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## Niche partitioning and stochastic processes shape community structure following whitefly invasions

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### Abstract

One of the most detrimental impacts of invasive species is the exclusion of native species, which reduces biodiversity and can alter community structure. Coexistence between invaders and native species across large scales, however, might be promoted by niche partitioning and/or stochastic processes, even when one species is excluded in some habitats. Here, we examined the effects of species traits, stochastic processes, and niche partitioning on coexistence of two morphocryptic whitefly species in the *Bemisia tabaci* complex: the invasive Mediterranean (MED) species and the native Middle East-Asia Minor 1 (MEAM1) species. These species engage in intense reproductive interference, which can result in the exclusion of one species or the other in shared habitats. Both species, however, have coexisted in sympatry in Israel for many years, where MED is invasive and MEAM1 is native. Using a spatially explicit model, we show that both stochastic processes and niche partitioning can promote coexistence between MEAM1 and MED, although predicted community structure differs drastically in each scenario. Comparison of field observations with model results indicated that variation in habitat use leading to niche partitioning was a primary factor driving coexistence between MEAM1 and MED across landscapes, although stochastic processes affected the establishment of rare species within habitats. In many systems, combining models with field surveys can be used to isolate and test mechanisms underlying patterns of community structure following invasions.

### Zusammenfassung

Eine der schädlichsten Auswirkungen von invasiven Arten ist der Ausschluss von einheimischen Arten, wodurch die Biodiversität verringert wird und die Gemeinschaftsstruktur verändert werden kann. Koexistenz von Invasoren und einheimischen Arten kann indessen über größere räumliche Skalen durch Nischenaufteilung und/oder stochastische Prozesse gefördert werden, und dies sogar wenn eine Art in einigen Habitaten ausgeschlossen wird. Hier untersuchten wir die Effekte von Arteigenschaften, stochastischen Prozessen und Nischenaufteilung auf die Koexistenz von zwei kryptischen Mottenschildlausarten aus dem Komplex von *Bemisia tabaci*: der "Mediterranean" Spezies (MED) und der "Middle East-Asia Minor 1" Spezies (MEAM1). Die beiden Arten sind durch eine intensive reproduktive Interferenz verbunden, die in gemeinsamen Habitaten zum Ausschluss der einen oder der anderen Art führen kann. Beide Arten koexistieren indessen seit Jahren in Israel, wo MED invasiv und MEAM1 einheimisch ist. Wir benutzten ein räumlich-explizites Modell und zeigten, dass sowohl stochastische Prozesse als auch

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Nischenaufteilung die Koexistenz von MEAM1 und MED bewirken können, wenn auch die vorhergesagte Zusammensetzung der Gemeinschaft sich stark je nach Szenario unterscheidet. Der Vergleich von Beobachtungen im Freiland mit den modellierten Ergebnissen zeigte, dass eine Veränderung in der Habitatnutzung, die zur Nischenaufteilung führte, der wichtigste Steuerfaktor für die Koexistenz von MEAM1 und MEM über Landschaftstypen hinweg war, auch wenn stochastische Prozesse die Etablierung der seltenen Art beeinflussten. In vielen Systemen kann die Kombination von Modellierung und Felduntersuchungen genutzt werden, um die Mechanismen herauszuarbeiten und zu testen, die den Mustern der Gemeinschaftsstruktur.

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## Introduction

Invasive species are one of the greatest threats to global biodiversity and the integrity of natural communities (Wagner & Van Driesche 2010). One of the most extreme outcomes of invasions is the exclusion of native species, which can alter food-web structure and other community properties (Reitz & Trumble 2002; Snyder & Evans 2006; Crowder & Snyder 2010). Yet, while invaders often drive species exclusion in some habitats, exclusion typically occurs in a subset of a species' available habitats rather than over its entire range (Reitz & Trumble 2002; Snyder & Evans 2006; Crowder & Snyder 2010).

Classical niche theory predicts that regional coexistence between species might occur if species differ in some traits affecting resource capture and/or reproduction in some environments (e.g., Levine & Rees 2002; Amarasekare 2003; Kneitel & Chase 2004; Tilman 2004). Niche theory therefore explains how native species might coexist with invaders that dominate in both resource and interference competition so long as there is some degree of niche differentiation. Patterns of coexistence between species under niche partitioning can be scale-dependent, whereby competing species exclude each other in some habitat patches but coexist at larger scales with greater environmental heterogeneity (Levine & Rees 2002; Amarasekare 2003; Kneitel & Chase 2004; Tilman 2004; Harrison, Cornell, & Moore 2010). Alternatively, purely stochastic processes can drive fluctuations in species abundance and allow species to coexist at varying levels of dominance across landscapes, even when no trait differences exist (Bell 2001; Hubbell 2001; Chave 2004). Stochastic processes, such as propagule pressure, might also influence the establishment and spread of invaders (Simberloff 2009), and may therefore contribute to interactions with native species.

