Mortality dynamics of a polyphagous invasive herbivore reveal clues in its agroecosystem success

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Abstract

BACKGROUND: The population dynamics of polyphagous pests such as *Bemisia argentifolii* (*B. tabaci* MEAM1) are governed by complex, interacting factors involving its cultivated and wild host plants, seasonality, movement and demography. To understand mechanisms contributing to population development and pest success within the agroecosystem, contiguous multi-host field sites were established in three environmentally distinct areas in Arizona. Life tables quantified and partition models described mortality sources and rates for immature insect stages on each host plant.

RESULTS: Predation and dislodgement were the largest sources of marginal mortality, supplied the highest irreplaceable mortality and predation was the key factor. Rates of mortality were best predicted, in order, by source, temperature, host plant and season. Marginal mortality was highest for fourth-stage nymphs followed by eggs. Mortality rates were predicted in descending order by stage, temperature and season. Survivorship patterns varied among host plants, and generational mortality averaged 70% on spring cantaloupes but nearly 95% on all other hosts. Population density varied seasonally, persisting at low levels on winter hosts and expanding beginning in the spring; perennial hosts and weeds bridge populations year-round.

CONCLUSION: Survival on winter hosts such as broccoli, albeit low, enables population continuity, whereas unusually high survivorship on spring crops like cantaloupe is an ecological release propelling population growth and driving regional dynamics in the summer and fall. This detailed understanding of mortality dynamics provides clues to the success of this invasive pest in our agroecosystems and facilitates opportunities for improved pest management at a broader landscape scale.
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Keywords: life table; *Bemisia argentifolii*; marginal mortality; survivorship; natural enemies; ecological release; decision tree partition models

1 INTRODUCTION

Many of our most intractable insect pests feed upon and move among a mosaic of annual and perennial host plants, leading to challenges in predicting population dynamics and applying this knowledge in pest management. A complex set of interacting factors that involve multiple cultivated and wild host plants, seasonality, environmental heterogeneity, dispersal and demography determine the population dynamics of mobile polyphagous pests. The temporal population changes of such pests in a single field cannot be disconnected from their dynamics over a much broader and inclusive landscape. Over 40 years ago, Rabb[1] urged us to refocus our attention on comprehensive area-wide approaches to integrated pest management (IPM) that account for a more expansive understanding of the ecosystem in which our crops are embedded. This landscape perspective includes the herbivores that impact plant systems and the community of natural enemies and other natural control elements impacting pest populations.[2–6] In general, we have a limited understanding of what makes polyphagous mobile pest successful in our agroecosystems.[7, 8]

The *Bemisia tabaci* species complex is found globally and species vary in the crops they inhabit and in the severity of their effects on these crops.[9] The silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring (=*B. tabaci* MEAM1), is a pest of worldwide significance and is invasive in many regions globally.[10, 11] The insect causes direct feeding

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damage, vectors more than 100 plant viruses, induces plant disorders, reduces yield and indirectly affects crop quality through honeydew excretion and the associated growth of sooty molds.[12] The pest potential of *B. argentifolii* is exacerbated by its high degree of polyphagy, rapid reproductive rate, ability to readily move between host patches and the lack of a quiescent stage. These qualities enable year-round population development on a broad sequence of host plants in the landscape.[13] The ability of the pest to readily develop resistance to a large array of insecticidal classes used for remedial population suppression makes management even more challenging.[14, 15] In the southwestern USA, the invasive *B. argentifolii* rapidly displaced the putatively native *B. tabaci* (Gennadius) in the late 1980s, allowing what was once an occasional pest to assume key pest status in many agronomic and horticultural crops.[10]

Learning how this pest has become so successful in our agroecosystems will depend on a more mechanistic understanding of the complex and spatiotemporally varying interactions among pest populations and a mosaic of host plants it utilizes throughout the year. We have a basic understanding of *B. argentifolii* biology and ecology, including its development and reproduction on a comparatively wide range of cultivated and non-cultivated host plants[13, 16] and its movement among these hosts.[17, 18] Host plant use by invasive *B. argentifolii* has been relatively well defined in the arid agricultural production regions of the desert southwestern USA.[19–21] During winter months, the insect inhabits vegetables such as broccoli, cauliflower and lettuce, various winter weeds and ornamental host plants in adjoining built environments. Late winter and early spring hosts include cantaloupes, vegetables and weeds. Cotton is the most abundant cultivated host during the summer, and cantaloupes and vegetables in fall complete the yearly cycle. Perennial crops such as alfalfa and citrus, and ornamental hosts such as lantana and hibiscus can host whiteflies year-round. The suitability of specific host plants for reproduction and survival varies.[22, 23] Field-based life table studies have provided a fundamental understanding of the survival and mortality dynamics on several hosts.[24–27] Finally, we have a basic knowledge of the role of abiotic environmental variables on population development.[28, 29] However, a comparative examination of the mortality dynamics in populations of *B. argentifolii* relative to host plant, season and other environmental variables such as temperature and their inter-relationships has not been done and would contribute to improved understanding and enhanced pest management approaches over the broader landscape.

Here, we use life tables to measure sources and rates of mortality impacting populations of *B. argentifolii* on an array of host plants over multiple seasonal cycles and in relation to environments represented by three agricultural production regions in Arizona. Life tables represent a robust approach for defining and estimating forces affecting populations and have long been used in ecology to understand and predict population dynamics in multiple systems.[30–34] Our objectives were to measure the biotic and abiotic mortality factors affecting pest populations in temporally and spatially varying environments. The overall goal was to understand what makes this pest so successful in a multi-host landscape to gain insight into changes we might effect for improved and more sustainable pest management in the agroecosystem.

2 MATERIALS AND METHODS

2.1 Study sites

Multi-year study sites were established at three geographically and climatically distinct agricultural production regions in Arizona, each associated with University of Arizona agricultural experiment stations. At each site, multi-host plant systems were established within a 1.6–2.4 ha total area consisting of a seasonal sequence of six representative hosts of *B. argentifolii* (Table 1). Plots (approximately 18 × 18 m) of each host plant were replicated four times in a randomized complete block design with approximately 1–2m borders between plots and blocks. Each host was seeded or transplanted, cultivated and harvested according to standard agronomic practices and timing for each site. Irrigation was facilitated using a flexible valve and pipe system that allowed each plot to be flood irrigated as needed. Weed seeds were scarified using a solution of 10% sulfuric acid, then broadcast in weed plots. Lantana plots were established with 3.79 liter transplants in 1-m spaced beds. No pesticides were used at any site.

2.2 Life tables and analyses

An established in situ life table technique was used to identify and quantify sources and rates of natural mortality affecting egg and nymphal stages of *B. argentifolii*[27, 35] on each host plant. A minimum of 50 eggs and 50 settled first-instar nymphs were marked in each plot per cohort with eggs and nymphs marked on a minimum of ten separate plants. Cohorts were generally established on a single day on host plants at a given site. Multiple cohorts were established at each site relative to the host's seasonality and the presence of *B. argentifolii* (Table 1). No alfalfa cohorts were completed in Yuma due to lack of insects and no fall cantaloupe cohorts were done in Marana because this region has a shorter growing season.

Each individual nymph was examined several times per week, or less frequently in cooler parts of the season when development was slower, in the field using a 15× Peak® loupe (Light Impressions) until the individual died or emerged as an adult. Eggs were difficult to observe clearly in the field and so leaves with eggs were collected and examined in the laboratory under a dissecting scope. This lag period between establishment and collection of eggs ranged from 10 to 68 days, depending on season; eggs were periodically observed in the field to note hatch. During observation periods, the instar of each live nymph and the instar and cause of death of each dead nymph were assigned to one of six categories (Table 2).[27, 36] A new mortality source, desiccation, was recognized for eggs and nymphs caused by senescence of the host leaf. This mortality was most frequently observed during cooler months.

Marginal mortality rates were estimated for each cause of death based on standard concepts and methods.[27, 37–39] The marginal rate estimates the level of mortality arising from a single factor as if that was the only factor operating (Table 2). Comparing measured generational mortality with that estimated from stage-specific, marginal death rates for the cohorts examined resulted in an average error of 0.34%. For some subsequent analyses, mortalities were expressed as k-values ($k = -\ln[1 - M]$), where M is the marginal rate of mortality. Survivorship data were generated for each host plant based on life tables and using accumulated degree days above 10°C (DD_{10}) from the initiation of each cohort.
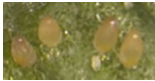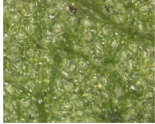
Irreplaceable mortality was estimated as an additional metric to assess the overall contribution of specific causes of death. It is the proportion of total generational mortality that would not occur if a given mortality factor or mortality during a given stage was eliminated.[34, 40] It is estimated as the difference between total mortality from all causes or stages and that due to all causes or stages but the factor or stage of interest.[27] The method assumes no density-dependent compensation in mortality.

TABLE 1. Summary of field sites, host plants and life table cohorts, 2001–2003 Arizona, USA

Site	Host plant	Cultivar/species	Planting date	No. cohorts[a]	Cohort start dates
Maricopa (33°04'11.3"N 111°58'22.2"W) Elevation 362 m Av. temp.: 21.3°C[b] Av. max.: 30.4°C Av. min.: 12.4°C Max.: 46.2°C Min.: −7.1°C Frost hours: 99.5	Alfalfa	SW-14 *Medicago sativa* L.	17 Nov 00	3	28 Aug 01, 23 Oct 01, 3 Sep 02
	Broccoli	Liberty *Brassica oleracea* L.	17 Nov 00, 9 Oct 2001	3	4 Apr 01, 21 Nov 01, 8 Jan 02
	Cantaloupe	Topmark *Cucumis melo* L.	12 Apr 2001, 2 Aug 2001, 25 Apr 2002	7	24 May 01, 19 Jun 01, 11 Sep 01, 2 Oct 01, 11 Jun 02, 2 Jul 02, 1 Oct 02
	Cotton	Deltapine 458BR *Gossypium hirsutum* L.	12 Apr 01, 16 Apr 02	5	10 Jul 01, 30 Jul 01, 14 Aug 01, 23 Jul 02, 3 Sep 02
	Lantana	New gold *L. hybrida*	13 Sep 00	9	16 Nov 00, 30 Nov 00, 24 Jul 01,14 Aug 01, 11 Sep 01, 13 Aug 02, 1 Oct 02, 29 Oct 02, 10 Dec 02
	Weeds	*Malva parviflora* L., *Physallis wrightii* Gray	18 Nov 00, 11 Apr 01	5	10 Jul 01, 6 Nov 01, 23 Jul 02, 29 Oct 02, 12 Nov 02
Marana (32°27'52.6"N 111°13'20.8"W) Elevation 622 m Av. temp.: 20.5°C Av. max.: 29.6°C Av. min.:11.9°C Max.: 45°C Min.: −9.1°C Frost hours: 101.8	Alfalfa	SW-14	3 May 01	1	4 Oct 01
	Broccoli	Liberty	11 Oct 01	2	21 Nov 01,18 Dec 01
	Cantaloupe	Topmark	3 Jun 01, 17 Apr 02	2	22 Aug 01, 31 Jul 02
	Cotton	Deltapine 458BR	3 May 01, 7 May 02	3	22 Aug 01, 5 Sep 01, 22 Aug 02
	Lantana	New gold	14 May 01	4	19 Sep 01, 24 Oct 01, 18 Sep 02, 16 Oct 02
	Weeds	*Sonchus asper* L.	3 May 01	5	19 Sep 01, 7 Nov 01, 18 Sep 02, 6 Nov 02, 11 Dec 02
Yuma (32°42'37.3"N 114°42'22.6"W) Elevation 36 m Av. temp.: 22.9°C Av. max.: 31.3°C Av. min.: 14.3°C Max. 46.4°C Min. −1.0°C Frost hours: 2.3	Broccoli	Liberty	7 Feb 01 9 Oct 01 12 Oct 02	4	20 Mar 01, 16 Nov 01, 7 Dec 01, 17 Jan 03
	Cantaloupe	Topmark	4 Apr 01 3 Aug 01 3 May 02 8 Aug 02	8	11 May 01, 15 Jun 01, 14 Sep 01, 19 Oct 01, 7 Jun 02, 28 Jun 02, 27 Sep 02, 25 Oct 02
	Cotton	Deltapine 458BR	4 Apr 01 3 Apr 02	3	13 Jul 01, 27 Jul 01, 19 Jul 02
	Lantana	New gold	9 Oct 00	6	27 Jul 01, 17 Aug 01, 5 Oct 01, 28 Jan 02, 9 Aug 02, 30 Aug 02
	Weeds	*Malva parviflora, Physallis wrightii*	9 Oct 00	3	13 Jul 01, 19 Jul 02, 22 Nov 02

a Studies conducted in four replicate plots per cohort.
b Annual temperature summaries based on AZMET[45] data for 2000–2003; frost hours are the total number of hours annually below 0°C.

