k} \quad \text{eqn. S8}$$

$$\frac{\partial \lambda}{\partial \gamma_i} = \frac{\partial \lambda}{\partial P_i}\left(-\prod_k s_{i,k}\right) + \frac{\partial \lambda}{\partial G_i}\prod_k s_{i,k} \qquad \text{eqn. S9}$$

generally. Recall that there are three sources of mortality for eggs (inviability, predation, dislodgement) and each of the first three nymphal instars (predation, dislodgement, unknown) and four sources of mortality for 4th instar nymphs (parasitism, predation, dislodgement, unknown). As an example, for the egg stage, *e,* the sensitivity of λ with respect to decomposed survival rates for inviability is

$$\frac{\partial \lambda}{\partial s_{inv}} = \frac{\partial \lambda}{\partial P_e}(1-\gamma_e)s_{pred}s_{dis} + \frac{\partial \lambda}{\partial G_e}\gamma_e s_{pred}s_{dis} \qquad \text{eqn. S10}$$

where the superscripts inv, pred and dis denote inviability, predation and dislodgement.

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Appendix S4. Factors contributing to program failure.

Several elements may have contributed to the lack of efficacy of these newly established parasitoids in the Arizona cotton system. First, aphelinid parasitoids are not strong dispersers (Hagler *et al.* 2002; Byrne and Bellamy 2003), which does not align well with annual crops such as cotton that must be recolonized each season by both the pest and its natural enemies. Low dispersal capacity is supported by studies where parasitism is enhanced when host crops are grown in closer proximity to one another over the seasonal cycle (Naranjo, Ellsworth & Cañas 2009), when cotton is embedded in a more diverse cropping system (Karut & Naranjo 2009), and when host plant diversity in the form of annual and perennial plant borders were deployed to promote parasitoid establishment (Roltsch *et al.* 2008). Ephemeral annual crops pose significant challenges to biological control in general and classical biological control specifically, because it selects for certain attributes in introduced natural enemies that are not often the focus of agent selection (Gilstrap 1997; Wiedenmann & Smith 1997). The relatively poor record of success of classical biological control in annual compared with perennial crops further highlights this challenge (DeBach 1964; Hawkins *et al.* 1999).

Second, one of the species established is an autoparasitoid (*E. sophia*) in this system. Data and models suggest that the outcomes of biological control that include autoparasitic species can be either positive or negative (Summy *et al.* 1983; Mills & Gutierrez 1996; Williams 1996; Bogran, Heinz & Ciomperlik 2002; Hunter, Collier & Kelly 2002; Zang, Liu & Wan 2011). By 2006, *E. sophia* had become the dominant aphelinid attacking *B. tabaci* in cotton (Naranjo & Li 2016), but life tables showed no clear change in parasitism rates or overall host mortality. Hence, there is no clear evidence that the introduction of this species played a role in the outcome of this program.

Third, life tables may not have adequately quantified host-feeding, and thus additional mortality imposed by both the native or exotic aphelinid parasitoid species. This behavior is common in aphelinid parasitoids attacking a wide range of insect species, including the parasitoid species examined here (e.g., Urbaneja *et al.* 2003; Ardeh, de Jong & van Lenteren 2005; Zang & Liu 2008). Life table observations failed to detect any obvious evidence of host-feeding in *B. tabaci* nymphs, although this mortality could have, on occasion, been incorrectly captured in the unknown category. Sucking predators would nearly, or most often completely, disrupt and evacuate the contents of nymphs, and this has a distinctly different appearance than cadavers on which parasitoids had feed (Naranjo & Ellsworth 2017). It is possible that host-fed nymphs were subsequently attacked by sucking predators or dislodged from the leaf before they could be observed. Nonetheless, even if exotic parasitoids engaged more readily in host-feeding than their native counterparts, this did not translate into higher overall rates of mortality or reduced population growth rates.

Fourth, the target pest is extremely polyphagous, a factor that complicates management by any control tactic. One of the initial rationales for implementing a classical biological control program was the fact that parasitoid diversity was low in crops impacted by the pest, particularly winter and spring vegetable crops (Hoelmer, Schuster & Ciomperlik 2008), and considerable research examined the fit of exotic parasitoids to specific crops (Gould, Hoelmer & Goolsby 2008). Nonetheless, the combination of ephemeral crops with a polyphagous pest well adapted to exploiting these crops may represent an extreme challenge for classical biological control. In contrast, the fact that native generalist arthropod predators inflict high levels of mortality on *B. tabaci* in cotton as well as a number of other crops (Naranjo, Ellsworth & Cañas 2009) suggest that this natural enemy community is well adapted to exploiting ephemeral prey resources.

A final consideration is the relatively widespread use of insecticides in the management of *B. tabaci* in all affected crops, albeit at lower use rates since the mid-1990s (Naranjo & Ellsworth 2009). While exotic parasitoid establishment appeared to be unaffected by insecticide use it almost certainly played a role in the dynamics of these host-specific parasitoids and thus the impact they can have on the pest suppression (Gerling & Naranjo 1998). Although the LTREs were conducted in insecticide free fields, they were embedded within a representative cropping system where insecticides were routinely used in adjacent fields for management of *B. tabaci* and other pests of cotton and other crops. This is a reality in commercial production systems affected by this pest and likely many other pest species that have been the subject of classical biological control efforts.

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