Models of invasive species often consider niche-based dispersal (e.g., Tilman 2004; Guisan & Thuiller 2005; Peterson 2006), and/or stochastic processes including propagule pressure (e.g., Bossenbroek, Kraft, & Nekola 2001; Rouget & Richardson 2003; Tilman 2004; Dullinger, Kleinbauer, Peterseil, Smolik, & Essl 2009). Such models, however, often focus on the spread of a single invader without considering biotic interactions, such as competition and reproductive interference, with native species (Guisan & Thuiller 2005). Furthermore, model predictions are rarely confronted with data on community structure following invasions. Thus, there

is a clear need to examine the roles of niche partitioning and stochastic processes on the spread of invaders, and the resulting structure of ecological communities, with both data and theory.

Here, we linked models with field data to examine factors affecting coexistence between two whitefly species, known as the Middle East-Asia Minor 1 (MEAM1) and Mediterranean (MED) species in the *Bemisia tabaci* complex (De Barro, Liu, Boykin, & Dinsdale 2011). In Israel, MEAM1 is native and MED is invasive (Simon, Cenis, & De La Rua 2007). In homogeneous habitats, these species rapidly exclude each other through competition and asymmetric reproductive interference (Horowitz, Kotsedalov, Khasdan, & Ishaaya 2005; Liu et al. 2007; Crowder, Horowitz, et al. 2010). Reproductive interference is any negative sexual interaction between species (Gröning & Hochkirch 2008). As reproductive interference is driven by encounter frequencies between species, it can be strongly impacted by niche partitioning in time and space. Asymmetrical reproductive interference can lead to the sexual exclusion of an inferior species (Ribeiro & Spielman 1986; Kuno 1992; Gröning, Lücke, Finger, & Hochkirch 2007; Hochkirch, Gröning, & Bücker 2007; Kishi, Nishida, & Tsubaki 2009), and has been shown to drive exclusion of native whitefly species by closely-related invaders (Liu et al. 2007; Crowder, Horowitz, et al. 2010; Sun, Xu, Luan, & Liu 2011). Yet, while MEAM1 and MED sexually exclude each other in some habitats (Liu et al. 2007; Crowder, Horowitz, et al. 2010), both species coexist when considering broader landscapes in the field (Khasdan et al. 2005). To reconcile these findings, we paired long-term field surveys with models to explore hypotheses about the effects of niche partitioning, dispersal limitation, differential colonization, and variation in species traits on coexistence between MEAM1 and MED. This approach allowed us to isolate the mechanisms that led to local exclusion of one species in some habitats but coexistence across regional landscapes.

## Materials and methods

### Natural history

The *B. tabaci* complex contains at least 24 cryptic species (De Barro et al., 2011), many of which broadly overlap in

their ecological roles (Liu et al. 2007; Crowder, Horowitz, et al. 2010). *B. tabaci* males court and mate with females of different species in the complex (Liu et al. 2007; Crowder, Horowitz, et al. 2010; Crowder, Sitvarin, & Carrière 2010). Because *B. tabaci* is haplodiploid, interspecific matings produce no fertile female offspring, and species with females that are more successful at mating with conspecifics produce the most fertile female offspring (Liu et al. 2007; Crowder, Horowitz, et al. 2010; Crowder, Sitvarin, & Carrière 2010). In turn, species whose mating is disrupted by reproductive interference have slower rates of population growth and are often excluded in shared habitats (Liu et al. 2007; Crowder, Horowitz, et al. 2010; Crowder, Sitvarin, & Carrière 2010). Indeed, empirical results from cage experiments with independent *B. tabaci* populations worldwide have demonstrated that behavioural traits drive sexual exclusion whenever two species occupy a single homogeneous habitat (Crowder, Horowitz, et al. 2010). In contrast, across broader scales in the field, species that exclude each other in shared habitats often coexist (Moya, Guirao, Cifuentes, Beitia, & Cenis 2001; Khasdan et al. 2005). Two such whitefly species, classified as the Middle-East Asian Minor 1 (MEAM1) and Mediterranean (MED) species in the *B. tabaci* complex by De Barro et al. (2011), are damaging and invasive crop pests that have spread throughout the world (Dalton 2006). The putative species MEAM1 and MED have previously been referred to as the B and Q biotypes of *B. tabaci*, respectively, but we use the new species designations here. In Israel, where these species have coexisted for many years, MEAM1 is native and MED is invasive (Simon et al. 2007; De Barro et al. 2011). The precise timeframe over which MED has invaded Israel is unknown, however, due to a lack of historical data that distinguish between these two species (Khasdan et al. 2005).

## Field surveys

Field surveys were conducted from 2003 to 2009 throughout seven regions of Israel (Fig. 1; see Appendix A: Table 1) to characterize distributions of MEAM1 and MED. These regions were previously identified based on significant variation in environmental conditions and climate (Khasdan et al. 2005). Fields sampled in each region were haphazardly chosen without regards to habitat type, such that sampled fields were a random representation of habitat variation in each region. The habitats sampled consisted of crop fields primarily from four plant families: Malvaceae, Asteraceae, Solanaceae, and Cucurbitaceae, all of which are suitable whitefly hosts. These four families accounted for over 95% of fields sampled. In each year, 3–70 fields were sampled in each region (see Appendix A: Table 1). A greater number of fields were sampled in regions with greater habitat variation to more accurately reflect habitat diversity. In most years, each field was sampled twice per season, once in late June and once in early September. The exception was in 2005 and 2006, when fields were sampled every month from June to October.