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TABLE 2. Description of causes of mortality, affected life stages and competing factors used for estimating marginal rates of mortality

Mortality source[a]	Stage affected	Description	Competing factors	Examples
Inviable	Egg	Normal appearance but failed to eclose in a timely manner	Predation, dislodgement	
Predation	Egg, nymph	Inflicted primarily by sucking predators, which leave behind a deflated and transparent nymphal cuticle or egg chorion; chewing predation leaves behind a partial cadaver	Dislodgement	
Parasitism	Nymph	Distinguished by the displacement of bacteriosomes in host, or the presence of parasitoid larvae or pupae within third-, or more commonly, fourth-instar hosts	Predation, dislodgement	
Desiccation	Egg, nymph	Senescence of the host leaf leaving behind an intact but shriveled/dehydrated insect	Dislodgement	
Unknown	Nymph	None of the other causes of death	Predation, dislodgement	
Dislodgement	Egg, nymph	Insects removed from the plant due to predation, usually chewing predators, or rain and/or wind; instar of nymph estimated as the average stadia of other dead nymphs on the same observation date	none	

[a] Marginal rate of mortality, $M_b = d_b/(1 - d_a)$, where d_b is the apparent (observed) rate of mortality from the cause of interest and d_a is the sum of apparent competing mortality rates.

Key factor analyses were conducted using the method of Podoler and Rogers,[41] which regresses individual k-values on total K (sum of all individual k-values for stages and causes of death). This method identifies the key factor as the one associated with the largest regression coefficient.

The density dependence of mortality factors was examined by regressing individual k-values on the natural log densities of eggs or nymphs near the beginning of the generation based on sampling data (described below) from each cohort. Interpolation between dates was used as needed, but density data was not available for all cohorts observed. A false discovery rate (FDR) of 5%[42] was used to correct for multiple tests of slope values different from zero within a mortality factor.

2.3 Insect sampling and population dynamics

The density of eggs and nymphs of *B. argentifolii* were estimated periodically on each host plant over the course of the study. Standard methods were used to estimate densities of eggs and small (instars 1 and 2) and large (instars 3 and 4) nymphs on cotton[43]

and cantaloupe.[44] Preliminary surveys were conducted for alfalfa, lantana and the weed species to identify leaf positions by node location for sampling that resulted in the highest abundance at the lowest variation. All nodes were counted from the top of the plant. For alfalfa, counts of all stages were made from the three whole leaflets on compound leaves on nodes 3–5. On lantana, eggs were counted on whole leaves from nodes 1 and 3, and all nymphs from node 3. For the three weed species, whole-leaf counts were made on leaves from nodes 2, 3 and 5 on *Sonchus asper*, 2, 3, 5 and 7 from *Malva parviflora* and 1–6 on *Physallis wrightii* for all stages. Finally, for broccoli, a single whole leaf in the top third of the plant was sampled for all stages. After counts were made in the laboratory under a dissecting microscope, the leaf area of each leaf or leaflet was measured with an area meter (Li-Cor). The final density of insects on all plants was then expressed as numbers per cm^2 to standardize counts from multiple hosts. Note that these are not absolute estimates because we did not measure and correct for total leaf area per unit of ground in the field. Because of resource limitations, insect density

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samples were collected from all host plants only during 2001 for Marana and Yuma; samples were collected from late 2000 to early 2003 in Maricopa.

The physiological time (degree days above a base of 10°C) from cohort initiation to the weighted average of adult emergence was estimated for each host plant at each site as a simple measure of generation time. This is not the generation time typically associated with demography as we did not measure reproduction and adult survivorship.

2.4 Statistical analyses and modeling

To understand patterns in mortality, decision tree partition models were produced to predict total, marginal or irreplaceable mortalities. In the case of the latter two, data were pooled across all life stages and across sources of mortality. A series of partition models was produced for each model effect in succession, starting with the effect of interest (host plant, mortality factor or life stage) and adding each fixed effect followed by measures of environment (temperatures and season). Multiple temperature metrics were produced for each cohort including chilling units below temperature thresholds of $-5°$ to 10°C at 1°C increments, as well as mean and mean minimum temperature for each cohort. These were calculated from site-specific hourly temperature records from the AZMET weather station system maintained by the University of Arizona.[45] A validation data set (25%) was randomly selected from the data, stratified by rep, and held out from the training data set. Default parameters controlled initial splitting behaviors in JMP Pro (v 15.2.1). Because of a tendency to overfit these data with automatic settings, decision trees were then pruned by removing the weakest split in the model successively until the tree was simplified without large losses in R^2 (less than 10% of the full model). User-controlled pruning of leaves also was used when default splits were based in logworth values below 1.3 (equivalent to $p > 0.05$), or when multiple successive and adjacent temperature splits were ostensibly over-fitting the data. A parsimonious model was produced and used to describe the variation in the mortality data.

Data were plotted to symbolize each branch and leaf of the resulting tree. Each split was depicted as means ± 95% confidence intervals (CI) in violin plots that represent the full distribution of the data for each significant contrast (logworth > 1.3 or $p < 0.05$). Splits at the highest level in the tree are the most significant contrasts; those close to the bottom are comparatively less important, although still significant (logworth > 1.3). Lower mortality rates are plotted on the left side of each contrast, with generally lower mortality rates on the left side of the tree compared with the right side of the tree. Violins are area-weighted based on relative sample sizes in the contrast and are color-coded to ease interpretation of the relative influence of each model effect. All charting was done in JMP Pro (v. 15.2.1).

SAS Lifetest (SAS Inc.) was used to compare immature survival curves across host plants for all sites combined. The log-rank test statistic was used to assess pairwise differences among hosts with a FDR = 0.05[42] to correct for multiple testing. The life table option was selected to generate data for plotting.

3 RESULTS

3.1 Life tables and analyses—mortality sources

The same causes of mortality were observed on all host plants; however, the relative contribution of each varied considerably (Figure 1). Predation (primarily by sucking predators) and

dislodgement (primarily due to weather and chewing predators) were consistently the largest sources of mortality on all host plants. Parasitism by aphelinid parasitoids (*Eretmocerus* spp. and *Encarsia* spp.) was moderately high in alfalfa, lantana, fall cantaloupe and cotton, and low on weeds and spring cantaloupes. Parasitism was extremely low or absent on broccoli. Egg inviability and unknown mortality were low throughout the study, with the exception of cohorts observed on weeds during the winter. Mortality due to desiccation was highly variable across and within host plants depending on season, with higher levels observed during late fall, winter and early spring (Figures 1 and S1). Irreplaceable mortality, or the mortality that would be absent if the source was missing, was greatest for predation and dislodgement on most host plants (Figure 1).

3.1.1 Decision tree models

Marginal mortality pooled over life stages was influenced by the source of mortality, whitefly host and environmental conditions, including various temperature metrics and season. Source mortality was the most important effect accounting for two-thirds of the R^2 of this model (Figure 2 and Table 3). Predation and dislodgement were responsible for more mortality than the remaining sources, with significantly more predation present in all seasons except spring. Predation rates were typically higher under warmer conditions, which also was reflected in significantly higher predation in cotton relative to other hosts. Dislodgement rates were higher in alfalfa and broccoli than in other hosts, which tended to support higher dislodgement rates under colder conditions.

Rates for egg inviability and unknown mortality were significantly lower than desiccation and parasitism. Under cooler conditions, mortality due to desiccation was more likely than parasitism. Under warmer conditions, the reverse was true, with a mean minimum temperature of 16.3°C separating these two trends—more parasitism was apparent during the summer and fall than in the spring and winter. Under warmer conditions, desiccation rates were higher in spring-planted cantaloupes and weeds than in other hosts. Under cooler conditions, desiccation was more common in broccoli and lantana than in weeds, and parasitism rates were higher in lantana than in broccoli, weeds and fall cantaloupes.

Natural enemies were less important in the spring when predation and dislodgement rates were lower irrespective of host. Parasitism rates also were lower in the spring compared with summer and fall. Mean (one split, 3% of R^2) and mean minimum temperatures (three splits, 7% of R^2), and chilling hours below three different thresholds (five splits, 14% of R^2), also influenced mortality rates (Figure 2).

Irreplaceable mortality rates from any source rarely exceeded 0.5 for any cohort, but were influenced by the same set of factors as marginal mortality with the exception that season was not a significant factor in this model (Table 3 and Figure S2). Instead, a series of temperature metrics (six splits, 32% of R^2) characterized environmental conditions, including mean (three splits, 2%) and mean minimum temperatures (two splits, 16%), and chilling hours below 6°C (one split, 14%). Other patterns were similar to the model for marginal mortality. Source mortality was most important to the model, and predation and dislodgement mortality rates exceeded all other sources (logworth = 83). Desiccation and parasitism rates were similar, higher than egg inviability or unknown rates (logworth = 28), and insensitive to any other temperature condition. By contrast, inviability and unknown
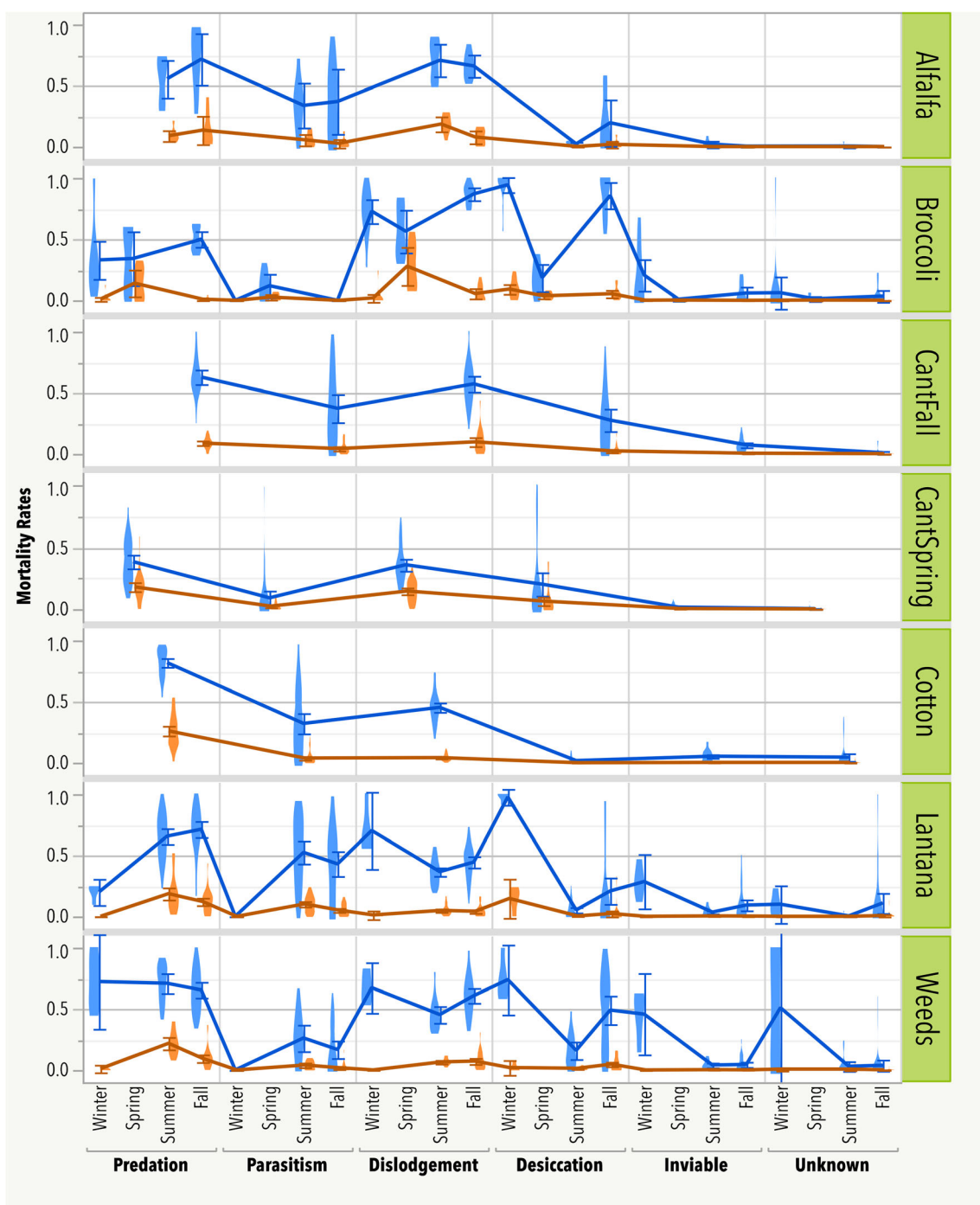
FIGURE 1. Mean marginal (blue) and irreplaceable (orange) mortality rates (±CI) by mortality source and season for whiteflies on each of seven hosts. Adjacent violins depict the full distribution of mortality rates for all cohorts. Cant, cantaloupes cultivated in either the fall or spring.

irreplaceable mortalities were higher when mean temperatures were below 9.8°C (logworth = 4.0).