Whiteflies were sampled randomly from plants in each field using an aspirator. Samplers performed a random walk diagonally through the centre of each field, beginning 50–100 m inside the field edge and working towards the centre, until a total of 80–100 whiteflies were sampled. The samples were kept in vials with 90% ethanol until specimens were identified to species based on differences in the mtCOI gene using the method of Khasdan et al. (2005). Briefly, this method amplifies the mtCOI gene using polymerase chain reaction, which is then followed by restriction endonuclease digestion with *VspI*. Following these reactions, MEAM1 and MED are readily distinguishable because PCR products for MEAM1 yield one fragment of around 100 bp, while PCR products for MED yield two fragments of around 300 and 500 bp (Khasdan et al. 2005). A total of 15–20 individuals per sample were used for molecular analyses. The average proportion of MEAM1 and MED was calculated across all fields in each region in each year, such that each region in each year was one experimental unit in the data analysis.

The field survey data were used to calculate several variables that served as inputs to the models. First, we calculated the mean percentage of each species in each habitat type (each field was one experimental unit). For each year, the percentage of MEAM1 in region  $r$  was:

$$\text{MEAM1}_r = \sum_{i=1}^n \text{MEAM1}_{i,r} \times P_{i,r} \quad (1)$$

where  $\text{MEAM1}_{i,r}$  is the percentage of MEAM1 in habitat type  $i$  in region  $r$ ,  $P_{i,r}$  is the percentage of habitat type  $i$  in the region, and  $n$  is the total number of habitat types. The value for  $\text{MED}_r$  was  $100 - \text{MEAM1}_r$ . We calculated the average number of insecticide sprays applied per field ( $S_r$ ) similarly:

$$S_r = \sum_{i=1}^n S_{i,r} \times P_{i,r} \quad (2)$$

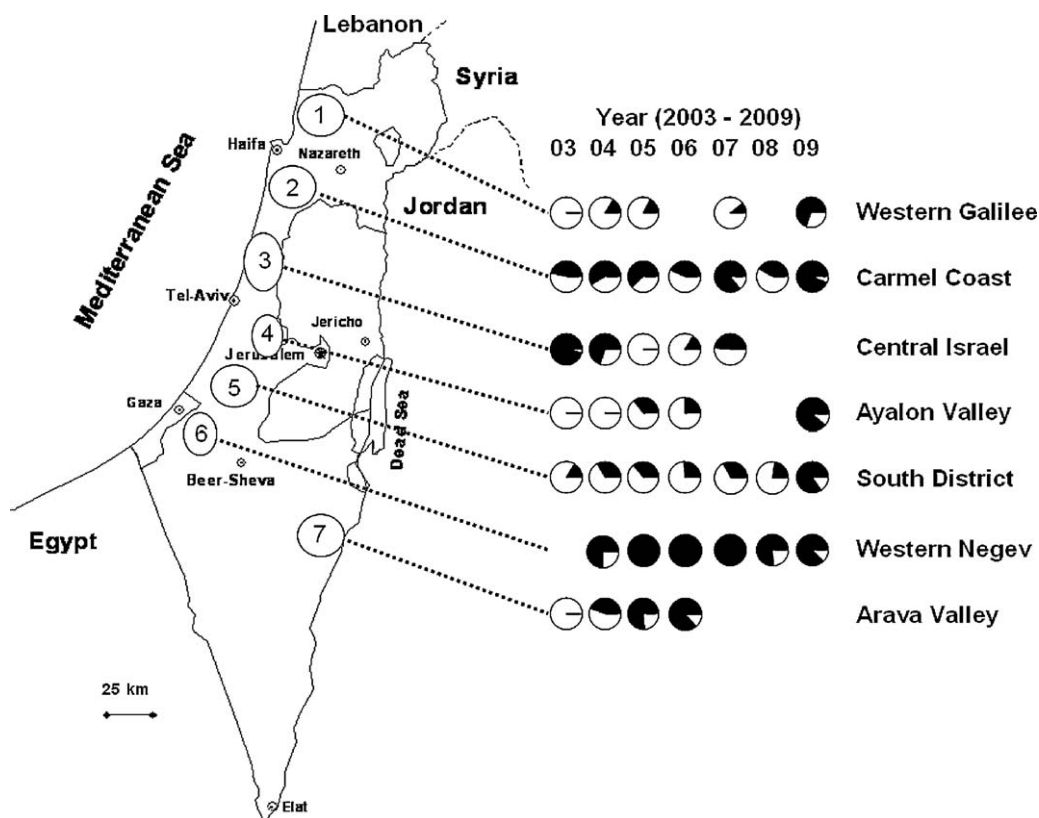
where  $S_{i,r}$  is the average number of insecticide sprays applied per year in habitat type  $i$  in region  $r$ . Thus, the percentage of each species and sprays in a region were weighted by the proportion of each habitat type to account for the fact that more-common habitats would affect the regional distribution of insects or number of sprays per field more than rare habitats. Data on the average number of insecticide sprays for each type of habitat in each region in each year were provided directly by growers. Habitat diversity was calculated using Shannon's diversity index ( $H'_r$ ):