Dislodgement supplied the second highest rate of irreplaceable mortality and similar to predation, irrespective of host, when conditions were cool (chilling hours below 6°C ≥19). Under warmer conditions, predation had the highest and most important irreplaceable mortality rate (logworth = 12). Dislodgement was higher in alfalfa, broccoli and spring-planted cantaloupes compared with other hosts (logworth = 13). In these other hosts, dislodgement rates were higher under cooler conditions of mean temperatures below 23.7°C (logworth = 5.2). Under warmer conditions, more dislodgement was found in weeds and fall-planted cantaloupes than in cotton and lantana (logworth = 2.2). Predation was the most important factor with a pattern of higher irreplaceable mortality at warmer temperatures (logworth = 9.5 and 6.3) and with higher rates in spring cantaloupes, cotton and weeds compared with fall cantaloupes, alfalfa and lantana (logworth = 3.4).

3.2   Life tables and analyses—life stage mortality

The life stages of *B. argentifolii* experienced different levels of total mortality from multiple causes and this mortality was
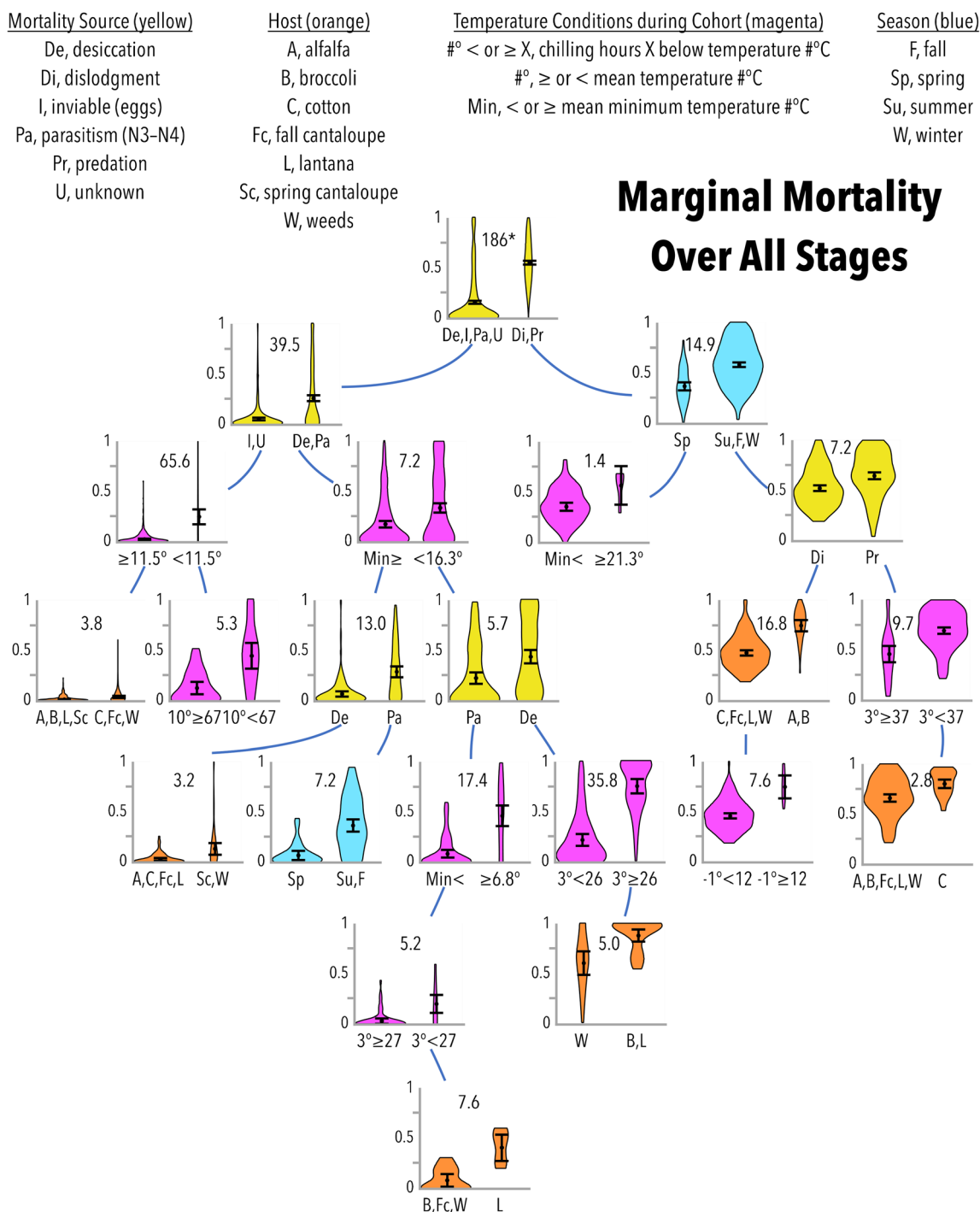
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FIGURE 2. Decision tree for partition model of marginal mortality with host (orange, six splits, 5% of R^2), mortality source (yellow, five splits, 66% of R^2), season (blue, two splits, 5% of R^2) and temperature conditions (magenta, nine splits, 24% of R^2) as factors. Each split (22 in total) depicted by area-weighted distributions (violins), mean marginality mortality ± 95% confidence intervals (CI) and logworths (*). $N = 1314$, $R^2 = 0.718$, corrected Akaike information criterion (AICc) = −936.

variable among cohorts and hosts plants (Figure 3). The highest level of marginal mortality was found during the fourth nymphal stadium followed by the egg stage. Mortality during the first nymphal stadium was generally the lowest with mortality during the remaining nymphal stadia moderate and similar. Egg mortality was highest on broccoli, alfalfa and weeds and lowest on spring cantaloupe. Mortality during the first nymphal stadium, was generally higher in the winter on hosts like broccoli and lantana. During the final nymphal stadium, mortality was two to three times lower on spring cantaloupes compared with all other host plants (Figure 3). Irreplaceable mortality followed patterns observed with marginal mortality with higher rates during the egg and fourth nymphal stadia. Irreplaceable mortality from the fourth nymphal stadium was greatest for fall cantaloupe, cotton and lantana.

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TABLE 3. Partition model decision tree summaries for mortality rates

Model effects	R^2	No. splits	AICc	Source	Stage	Host	Temperature metrics	Season
				Proportion of model				
Pooled over stages								
Marginal	0.718	22	−936	0.66	n/a	0.05	0.24	0.05
Irreplaceable	0.575	12	−3871	0.59	n/a	0.09	0.32	0.00
Pooled over sources								
Marginal	0.592	16	−649	n/a	0.43	0.01	0.42	0.14
Irreplaceable	0.609	13	−3269	n/a	0.61	0.04	0.19	0.16
Total mortality	0.532	9	−496	n/a	n/a	0.76	0.22	0.02

Abbreviations: AICc, corrected Akaike information criterion; n/a, not available.

The distribution of mortality by cause was variable within each life stage and host plant (Figure S3). As expected, predation assumed a large portion of the mortality in most stages. For cool season hosts like broccoli, desiccation was the major mortality source in all stages. Because parasitism can only be observed in older nymphal stages, it was relatively high in the final nymphal stages, especially in hosts observed during warmer months (Figure S1).

3.2.1 Decision tree models

Marginal mortality pooled over sources of mortality was impacted by whitefly life stage, host and environmental conditions, including season (Figure 4 and Table 3). Stage was a very important factor in the decision tree splitting six times, including first where mortality rates were much higher in the fourth instar (N4) than in the other life stages. Mortality was much lower in the fourth instar during the spring and in the other seasons when mean temperatures were below 10.9°C. Under cooler conditions in general, eggs experienced significantly more mortality than N1–N3. However, under warmer conditions, eggs and N3 mortality rates were similar and higher than for N1–N2. When host plant is considered, egg mortality rates were once again higher than in N3 for all crops except spring-planted cantaloupes. N1–N2 mortality rates during the spring, summer and fall were significantly lower compared with the winter.

Temperature conditions were about as important to the model as whitefly stage, each representing approximately 42%–43% of the R^2 and involving mean temperature (three splits, 35%), mean minimum temperature (one split, 1%) and chilling hours below three different thresholds (three splits, 6%). Host was much less influential with only one split, but it showed significantly lower mortality in spring-planted cantaloupes and the spring season generally, when mortality rates were lowest (Figure 4).

Relative importance and patterns of model effects in the decision tree for irreplaceable mortality rates were similar to the decision tree for marginal rates (Table 3 and Figure S4). Whitefly life stage was even more important in this model (three splits, 61% of R^2) and temperature metrics were less influential (six splits, 19%). The fourth instar was once again the most important stage for irreplaceable mortality (logworth = 110), with the highest rates emerging under warmer conditions, especially during the summer and fall (logworth = 14.2). At more than 0.25, irreplaceable mortality rates were highest for these large instars in lantana, significantly higher than for alfalfa, broccoli, cotton, weeds and fall-planted cantaloupes (logworth = 4.8). By contrast and although still higher than in other stages, irreplaceable rates were much

lower in the winter and spring for the fourth instar at around 0.10. Rates were significantly lower for other stages (mean = 0.03), which were higher in the spring (logworth = 48), and generally higher for eggs than N1–N3, especially under warmer conditions (logworth = 9.4). Mean temperature (two splits, 17% of R^2) and season (two splits, 16%) had similar influence on the model, whereas chilling hours below four different thresholds were less important (four splits, 2.4%).

3.3 Life tables and analyses—total mortality

Total generational mortality was lowest on spring cantaloupes and differed from all other host plants (Figure 5). Survival curves that track the probability of survival over time for a cohort varied among host plants. Error-corrected pairwise comparisons between host plants indicated that survival curves generally differed between all host plant pairs except cotton and alfalfa. Consistent with total mortality, the probability of survival was lowest on broccoli and highest on spring cantaloupes (Figure 5).

3.3.1 Decision tree models

Total mortality rates were generally high, well above 0.90. However, the decision tree identified important differences among factors (Table 3 and Figure 6). At just one split (logworth = 26), host dominated the model (76% of R^2) with whiteflies in spring-planted cantaloupes dying at rates of just 0.733 ± 0.066 (95% CI) compared with 0.942 ± 0.009 in other hosts. For these other hosts and during warmer conditions, there was less mortality (logworth = 2.3) during the spring (0.853 ± 0.025) than in the summer and fall (0.926 ± 0.011). The highest total mortalities were measured in the winter (0.999 ± 0.0004), when cooler conditions prevailed with mean temperatures below 11.5°C, and were significantly higher than in the fall (0.994 ± 0.004; logworth = 1.5).

Environmental conditions were represented in the model by temperature metrics (five splits, 22% of R^2) and season (three splits, 2.3%). Low temperature metrics were important to the model with one split each for two thresholds for chilling hours (3°C and −2°C, at 12% and 1%, respectively) and one split for mean minimum temperature (5.1%). Two splits for mean temperature constituted 3.4% of the model.