$$H'_r = \sum_{i=1}^S (-P_{i,r} \times \ln[P_{i,r}])$$

$H'_r$  increases when the number of habitat types or the evenness of habitat types increases.

## Data analysis

Data from the field surveys and the habitat analysis were input into a multiple regression model to determine the effects of various factors on the distribution of MEAM1 and MED across Israel. The proportion of MEAM1 was the response



**Fig. 1.** Distribution of two whitefly species (MEAM1 and MED) in the *Bemisia tabaci* complex from the field-surveys. The location of each of the seven regions is shown with an oval. Each pie-circle shows the proportion of whiteflies that were MEAM1 (black area) and MED (white area) in each sampled region, for each year that region was sampled.

variable, and region (categorical), year (categorical), habitat diversity, weighted sprays, and presence/absence of each habitat type (each of four plant families) were explanatory variables. Including region and year into models allowed us to account for potential effects of spatial and temporal autocorrelation in the dataset. A significant effect of any habitat type would indicate that variation in habitat use, which could lead to niche partitioning between the species, might influence distribution of MEAM1 and MED in the field. In this context, and throughout the manuscript, we use the terms “habitat use” and “habitat association” to describe the distribution of species in habitats, which may or may not be influenced by species interactions. In contrast, we use the term “niche partitioning” to broadly indicate segregation of resources and habitats between species, which could result from evolutionary diversification between species or competitive exclusion in current ecological time.

To further look if habitat use varied between MEAM1 and MED, we compared the percentage of MEAM1 or MED in specific habitats (plant species) to the overall proportion of each species in the region where the fields were located. We used one-sample *t*-tests to determine if the percentage of MEAM1 and MED in particular habitats differed significantly from the regional percentage of each species. If the percentage of MEAM1 or MED in a particular habitat was significantly greater than the regional averages, it would

suggest that plant species was more commonly associated with that particular species. This analysis was done for each habitat type where at least five fields were sampled.

### Spatially explicit model

We used a simulation model to explore whether community patterns seen in the field-data could be explained by purely stochastic processes, niche partitioning stemming from segregation in habitat use, and variation in species traits. The stochastic model of Crowder, Horowitz, et al. (2010) and Crowder, Sitvarin, and Carrière (2010) was expanded to include a grid of 100 cells (10 × 10), each cell representing a unique habitat patch. Each habitat patch conformed to one of the following three types (based on results from the field surveys): (1) fitness of MEAM1 = MED, (2) fitness of MEAM1 > MED, and (3) fitness of MEAM1 < MED. Thus, habitat types were characterized based on their suitability and use by each species. At the beginning of each simulation, habitat patches were randomly distributed to the 100 grid cells based on the relative proportion of each habitat type (described below).

The time step of the model was 1 h. At the beginning of each day, whiteflies developed and moved between patches. In simulations with dispersal, we assumed that 6% of adults

**Table 1.** Results of multiple regression models on factors affecting the proportion of MEAM1 across regions. Regression coefficients are reported for habitat diversity, insecticide sprays and presence/absence of particular habitats. For the categorical variables region and year, we report for brevity the sum of squares from overall effect tests.

| Factor             | Coefficient | SE   | F    | df    | P       |
|--------------------|-------------|------|------|-------|---------|
| Region             | 10,737.0    | –    | 10.3 | 6, 20 | <0.0001 |
| Year               | 7257.1      | –    | 6.99 | 6, 20 | 0.0004  |
| Habitat diversity  | 13.7        | 8.12 | 2.84 | 1, 20 | 0.11    |
| Insecticide sprays | –0.62       | 1.47 | 1.09 | 1, 20 | 0.17    |
| Malvaceae          | –10.3       | 5.01 | 4.24 | 1, 20 | 0.053   |
| Asteraceae         | –16.3       | 4.23 | 14.9 | 1, 20 | 0.0010  |
| Solanaceae         | 1.47        | 4.49 | 0.11 | 1, 20 | 0.75    |
| Cucurbitaceae      | 12.6        | 5.27 | 5.75 | 1, 20 | 0.026   |

aged 5 days old were capable of dispersal (Crowder, Carrière, Tabashnik, Ellsworth, & Dennehy 2006), and dispersing adults moved randomly between adjacent cells. Variation in this assumption (i.e., adults moving more than one cell or moving on multiple days) did not qualitatively affect model simulations. Mating and oviposition were simulated every hour. Based on behavioural observations of females (Crowder, Sitvarin, & Carrière 2010), we assumed that each virgin female was courted once per time step until she was mated. The probability of a courtship ending in copulation ( $P_{success}$ ) was:

$$P_{success} = P_{intra} \times P_{cop}$$

where  $P_{intra}$  is the probability of an intraspecific courtship, and  $P_{cop}$  is the probability of copulation in intraspecific courtships. In models without trait variation (purely stochastic neutral models),  $P_{intra}$  and  $P_{cop}$  were the same for both species (see Appendix A: Table 2). In models with trait variation, estimates were based on behavioural observations conducted with both species (Crowder, Horowitz, et al. 2010) (see Appendix A: Table 2). For each courtship, a random number was drawn from a uniform distribution between 0 and 1 and compared with the probability values for  $P_{intra}$  and  $P_{cop}$ . If either random number was greater than the observed probability, the courtship ended before mating, otherwise the courtship ended in copulation. Mated females laid both male and female eggs (see Appendix A: Table 2), while unmated females laid only male eggs. Adults survived for 20 days, and females 2–20 days old laid eggs (Crowder et al. 2006). The number of eggs laid by females per day depended on female age with females 2–7 days old laying the majority of eggs (Crowder et al. 2006).

We modelled five scenarios to test the effects of colonization, dispersal limitation, variation in species traits, and niche partitioning on coexistence and community structure between MEAM1 and MED (see Appendix A: Table 3). In the first two scenarios (stochastic neutral scenarios), there were no trait differences between species, and dispersal was either limited or not (see Appendix A: Table 3). In the third scenario, there were no differences between species in habitat use, but species differed in life-history and behavioural traits. In the fourth scenario (complete niche partitioning),

all of the patches were more commonly associated with one species (0, 20, 40, 60, 80, or 100% of patches were more commonly associated with MEAM1 than MED, the remainder more commonly associated with MED than MEAM1) and traits varied between the species. In the final scenario (partial niche partitioning), 20% of the habitat patches were equally associated with MEAM1 and MED, and 0, 20, 40, 60, or 80% of the remaining habitat was more commonly associated with MEAM1 than MED (the remainder was more commonly associated with MED than MEAM1). In niche-partitioning scenarios, for all patches more commonly associated with one species than the other, we assumed that the fitness of the inferior species was 0, 20, 50, or 80% of the fitness of the superior species (a value of 0 indicates the patch was completely unassociated with the inferior species). These values were based on results from the field surveys, where habitat use between species varied widely depending on the type of habitat, which lead to varying degrees of niche overlap based on variation in habitats across landscapes. In the three scenarios with no variation in habitats, the initial percentage of MEAM1 was 5–95 (in increments of 5%). In the two niche partitioning scenarios, the initial percentage of MEAM1 was 10, 50, or 90% (variation in initial MEAM1 had a smaller effect with niche partitioning than in neutral models; see “Results”).

The model was written in Visual Basic (Microsoft Excel 2002). Each simulation was run until one species was excluded in all habitat patches, or for 1000 days (whichever occurred first). One thousand days represents approximately 40 whitefly generations, much longer than when species exclusion typically occurs in cage experiments with these species (Crowder, Horowitz, et al. 2010). The models were simulated 100 times for each scenario and set of initial conditions tested.

## Results

### Distribution of MEAM1 and MED in the field

Both MEAM1 and MED were found in every region of Israel, and both species were typically found in each region every year of the survey (Fig. 1). The multiple regression

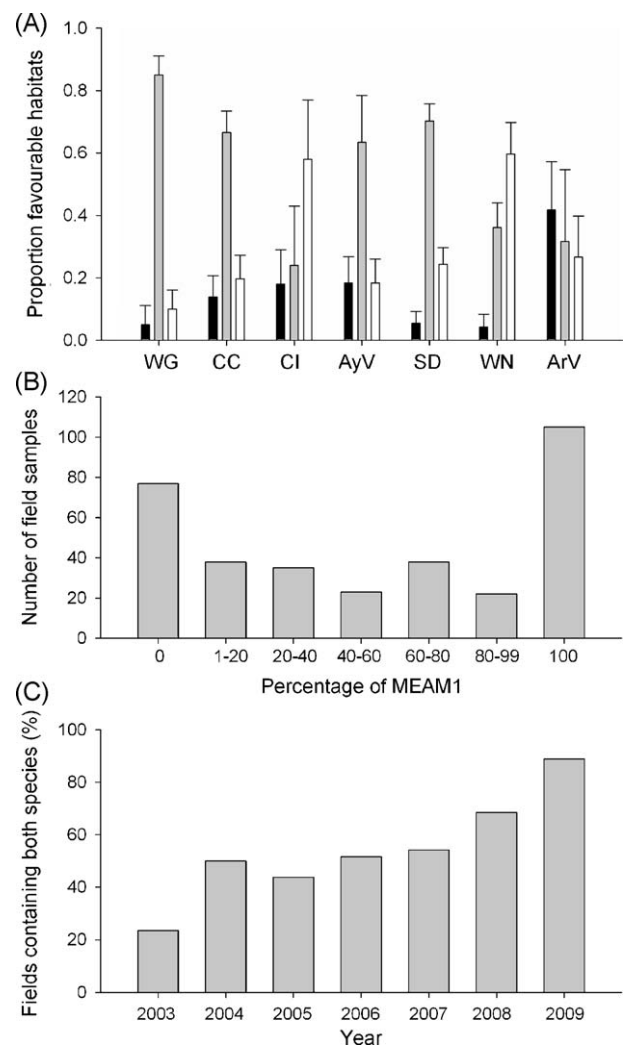
model accounted for 93% of the variation in the distribution of MEAM1 and MED across regions ( $r^2 = 0.93$ ). The abundances were affected by year, region, and the presence of three plant families (Table 1). MED was more common in northern regions, while MEAM1 was more common in southern regions (Fig. 1). In every region except Central Israel, the relative abundance of MEAM1 increased over time, while MED became less common (Fig. 1). The percentage of MEAM1 increased with the presence of Cucurbitaceae habitats, and decreased with the presence of Malvaceae and Asteraceae habitats (Table 1). Habitat diversity and insecticide sprays, however, did not significantly impact the distribution of MEAM1 and MED (Table 1).