3.4 Life tables and analyses—key factors and density dependence

Predation and desiccation in the final nymphal stage were the most common key factors to emerge (Table 4). The only exception was lantana, where predation in the third nymphal stage was the key factor.
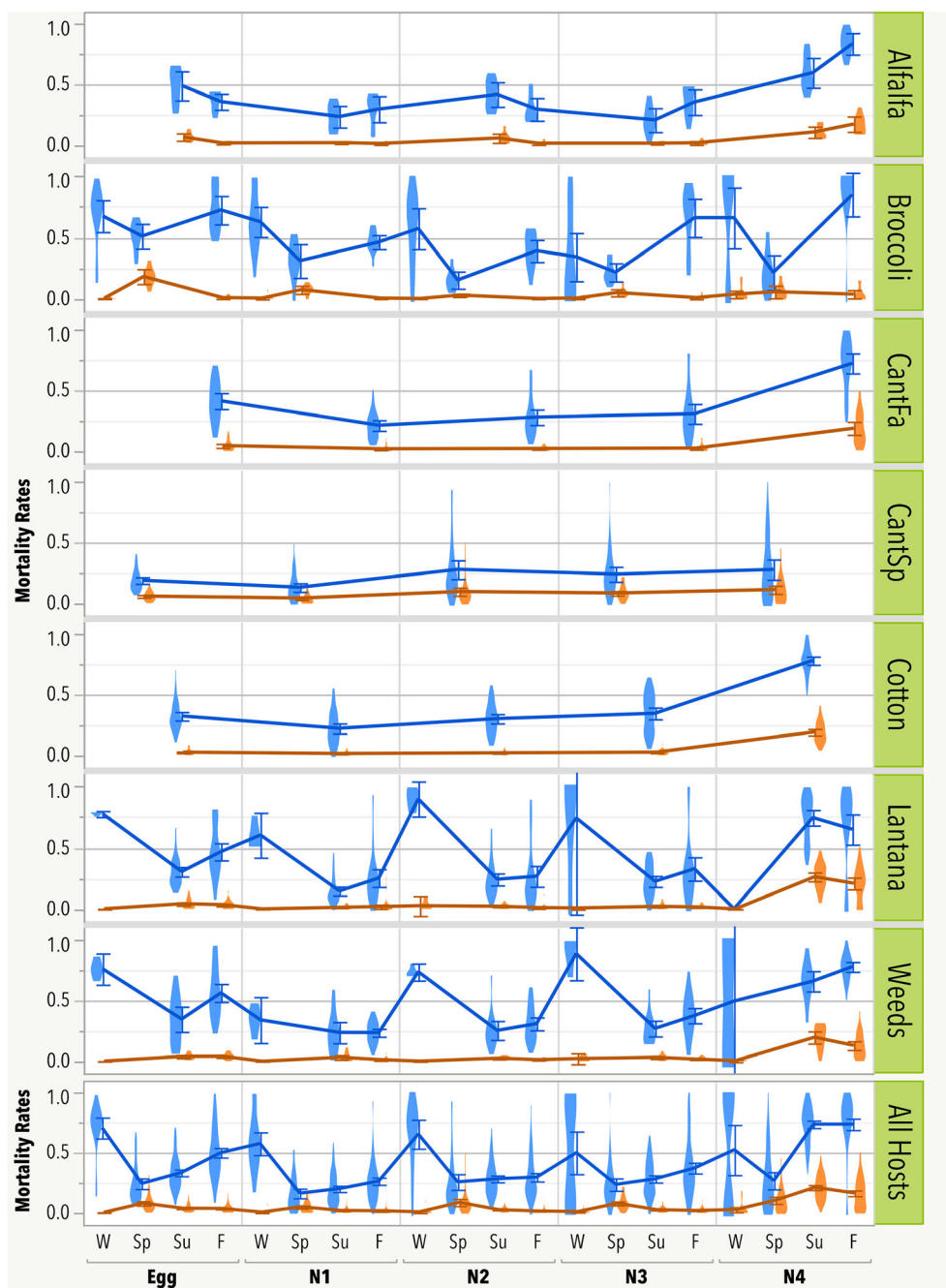
FIGURE 3. Mean marginal (blue) and irreplaceable (orange) mortality rates (±CI) by whitefly stage and season on each of seven hosts and overall hosts. Adjacent violins depict the full distribution of mortality rates for all cohorts. Cant, cantaloupes cultivated in either the fall or spring. N1 - N4 denotes first through fourth nymphal stadia.

There was little evidence of density dependence in any mortality factors on any host plant (Table S1). After correcting for multiple testing, density dependence was only observed for dislodgement of eggs in alfalfa and fall cantaloupes, and desiccation of nymphs for spring cantaloupes. Inverse density dependence was noted for desiccation of nymphs for alfalfa and weeds, predation of eggs in broccoli, and predation of nymphs in broccoli and lantana. In all cases, the slopes of the regressions of mortality k-values on ln density of the insect were very small suggesting weak relationships between mortality and insect density. Delayed density dependence could not be reliably tested given the infrequency of sampling for immature life stages.

3.5 Population dynamics

The density of immature life stages of *B. argentifolii* varied relative to host plant and seasonality. The magnitude of differences from eggs through small nymphs to large nymphs was consistent with observed patterns in mortality dynamics (Figure 7). Populations exist at low densities during the cooler winter months, and at higher densities in early spring and late fall periods with the highest density in mid to late summer. Insects can be found on perennial hosts such as alfalfa and lantana and on a sequence of annual and perennial weeds throughout the year. The highest populations were found on cantaloupes, followed by lantana, weeds and cotton. The large variation in
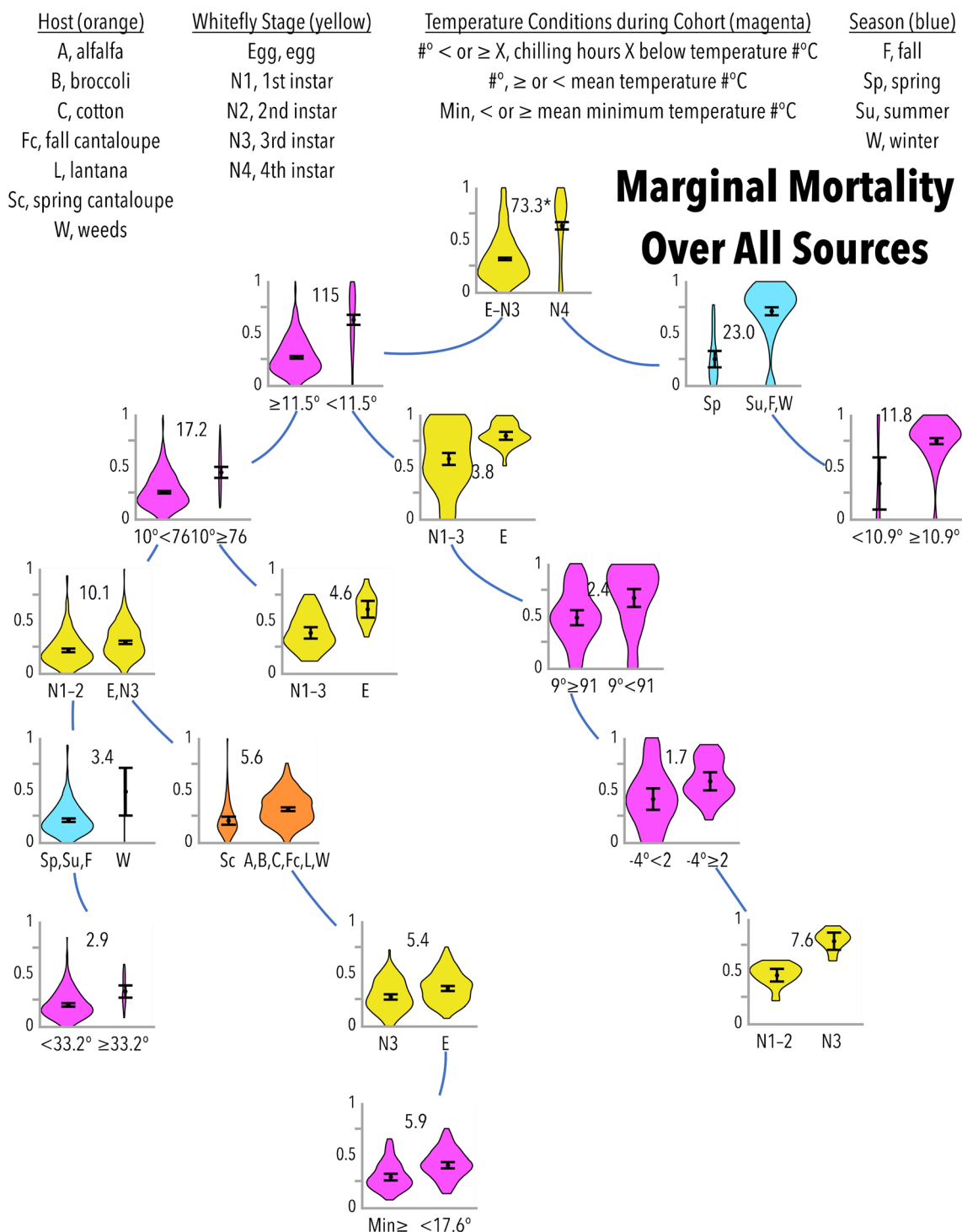
FIGURE 4. Decision tree for partition model of marginal mortality over all sources of mortality with whitefly stage (yellow, six splits, 43% of R^2), host (orange, one split, 1.3% of R^2), season (blue, two splits, 14% of R^2) and temperature conditions (magenta, seven splits, 42% of R^2) as factors. Each split (16 total) depicted by area-weighted distributions (violins), mean marginality mortality ± 95% confidence intervals (CI) and logworths (*). $N = 1095$, $R^2 = 0.592$, corrected Akaike information criterion (AICc) = −649.

magnitude among hosts and season under-represents the low but generally consistent presence of the insect on hosts such as alfalfa, lantana and weeds. In all host plants, there were periods during the year when we observed no whiteflies and this is depicted by the divots in the host plant bars along the bottom of Figure 7.

Based on simple degree day estimates, the average number of "generations" (egg–adult) annually was 10.5, 11 and 12 for Marana, Maricopa and Yuma, which is consistent with the seasonal temperature profiles for each site (Figure S1). The number and timing of generations was consistent with increases and decreases in population size over the year. The physiological time
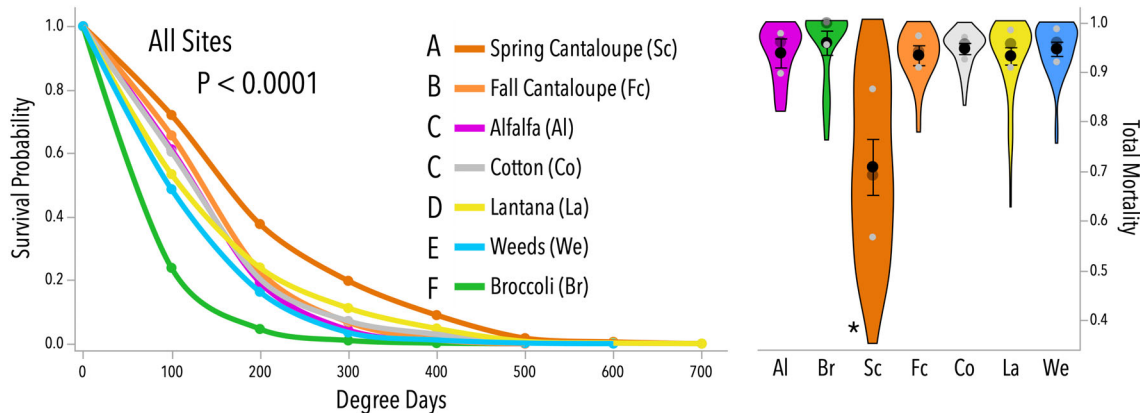
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FIGURE 5. Survivorship curves for immature *Bemisia argentifolii* on various host plants in Arizona. Survival varied among host plants (log-rank = 10 942.5, d.f. = 6). An upper case letter next to the host plant name denotes differences between curves based on error-corrected pairwise tests. Distribution and mean ± confidence intervals (CI) of total immature mortality. A large gray dot represents the median, small gray dots denote the 25th and 75th percentiles. *Significantly lower whitefly mortality in spring-planted cantaloupe.

from egg to adult varied among crops with the shortest development time on weeds (344 DD_{10}) and the longest on spring cantaloupe, cotton and lantana (392–402 DD_{10}) (Table S2). Generations were completed in as little as 18 days during summer months or as long as 133 days during the winter.

4 DISCUSSION

We used life tables to enhance our understanding of the population ecology and dynamics of an invasive whitefly pest within a heterogeneous agricultural production system and sought to find insight into what has made this pest successful in our agroecosystem. We measured the differential mortality forces impacting pest populations over time and space in a mosaic of crop, wild and ornamental host plants. *B. argentifolii* is tropical and subtropical in distribution with no quiescent stage to avoid potentially inhospitable conditions. Thus, populations persist by contemporaneously and sequentially colonizing an array of hosts plants in the environment. We found that rates of predation and total mortality were remarkably similar among host plants with one notable exception. Survival on spring-planted cantaloupes was consistently high relative to other hosts and may represent a critical point of population expansion affecting pest dynamics throughout the landscape. This points to one phenomenon that makes *B. argentifolii* successful in this multi-host system, but also may improve our understanding of how these dynamics provide opportunities for improved pest management.