### Niche differences between MEAM1 and MED

Supporting results of the multiple regression models, several plant species that were commonly sampled were more commonly associated with either MEAM1 or MED (Fig. 2A; Table 2). Indeed, only 2 out of 11 plant species that were commonly sampled were not more commonly associated with one species or the other (Table 2). In turn, plant species more commonly associated with MEAM1 and MED were found in each region of Israel (Fig. 2A). Consistent with the multiple regression analysis, plant species in the Cucurbitaceae were generally more commonly associated with MEAM1 than MED, and species in the Asteraceae and Malvaceae were more commonly associated with MED than MEAM1. In most regions, a higher proportion of plant species were more commonly associated with MED than MEAM1 (Fig. 2A), which could explain how MED is able to coexist with MEAM1 despite the strong effects of reproductive interference from MEAM1. Although habitat types were often more commonly associated with one species or the other, both species co-occurred in 54% of fields sampled, while 23% of fields sampled contained only MEAM1 and 23% contained only MED (Fig. 2B). Indeed, the proportion of fields containing both species increased over time (Fig. 2C), which corresponded with increased dominance of MEAM1 across Israel (Fig. 1) and a concurrent reduction in fields containing only MED.

### Stochastic meta-population model

Under the neutral models (see Appendix A: Table 3), coexistence was only possible when there was no variation in species traits and no dispersal (see Appendix A: Fig. 2A–C). In each case, stochastic processes governed which species was excluded: the species that was more abundant initially was more likely to exclude the rarer species. Variation in species traits also did not singly promote coexistence in a homogeneous landscape (see Appendix A: Fig. 2C). In this case, MEAM1 was more likely to exclude MED due to strong asymmetrical reproductive interference, although



**Fig. 2.** (A) Proportion of habitats more commonly associated with MEAM1 (black bars), MED (gray bars), or neither species (white bars) in each of Israel's seven regions (WG: Western Galilee; CC: Carmel Coast; CI: Central Israel; AyV: Ayalon Valley; SD: South District; WN: Western Negev; ArV: Arava Valley). Values shown represent the average (and SE) for each region across all the years of sampling. (B) Number of field samples that were composed of various percentages of MEAM1, across all regions in Israel. Values shown represent the total number of samples across years. (C) Percentage of field sites containing both species in each year of the field-surveys.

MED could exclude MEAM1 through priority effects when MED was initially very common (see Appendix A: Fig. 2C).

Coexistence between MEAM1 and MED was possible when variation in habitat use leading to niche partitioning occurred, and large differences in fitness between the species were present (Fig. 3). These results were similar when either 0 or 20% of habitats were used equally by both species (Fig. 3; see Appendix A: Fig. 3). Coexistence occurred when some habitats were more commonly used by one species compared with the other, and fitness differences were large (relative fitness of 0–0.5 in uncommon habitats) (Fig. 3). These results

**Table 2.** Results of *t*-tests to determine if the proportion of MEAM1 and MED in various habitat types differed significantly from the regional proportion of MEAM1 and MED.