Recursive partition modeling is a powerful non-parametric regression approach to resolving relationships among many predictors and a response variable, without many of the limitations of other approaches, even when faced with many and complex interactions. Although these methods have been broadly applied in the sciences,[46] few examples exist in the ecological, entomological or pest management literature.[47] Here we used partition modeling to better characterize the relative influence of both biotic and abiotic factors on whitefly mortality in our agroecosystem. The resultant decision trees transparently order and assemble key contrasts (splits) within the life table data, confirming and elucidating findings from the more traditional demographic analyses.

4.1 Demographics and population dynamics

A similar set of mortality sources affected populations of *B. argentifolii* on all host plants, but the relative magnitude and importance of the different forces varied by host, season and environmental factors such as temperature. Predation by sucking predators and dislodgement due to weather events and chewing predation were consistently the largest sources of marginal and irreplaceable mortality. Predation was consistently identified as the key factor associated with variations in total generational mortality. Partition tree analyses showed that source and stage are strongly predictive of both marginal and irreplaceable rates of mortality, followed by temperature metrics, including mean temperature, minimum temperature and the duration of time at various temperatures below 10°C. Host plant and season, which are correlated to some extent, account for relatively lesser amounts of variation in mortality overall, with season being more important than host in predicting mortality among developmental stages.

Survivorship analyses and partition trees showed us that total mortality was highest during the winter on hosts such as broccoli, lantana and weeds, and lowest on spring-planted crops such as cantaloupes. Total survival also was impacted by environmental variables like temperature and less so by changing seasons. These mortality dynamics are consistent with general population trends in which very low populations are found on winter hosts and rapidly growing populations are observed during spring and early summer on hosts such as cantaloupe and other cucurbit crops.[20, 21, 48, 49] Seasonal population dynamics are clearly connected to temperatures affecting development and reproduction, but now we understand the additional importance of differential survivorship.

The success of the invasive *B. argentifolii* in our agroecosystem has been tied to its much broader host use.[10, 13] For example, broccoli was never a host of the putatively indigenous *B. tabaci*[16] but now likely serves a critical role in bridging pest populations during the winter. Likewise, crops like cucurbits, which are exceptionally good hosts of the invasive *B. argentifolii*[10] provide a key bridge in the adjacent spring season. Not only do these spring crops provide an important reproductive bridge, but our findings of high survivorship in cantaloupes and perhaps other cucurbits suggest a route of rapid population expansion that ultimately drives dynamics in the
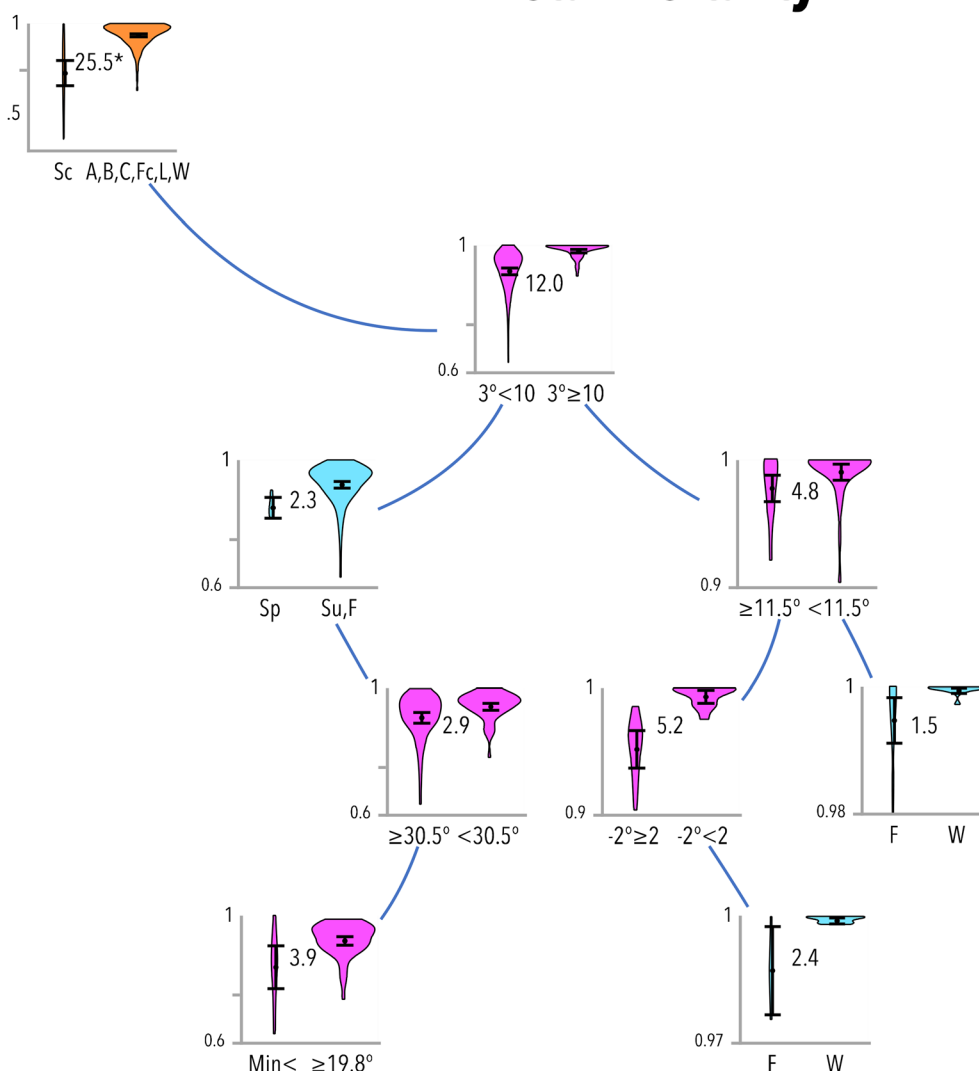
FIGURE 6. Decision tree for partition model of total mortality over all whitefly stages and sources of mortality with host (orange, one split, 76% of R^2), season (blue, three splits, 2.3% of R^2) and temperature conditions (magenta, five splits, 21% of R^2) as factors. Each split (nine total) depicted by area-weighted distributions (violins), mean marginality mortality ± 95% confidence intervals (CI) and logworths (*). Note, y-axis scales are variable among splits to accommodate plotting. $N = 219$, $R^2 = 532$, corrected Akaike information criterion (AICc) = −496.

agroecosystem. This expansion can lead to economic infestation in summer grown cotton,[27, 50] which in turn can affect pest abundance and virus transmission in crops like fall cantaloupes.[51] By contrast, although populations decline on winter hosts, cultivated or wild, they represent a crucial bridge to sustaining populations that later infest more-productive crop hosts into the spring. We found a significant relationship between cold temperatures and increased mortality so the severity or mildness of winter temperatures may modulate dynamics from year to year. Knowledge of both these extreme

patterns offers insights for improved pest management within the landscape.

Other field-based life table studies of *B. argentifolii* have demonstrated similar sources and rates of immature mortality. Mortality from sucking predators occurs at relatively high levels in cotton in Turkey,[25] cassava in Uganda[52] and cucumber in China.[53] Parasitism by aphelinid parasitoids was more prevalent in cotton from Turkey and cassava from Uganda where these studies identified parasitism as the key factor. Our findings for parasitism were

TABLE 4. Key factor analyses on each host plant using the regression method of Podoler and Rogers.[41]

		Predation	Parasitism	Dislodgement	Desiccation	Inviability	Unknown	N
Alfalfa	Egg	−0.0049	0	0.055	0.0001	0.0052	0	16
	N1	0.0393	0	0.0413	−0.0021	0	0	16
	N2	0.0198	0	−0.0235	−0.0024	0	0	16
	N3	0.1337	0	−0.0168	−0.0017	0	0	16
	N4	**0.4754**	0.2448	0.0536	−0.0149	0	−0.0026	16
Broccoli	Egg	−0.0142	0	−0.0072	0.2058	0.0233	−0.0015	36
	N1	0.0009	0	0.0478	0.0821	0	0	36
	N2	0.0081	0	0.0543	0.0841	0	0	36
	N3	0.0051	−0.0019	0.0151	0.0692	0	0.0025	36
	N4	0.0232	−0.0111	0.0442	**0.3365**	0	0.0335	36
CantSpr	Egg	−0.0046	0	0.0458	0.0008	0.0012	−0.0005	40
	N1	0.0066	0	0.0200	0.0117	0	0	40
	N2	0.0185	0	0.0092	0.2467	0	0	40
	N3	0.0039	−0.0041	0.0341	0.0144	0	0	40
	N4	**0.3192**	0.2711	−0.0036	0.0097	0	−0.0004	40
CantFall	Egg	0.0357	0	−0.0018	0.0526	−0.0068	−0.0001	28
	N1	0.0077	0	0.0099	−0.0007	0	0	28
	N2	0.0196	0	0.0487	0.0334	0	0	28
	N3	0.0261	−0.0001	0.07947	0.0432	0	0	28
	N4	**0.2799**	0.1703	0.2159	−0.0111	0	−0.0021	28
Cotton	Egg	−0.0003	0	0.0226	−0.0023	0.0001	−0.002	44
	N1	0.0082	0	0.0045	−0.0047	0	0	44
	N2	0.0723	0	0.0207	−0.0009	0	−0.0001	44
	N3	0.0982	−0.0032	0.0215	−0.0001	0	0.0048	44
	N4	**0.3727**	0.3507	0.0416	0.0011	0	−0.0053	44
Lantana	Egg	0.0009	0	0.0118	0.0788	0.0452	0.0093	76
	N1	0.0134	0	0.0324	0.0403	0	0.0114	76
	N2	0.0288	0	0.0114	0.194	0	0.0243	76
	N3	**0.2027**	−0.001	0.0723	0.1757	0	0.0615	76
	N4	−0.0005	−0.0002	−0.01272	−0.0017	0	0.0003	76
Weeds	Egg	−0.0109	0	0.0931	0.0972	0.0573	0.0004	52
	N1	0.0008	0	0.0099	0.0098	0	0	52
	N2	0.0326	0	0.0158	0.0888	0	0.0042	52
	N3	0.1345	−0.0023	0.0141	0.0593	0	0.0839	52
	N4	0.0972	−0.0578	−0.0104	**0.1566**	0	0.1254	52

Note: Slope values in bold text indicate the key factor for each host plant.

inconsistent with rates above 0.40 on lantana, but lower and more variable on other host plants. Overall, we found higher levels of parasitism generally than we had observed when cotton was the sole, and largely isolated, crop of focus.[26, 27, 36] Aphelinid parasitoids are not strong dispersers[54, 55] and the close juxtaposition of host plants in our model ecosystems may have facilitated higher parasitoid populations that were able to better track host insect resources and thus contribute more to pest mortality. By contrast, predation occurred at similar levels in relatively isolated cotton fields[27] and those embedded in a mosaic of other host plants here. Meta-analyses[56] suggest that specialist natural enemies, such as the aphelinid parasitoids here, respond to spatial diversity at smaller scales compared with generalist natural enemies. The predators in our system, as in many others, are mostly generalist feeders that are well adapted to disturbance and readily disperse among host plants to take advantage of the changing abundance of prey populations.[57, 58] For instance, it is not uncommon to see several species of generalist predators colonizing cotton

seedlings in isolated fields along with whiteflies, mites, aphids and thrips. Perennial alfalfa systems provide a relatively continuous habitat for many natural enemies.[59, 60] Our managed ecosystems were small in scale (approximately 2 ha) and although not designed to specifically test effects of landscape complexity on pest control, our results are consistent with emerging ecological patterns.

Dislodgement from the plant surface is a common cause of mortality in the sessile immature stages of *B. argentifolii* and recent studies on cassava identified disappearance to be the key factor.[61] Naranjo and Ellsworth[27] showed that death of all immature stages by dislodgement on cotton is associated with wind and blowing dust generated by monsoon storms in our region, whereas rainfall can contribute to dislodgement of eggs and first-instar nymphs. Predation from beetles and lacewings was associated with removal of larger nymphs from the plant surface. Here, rates of dislodgement were higher on host plants during the winter and fall but were generally high on all host plants in all seasons. It is unclear what differential role wind, rain or chewing predators played during the
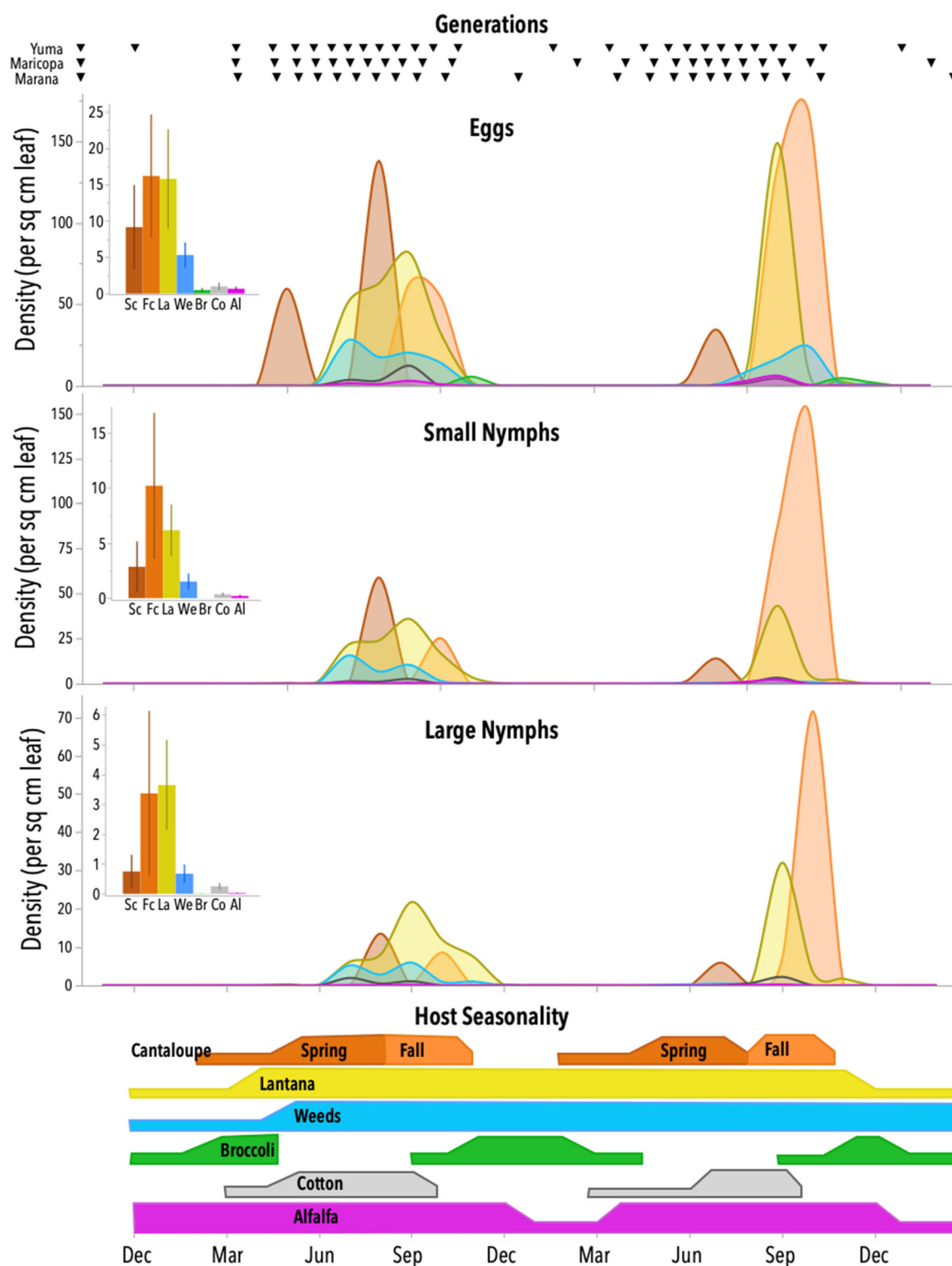
FIGURE 7. Seasonal mean densities (no. per cm^2 leaf) of immature *Bemisia argentifolii* on a sequence of host plants over a 3-year period pooled over three geographic regions in Arizona. The inset small charts depict grand mean densities of insects over the entire study. The upper panel shows the number and timing of insect generations (egg to adult) beginning from mid-October and assuming a mean physiological time of 380 DD$_{10}$; the lower panel denotes the seasonality of the host crops over time from planting to harvest. The shallow heights in seasonality bars for host plants denote true zeros for total whitefly densities. If the bar is intact, insects were present, but the counts were too low to be seen in the density plots above.

cooler months of the year, but higher rates of dislodgement during winter months were associated with cooler temperatures.

Until life tables were conducted in colder parts of the season, the loss of host material through leaf desiccation was a suspected but unresolved source of mortality. The immature stages of the insect are dependent on a consistent source of phloem sap, and any disruption of this supply leads to death. On some occasions the plant foliage containing insects were disrupted by weather

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events, natural senescence and possibly cultivation activities during warmer months, but the bulk of this mortality occurred during cooler seasons. The effects of freezing temperatures have not been studied extensively in this species, but limited data suggest that a combination of subzero temperature levels and duration of exposure can have negative consequences on all life stages[62, 63] (Ellsworth, unpublished). Our partition models consistently demonstrated that cooler temperatures were predictive of desiccation mortality. Although some of the conditions we observed were clearly sufficient to cause death of host plant tissue and thus the insect, it remains uncertain whether this range of conditions could have a direct effect on the survival of eggs or nymphs on more cold-hardy host plants.

Partition models are useful for understanding the relationship among factors, even ones that are correlated. For example, the temperature metrics in our models served, at times, as a proxy for the effects of season in some decision tree branches. Nevertheless, the inclusion of both season and temperature metrics did significantly increase model performance.

Season also had a substantial equivalency with host, specifically spring-planted cantaloupes and the spring season. This is, in part, because most of the successful cohorts measured during the spring were in spring-planted cantaloupes. Only two other cohorts were measured in the spring, both in broccoli at each of two locations, and both with reduced mortality rates. Our use of partition models allowed the identification and quantification of these proxy relationships, such that we now know that although spring cantaloupes are a major ecological release point for *B. argentifolii* in our agroecosystem, the spring period itself could be a contributing factor in the reduced levels of mortality observed. Spring may be when whiteflies more efficiently move to and exploit a new host resource relative to its natural enemies, which may lag in response. This lag could be due to temperature limits on natural enemy movement and dispersal or due to relative suitability of prey in other hosts such as alfalfa. Alfalfa during late winter and spring harbors an abundant array of prey such as alfalfa weevils, multiple species of aphids and lepidoptera. These push–pull forces could be at the root of why hosts in the spring, and especially spring cantaloupes, support whitefly populations subject to far less mortality.

4.2 Pest management considerations

Current IPM programs for *B. argentifolii* are based on scouting of individual crop fields and implementing remedial control actions based on pest abundance,[50] but elements of the landscape play a role as well. First, threshold-based control decisions are practiced widely, and simultaneous actions taken by growers throughout the landscape enable area-wide suppression.[48, 64] Management also considers important population sources and regional strategies for sharing of control chemistry to preserve efficacy.[14] For instance, anecdotally, it has long been recognized that infestations in summer crops such as cotton can be precipitated from unmanaged populations in nearby cucurbit fields.[19, 48] As such, growers are encouraged to suppress whiteflies at the end of the growing cycle and quickly plow under vines to help manage regional source populations. Our findings confirmed that large populations of the pest in spring cantaloupes were subject to the lowest total mortality. Despite predation acting as a key factor in this crop, overall levels of natural enemy induced mortality were low compared with other crops and hosts. The result was survivorship rates of around 30% on this crop compared with an average of around 5% on all other hosts. It was hypothesized that

introduction of more host-specific parasitoid species from the invasive range could potentially increase biological control services on cantaloupes and other crops such as broccoli,[65] but the overall value of the classical biological control program for this insect is uncertain.[26] Given the high levels of additional natural mortality that would be needed to dampen population growth on cantaloupe, more viable approaches might involve altering its temporal and/or spatial distribution to minimize pest population sources for nearby crops.[51] Broccoli is an equally good host of *B. argentifolii* as cotton or cantaloupes,[23] but high mortality on this crop, especially during the winter, may make it a good target for enhancing mortality further.

Alfalfa could represent a year-round source of whiteflies, but based on our observations and those of others,[23, 66] this crop appears to be a relatively poor host. Consistent with previous surveys in Arizona and California, populations of *B. argentifolii* are highest on alfalfa during the late summer and fall, and lowest during winter and spring. In fact, we never managed to find sufficient whiteflies during winter or spring months to complete a cohort at any of our research sites. This suggests alfalfa does not act as a viable overwintering host, despite its perennial availability. In addition, alfalfa is harvested at intervals ranging from less than 30 days in the summer and fall to more than 45 days in the winter and spring. As a result, very little to no reproduction occurs on this host.[66] We managed to complete cohorts to adult emergence, but only because we shifted harvest intervals for experimental purposes and focused establishment of cohorts on the crowns of the plant that had a better chance of escaping harvest removal. Finally, what relatively few immature whiteflies are found in alfalfa are subject to high levels of mortality (94%). This all suggests that alfalfa contributes almost nothing to the population dynamics of this insect in the larger landscape other than acting as a bridge for adults as they move through the landscape and feed during the summer and fall.[51, 66] Lettuce is another common, but poor host of *B. argentifolii* during the late fall and winter that contributes little to nothing towards population growth or regional dynamics.[21] Although alfalfa may be a poor host of *B. argentifolii*, our life table results and previous work identify it as an important source of natural enemies that could have far-ranging impacts on pest suppression within the broader landscape.[59, 60]

A large array of ornamental plants host populations of *B. argentifolii* in the landscape[67–69] and may be especially important in the dynamics of regional populations near built environments. We observed populations on the popular ornamental lantana year-round and completed cohorts on this host plant in all seasons except the spring. Typically, we find the highest populations on lantana in the fall immediately following cotton harvest (personal observation). Mortality rates exceeded 99% on lantana during winter months largely driven by leaf desiccation and predation. Lower levels of abiotic-related mortality are likely in the built environment, where microclimates may shelter plants from extreme temperatures during the winter. Unlike findings from Israel,[67] we found essentially no mortality from parasitism on this host during the winter, likely due to differing temperature profiles and parasitoid communities. Ornamental hosts likely act as both sources and sinks for the pest at different times during the seasonal cycle, but the direct management of populations on ornamental hosts, primarily in the urban environment, is problematic. This is perhaps an area where additional biological control services could be explored.

Finally, weedy host plants are abundant in agricultural landscapes and in associated urban environments and many host *B. argentifolii* throughout the year.[68, 70, 71] Densities in our study

were moderate over many months of the year with immature mortality ranging from just over 90% on *M. parviflora* and *P. wrightii* during the summer to over 99% on *S. asper* during the winter. Given the close juxtaposition of weeds to crops in our irrigated landscape, weeds have the potential to act as both sinks and sources of whiteflies. They also may serve as sources of natural enemies. We found high levels of predation, moderate to high levels of dislodgement (partially due to chewing predators) and moderate levels of parasitism on three representative weed species. Weeds also may represent important reservoirs of plant viruses that can be transmitted to crop plants.[72, 73] Good agricultural practices typically suppress weed populations within crop fields and IPM recommendations also call for careful management of weeds surrounding fields. Compared with more abundant alfalfa, it is unclear how significantly weeds function as reservoirs of natural enemies in irrigated systems like ours.

4.3 Study limitations

Dispersal by adults is a critical component in the meta-population dynamics of *B. argentifolii*, enabling the use of multiple hosts in the landscape and maintaining population continuity over the season. Our understanding of movement in this insect is limited to a few experimental studies,[17, 18] anecdotal observations from larger scale surveys,[20, 21, 49] or predictions of patterns from spatial models and life tables.[27, 74, 75] Our small experimental study sites provided a ready year-round habitat such that *B. argentifolii* and its natural enemies needed to move relatively short distances to find suitable hosts as others became unsuitable. The degree to which larger inter-host distances would influence outcomes is unclear, but we did observe relatively consistent levels of many mortality factors across our widely separated and climatically distinct production regions, suggesting that we observed representative patterns. Recent studies examining the effects of plot size on arthropod dynamics in cotton suggest that 12×12 m^2 plots are sufficient for assessing insecticide non-target effects (Bordini et al., unpublished). Our plots here were over two times larger. This insect also has literally hundreds of hosts and we examined only a few representative plants. However, those hosts examined dominate in our production systems where off-crop plant growth is extremely limited by our desert environment. Other host plants likely play only a small role in overall regional dynamics.