| Habitat                    | Estimate | SE    | <i>t</i> | <i>df</i> | <i>P</i> | Associated species |
|----------------------------|----------|-------|----------|-----------|----------|--------------------|
| Cotton (Malvaceae)         | −8.42    | 2.76  | −3.05    | 100       | 0.0030   | MED                |
| Cucumber (Cucurbitaceae)   | 18.1     | 5.61  | 3.23     | 14        | 0.0061   | MEAM1              |
| Dalorit (Cucurbitaceae)    | 55.0     | 5.91  | 9.31     | 6         | <0.0001  | MEAM1              |
| Eggplant (Solanaceae)      | −7.48    | 6.32  | −1.18    | 36        | 0.24     | Neither            |
| Melon (Cucurbitaceae)      | 23.3     | 3.09  | 7.55     | 7         | <0.0001  | MEAM1              |
| Pepper (Solanaceae)        | 20.8     | 2.63  | 7.93     | 51        | <0.0001  | MEAM1              |
| Salvia (Lamiaceae)         | −53.2    | 16.45 | −3.23    | 4         | 0.032    | MED                |
| Sunflower (Asteraceae)     | −21.8    | 3.97  | −5.49    | 32        | <0.0001  | MED                |
| Tomato (Solanaceae)        | 15.6     | 4.52  | 3.46     | 21        | 0.0023   | MEAM1              |
| Trachelium (Campanulaceae) | −73.1    | 3.33  | −21.9    | 5         | <0.0001  | MED                |
| Zucchini (Cucurbitaceae)   | 10.0     | 5.80  | 1.73     | 4         | 0.16     | Neither            |

were impacted by the initial frequency of each species, as the range of fitness and habitat conditions allowing coexistence was much narrower when one species was initially very common (90%) (Fig. 3A and C) compared to when each species was initially equally common (50%) (Fig. 3B).

Although neutral models without dispersal and niche partitioning models led to coexistence under some conditions, species abundance distributions across the landscape were drastically different in each scenario (Fig. 4). In the neutral model, one species was always excluded in every habitat patch, although coexistence occurred across the landscape (Fig. 4A). In niche partitioning scenarios, both species coexisted in all, or nearly all, habitat patches (Fig. 4B).

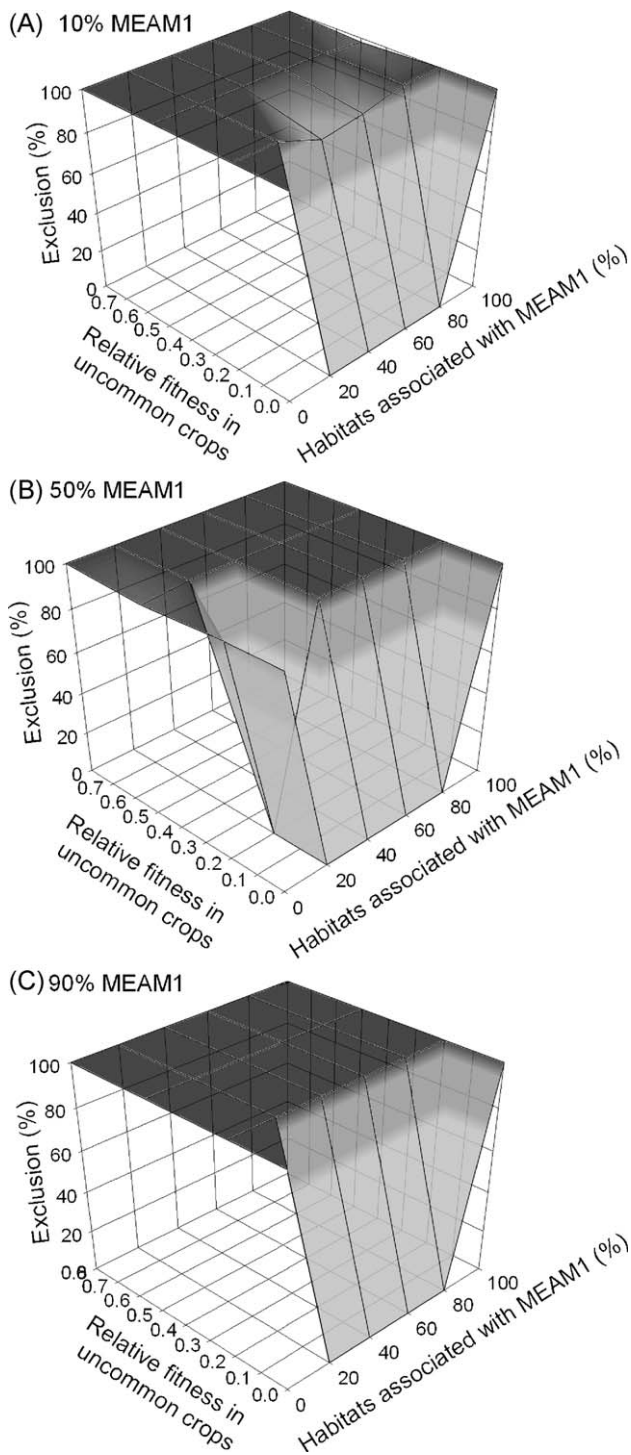
## Discussion

Here we showed that both neutral stochastic processes and niche partitioning, stemming from variation in habitat use, could promote coexistence between the invasive MED and the native MEAM1 species in the *B. tabaci* species complex. Yet, long-term field observations did not support neutral processes as the sole factor promoting coexistence for several reasons. First, when niche-partitioning and trait variation were not included in models, coexistence only occurred when dispersal did not occur (see Appendix A: Fig. 1A). This limitation is not realistic, however, as individuals of *B. tabaci* often travel long distances in migratory flight (Blackmer & Byrne 1993). Second, although species could coexist due solely to stochastic processes, single habitat patches always only contained one species under these conditions (Fig. 4A). Thus, if stochastic processes were the sole driver of coexistence between MEAM1 and MED, we would have expected to find only one species or the other in all, or nearly-all, fields from the long-term field surveys, which was not the case (Fig. 2B and C). In contrast, both MEAM1 and MED were found in many fields from the surveys, which is in accord with predictions of coexistence driven by niche partitioning (Fig. 4B). Variation in the proportion of fields containing both species across time likely reflected variation in the abundance of habitats