Our partial life table studies did not measure adult survivorship or resultant reproduction, two additional key features of the insect's demography. Although such parameters have been measured in many laboratory studies,[13] there is a dearth of information on these vital rates in the field and in the additional mortality incurred by adults moving among host plants in the landscape. Adults are subject to predation[76, 77] and the correlation of adult mortality and predators has been used to develop improved pest management decision-making involving sampling of both the pest and a group of key predators.[78] However, further study of vital rates in the field, as well as an explicit understanding of rates and extents of movement will be crucial to developing predictive models that can aid our understanding of this insect's population dynamics and be used as tools for broader-scale management within the landscape.

5 CONCLUSIONS

Our year-round studies with this polyphagous invasive whitefly pest emphasize the importance of an area-wide perspective

rooted in a detailed and mechanistic understanding of its key host plants for understanding its population dynamics and possibly exploiting this knowledge for improving pest management. Populations on one host plant are inexorably tied to those surrounding it in space and time. Populations of *B. argentifolii* are extremely low during winter months as a result of slow development and reproduction, and high levels of natural mortality. The combination of increasing temperatures and high survival rates on key host plants such as spring-planted cantaloupe allow populations to rapidly expand during the spring while perhaps outpacing their natural enemies, setting the stage for economic densities and a greater need for remedial control tactics on crops during the summer and fall.

A foundational element of IPM is pest avoidance.[5] The vulnerable winter mortality dynamics of this insect suggests areas for further exploitation. In terms of population control, Morris[33] suggested that adding a small amount of mortality to a population already experiencing a low rate of survival could have a disproportionately larger impact on control than adding that same mortality to a population with higher survival. Thus, strategies to enhance winter mortality, even by a small amount, could disrupt population development and dampen expansion later in the season. Tactics might include better management of winter weeds and ornamentals, conservation or augmentation of natural enemies, or the deployment of ice-nucleating agents that might reduce insect cold-tolerance.[79] However, it is the rapid expansion of populations on cucurbits during the spring that ultimately drives dynamics in the agroecosystem and contributes to the success of this pest in our agroecosystem. Unfortunately, a large amount of additional mortality would be required here to effect useful change. Currently, this is supplied by insecticides, but further research should explore the mechanisms behind the low levels of natural mortality overall on spring cucurbit hosts and seek solutions that could increase this mortality. Additional approaches to population management might include limiting cucurbit crops in certain regions, altering the timing of planting, or manipulating the spatial arrangement of these source crops to minimize inter-host movement.[51] There appears to be exchange of genetic material for insecticide resistance in *B. argentifolii* populations from distances as great as 3 km.[80] This suggests that further study is needed to determine optimal cropping layout and intercrop distances over fairly large scales to optimize avoidance of economic densities in the receiving crop. Similar considerations would be involved for understanding the impacts of ornamental hosts on pest populations in crops cultivated near built environments.

Regardless of the value of spatial and temporal manipulations of host plants in the landscape, our results clearly demonstrate that while overall rates of natural mortality are large on most host plants, additional pest control tactics are likely to be needed for crop hosts.[27, 36] When needed, consideration should be made for the use of selective insecticides that will preserve natural enemies,[81, 82] key factors in our system, and facilitate the important ecological services they provide in pest mortality across an array of host plants in the landscape. Working to preserve and potentially enhance natural mortality forces may help us to counter the success of this invasive pest.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in AgDataCommons at https://doi.org/10.15482/USDA.ADC/1526553.

SUPPORTING INFORMATION
Supporting information may be found in the online version of this article.

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Supplemental Material

Table S1. Density dependence analyses for *B. argentifolii* mortality factors on six host plants. Values denote the slope of regressions (95% confidence interval) of mortality factor k-values (-ln[1-marginal mortality]) on ln density of eggs or nymphs[a].

Host plant	Predation	Parasitism	Inviable	Desiccation	Unknown	Dislodged	N
Alfalfa							
Egg	-0.017 (-0.037, 0.003)	–	0.007 (-0.003, 0.018)	0.0028 (-0.004, 0.009)	–	0.1429* (0.060, 0.226)	16
Nymphs	0.090 (-0.215, 0.395)	0.0395 (-0.131, 0.210)	–	-0.0911* (-0.152, -0.030)	0.0001 (-0.003, 0.003)	-0.0063 (-0.119, 0.106)	16
Broccoli							
Egg	-0.0471* (-0.076, -0.019)	–	0.0053 (-0.028, 0.038)	0.0328 (-0.084, 0.149)	–	0.0619 (-0.014, 0.138)	16
Nymphs	-0.5668 (-1.011, -0.112)	0.0426 (-0.012, 0.098)	–	-0.5289 (-1.742, 0.684)	0	-0.3412 (-1.107, 0.425)	11
Spr. Cantaloupe							
Egg	0.0001 (-0.009, 0.010)	–	0.0004 (-0.004, 0.005)	0.0002 (-0.001, 0.002)		0.01503 (-0.010, 0.040)	19
Nymphs	-0.0131 (-0.111, 0.084)	0.0164 (-0.001, 0.033)	–	0.0222* (0.010, 0.034)	0	0.0282 (-0.033, 0.090)	16
Fall Cantaloupe							
Egg	0.0545 (-0.029, 0.138)	–	0.0229 (-0.002, 0.048)	-0.0086 (-0.080, 0.062)	–	0.0883* (0.013, 0.163)	20
Nymphs	0.0237 (-0.170, 0.217)	-0.3122 (-0.671, 0.047)	–	-0.0091 (-0.179, 0.160)	0.0078 (-0.007, 0.022)	0.0139 (-0.189, 0.216)	11
Cotton							
Egg	-0.0116 (-0.031, 0.007)	–	0.0103 (-0.004, 0.025)	0.0020 (-0.002, 0.006)	–	-0.0186 (-0.045, 0.008)	32
Nymphs	-0.0655 (-0.219, 0.088)	0.0825 (-0.073, 0.238)	–	0.0036 -0.003, 0.010)	0.010 (-0.018, 0.039)	0.0192 (-0.032, 0.070)	32
Lantana							
Egg	-0.004 (-0.026, 0.018)	–	0.0033 (-0.003, 0.010)	-0.0003 (-0.007, 0.006)	–	0.0177 (-0.005, 0.040)	44
Nymphs	-0.1343* (-0.237, -0.031)	0.0460 (-0.112, 0.204)	–	0.0009 (-0.007, 0.009)	0.0041 (-0.002, 0.010)	0.0160 (-0.020, 0.052)	44
Weeds							
Egg	-0.003 (-0.030, 0.024)	–	-0.0057 (-0.024, 0.013)	-0.0373 (-0.186, 0.112)	–	0.0188 (-0.134, 0.172)	23
Nymphs	0.0149 (-0.091, 0.120)	0.0589 (0.020, 0.098)	–	-0.2480* (-0.382, -0.114)	0.0016 (0.000, 0.004)	-0.0308 (-0.122, 0.060)	22

[a] * indicates the slope was significantly different from zero (within a mortality factor) with FDR = 0.05. Based on all reps per cohort at all sites; insect sampling data not available for all cohorts.

Table S2. Mean physiological time from egg to adult based on life table data.

Host plant	Generation time DD_{10}[a] (95% CI)	N
Weeds	343.8 (320.9 – 366.8)	12
Broccoli	368.7 (321.8 – 415.6)	6
Alfalfa	372.4 (320.8 – 423.9)	4
Spring cantaloupe	377.5 (375.9 – 428.9)	7
Cotton	392.3 (369.0 – 415.6)	11
Lantana	397.3 (378.8 – 415.7)	16
Fall cantaloupe	402.4 (330.2 – 424.7)	9
Mean	**380.9 (370.7 – 391.3)**	**65**

[a] Estimated time from egg to the weighted emergence time of adults; results based on life tables pooled over four replicate plots with some cohorts not producing adults.
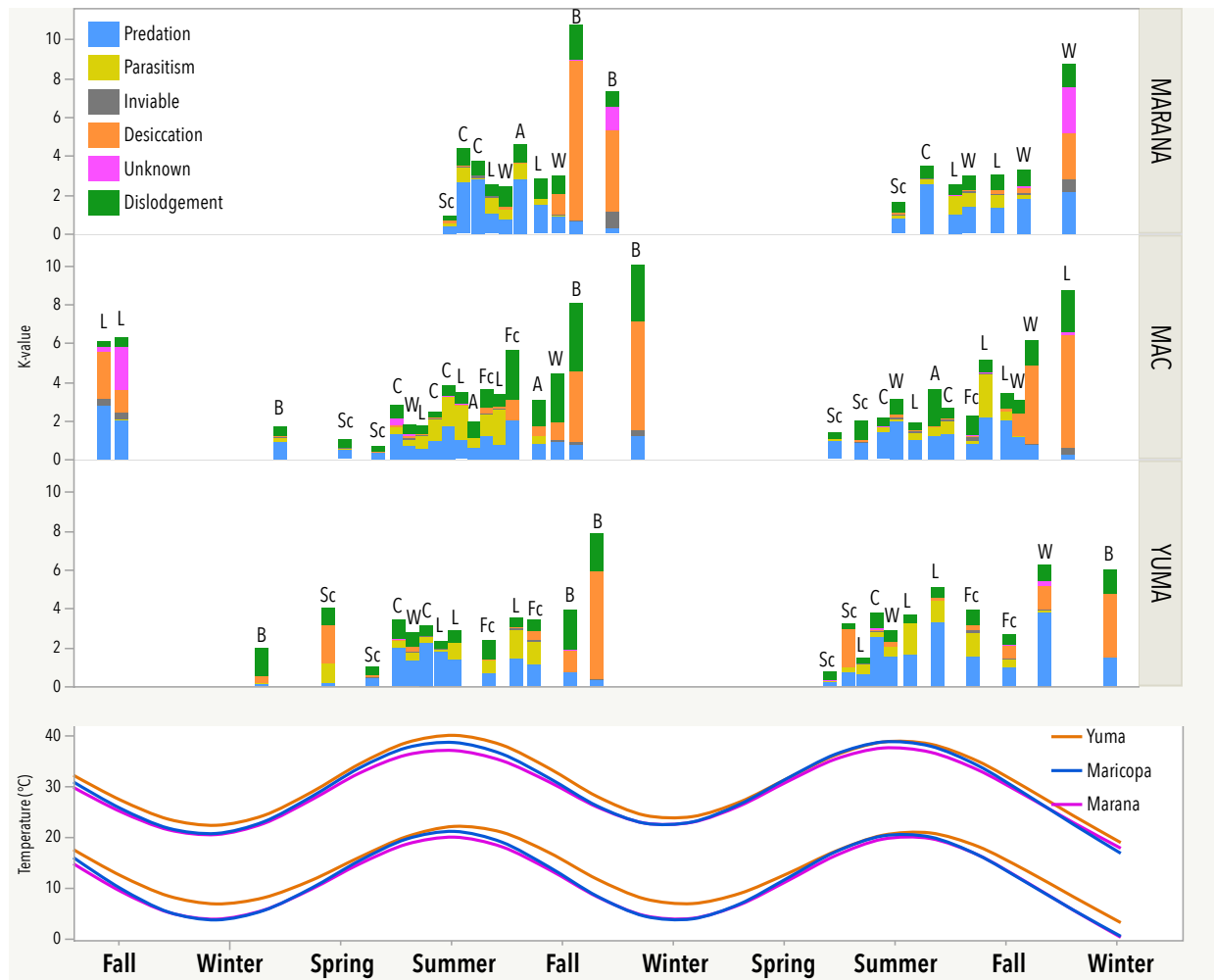
Figure S1. Seasonal summary of marginal mortality displayed as k-values for all host plants at the three sites. Each bar represents results from four replicate plots of each host plant. Bottom panel shows loess smoothed seasonal maximum and minimum temperature profiles at the three sites over the course of this study. A = alfalfa, B = broccoli, Sc = spring cantaloupe, Fc = fall cantaloupe, C = cotton, L = lantana and W = weeds.
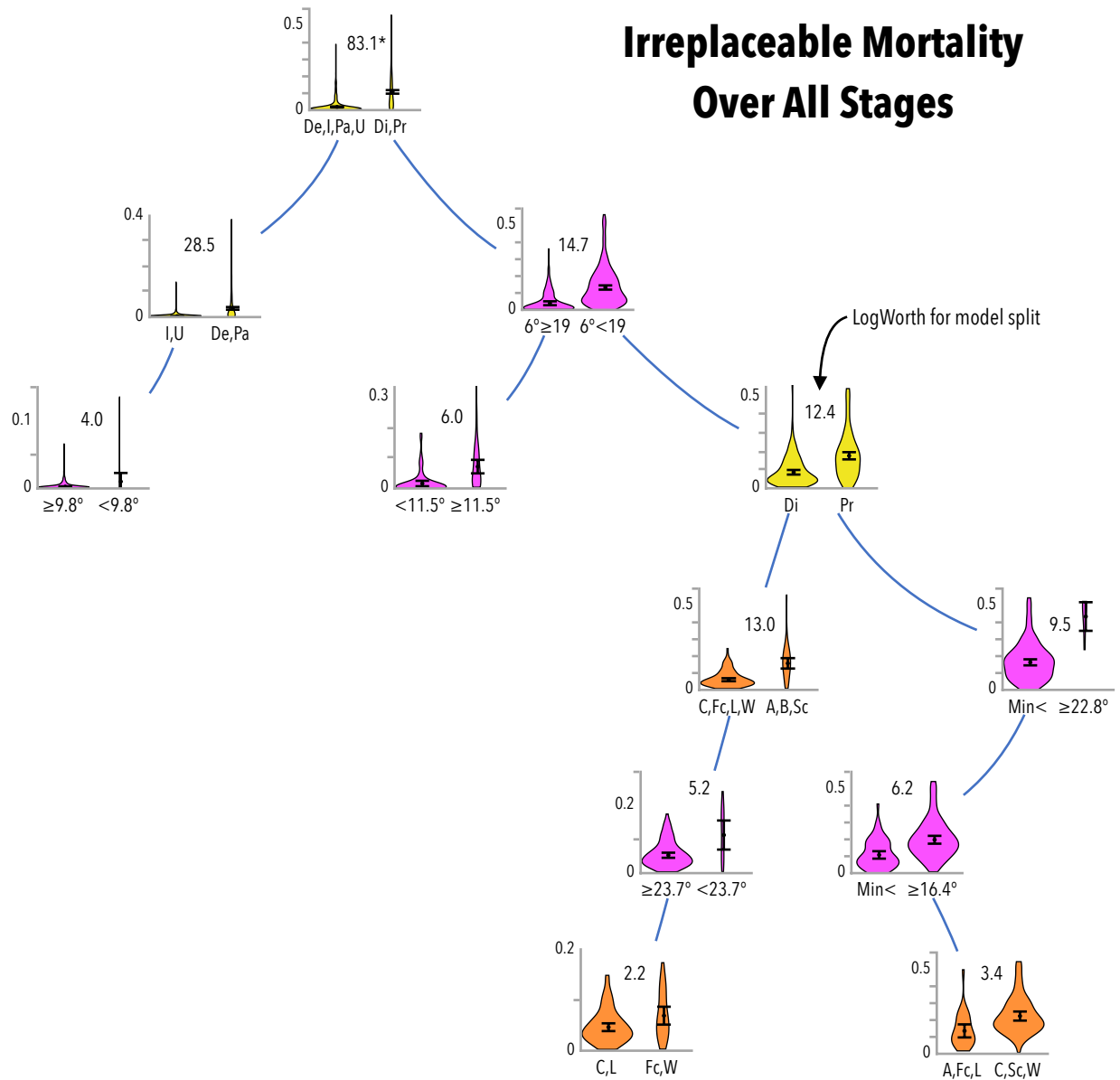
Figure S2. Decision tree for partition model of irreplaceable mortality over all whitefly stages with mortality source (yellow, 3 splits, 59% able R²), host (orange, 3 splits, 9% of R²) and temperature conditions (magenta, 6 splits, 32% of R²) as factors. Each split is depicted by area-weighted distributions (violins), mean marginality mortality ± 95% CI, and logworths (*). Note, y-axis scales are variable among splits to accommodate plotting. N = 1314, R2 = 0.575, AICc = -3871.
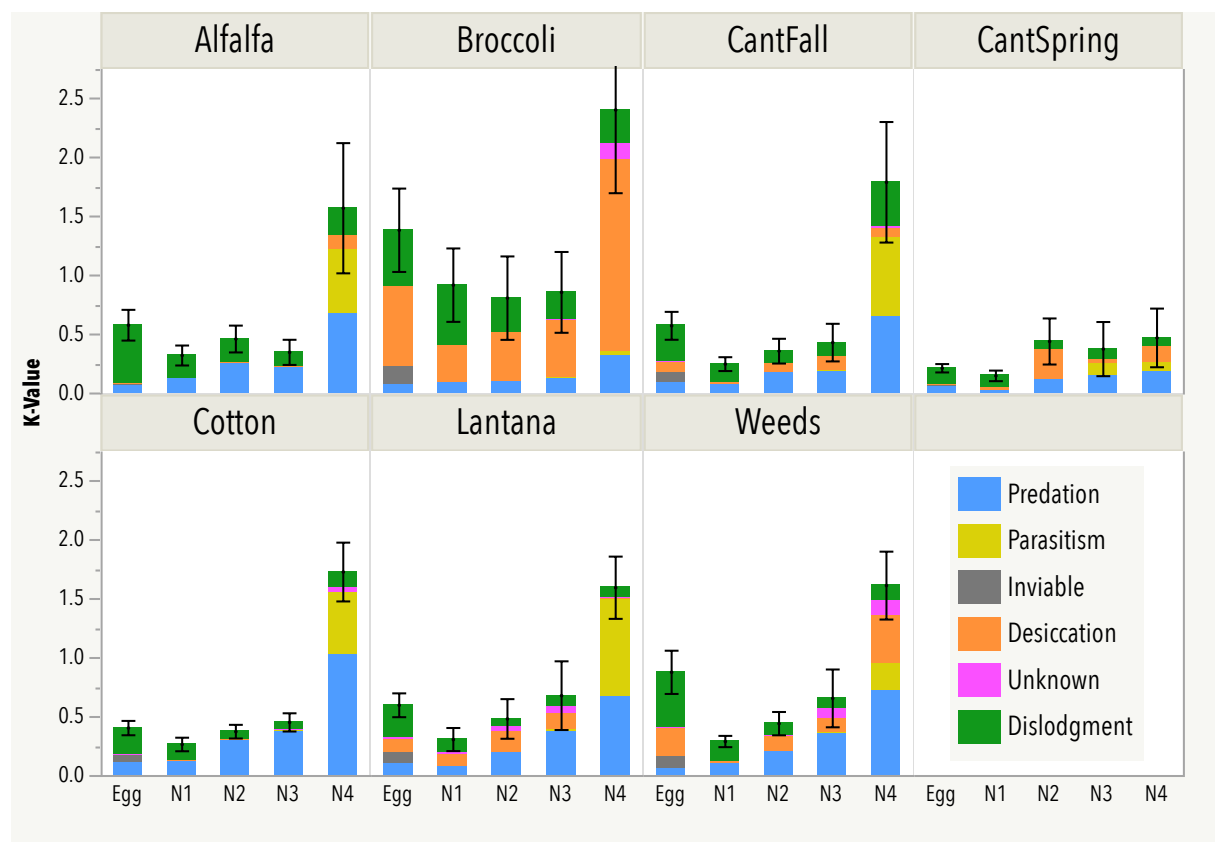
Figure S3. Marginal rates of morality depicted as k-values for mortality factors during each immature stadia, ± 95% CI for mean total K; N = 16–76.

Whitefly Stage (yellow)
Egg, egg
N1, 1st instar
N2, 2nd instar
N3, 3rd instar
N4, 4th instar

Host (orange)
A, alfalfa
B, broccoli
C, cotton
Fc, fall cantaloupe
L, lantana
Sc, spring cantaloupe
W, weeds

Temperature Conditions during Cohort (magenta)
#° < or ≥ X, chilling hours X below temperature #°C
#°, ≥ or < mean temperature #°C
Min, < or ≥ mean minimum temperature #°C

Season (blue)
F, fall
Sp, spring
Su, summer
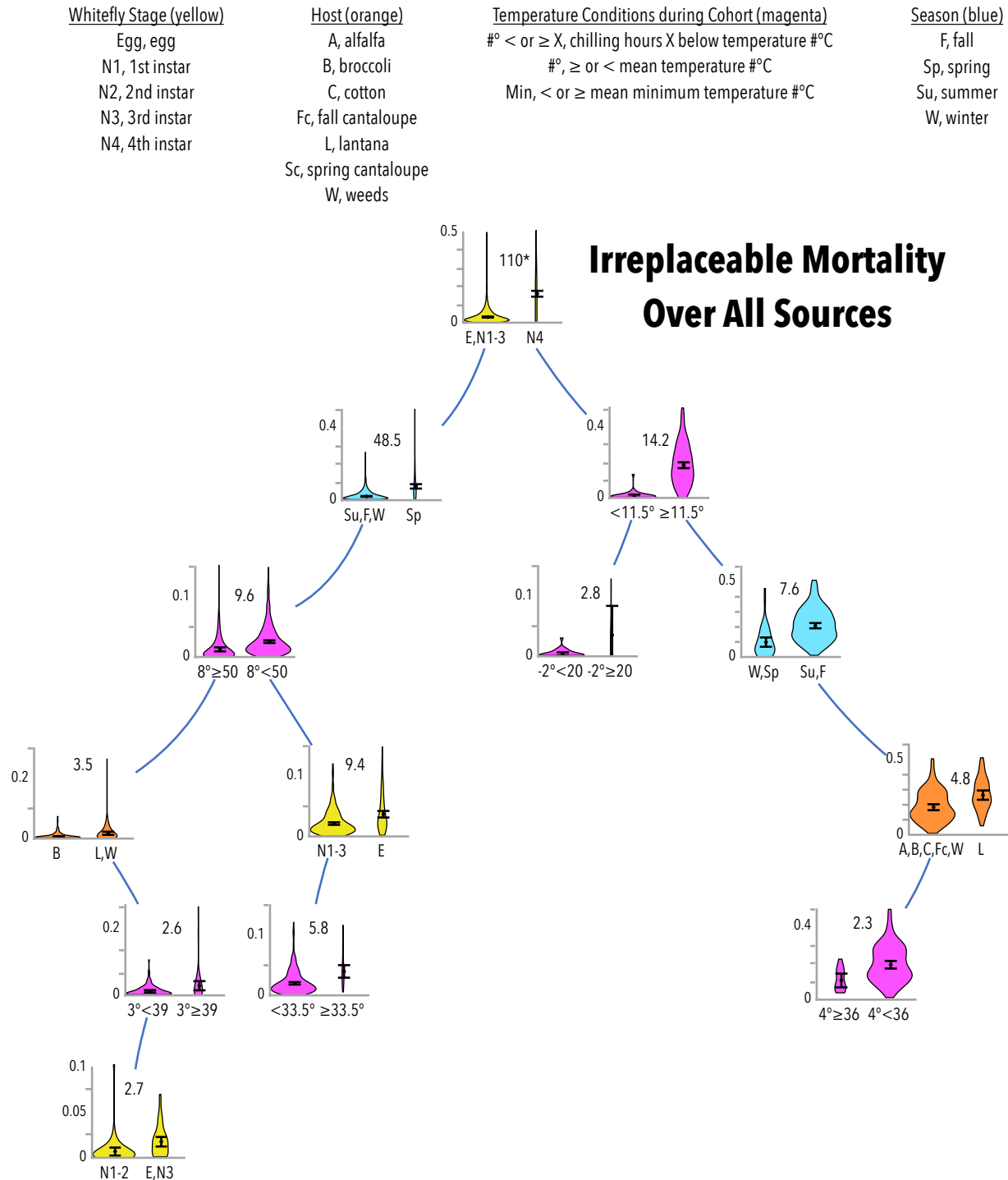W, winter

Irreplaceable Mortality Over All Sources

Figure S4. Decision tree for partition model of irreplaceable mortality over all mortality sources with whitefly stage (yellow, 3 splits, 61% of R^2), host (orange, 2 splits, 4.4% of R^2), season (blue, 2 splits, 16% of R^2) and temperature conditions (magenta, 6 splits, 19% of R^2) as factors. Each split (13 total) depicted by area-weighted distributions (violins), mean marginality mortality ± 95%CI and logworths (*). Note, y-axis scales are variable among splits to accommodate plotting. N =1095, R2=0.609, AICc=-3269.