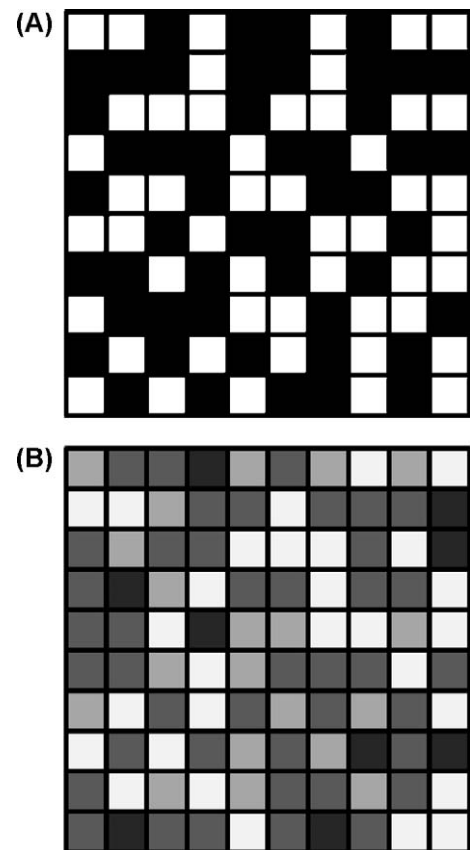
across regions and surrounding individual fields, as well as the intensity of reproductive interference and speed of sexual exclusion in areas of species overlap.

We observed that the majority of habitats found in the landscape were more commonly associated with one species compared with the other, and presence of certain habitat types significantly affected the distributions of MEAM1 and MED. These results suggest that coexistence is fostered, at least in part, by variation in habitat use leading to niche partitioning. As is typical of many invasive species that have broader resource niches than native species (Snyder & Evans 2006; Crowder & Snyder 2010), MED had a broader range of associated habitats compared with MEAM1 (Fig. 2A). In turn, broad resource niches can provide refuges from competition and promote establishment and spread of invaders (Crowder & Snyder 2010). Variation in the breadth of resource and habitat niches can also impact encounter frequencies between species and mitigate the negative effects of reproductive interference (Gröning et al., 2007). In our system, the establishment of the invasive MED may therefore be more likely in areas with a broad variation in plant habitats. In contrast, persistence of MEAM1 may be more likely in regions with few plant species, where MEAM1's competitive dominance (Crowder, Horowitz, et al. 2010; Crowder, Sitvarin, & Carrière 2010) allows it to out-compete sympatric species in shared habitats.

Our findings suggest that a species that is superior at interference competition can coexist with a superior resource competitor if the weak resource competitor benefits from interference competition, as has been predicted with models (Case & Gilpin 1974; Amarasekare 2002). Here, while the invasive MED has a broader range of associated habitats, MEAM1 is superior at reproductive interference, which limits the ability of MED to reproduce in shared habitats (Crowder, Horowitz, et al. 2010; Crowder, Sitvarin, & Carrière 2010). Similar trade-offs between ecological traits are often associated with coexistence between species (reviewed by Kneitel & Chase 2004). For example, Gröning et al. (2007) showed that a leafhopper species with a reduced habitat breadth occurred in tight aggregations, which reduced



**Fig. 3.** Effects of habitat variation and relative fitness on sexual exclusion of MEAM1 and MED in niche partitioning models where 0% of the habitat was equally used by both species and (A) 10%, (B) 50%, and (C) 90% of individuals were initially MEAM1. The *x*-axis shows the % of habitats in the region more commonly associated with MEAM1, and the *y*-axis shows the relative fitness for both species in uncommonly used habitats. The *z*-axis shows the percent of simulations where one species was excluded within 40 generations. The planes show the 3-dimensional trends in the data, where lighter values indicate lower probability of exclusion (i.e., higher probability of coexistence).



**Fig. 4.** Typical species distributions with (A) the neutral model without dispersal and (B) the complete niche partitioning model. For both cases, the regional percentage of MEAM1 was approximately 50%. (A) black squares indicate the patch was 100% MEAM1, white squares indicate the patch was 100% MED. (B) no species occupied more than 70% of a single patch. The four increasingly dark shades of gray represent 60–70% MEAM1, 50–60% MEAM1, 40–50% MEAM1, and 30–40% MEAM1.

its interspecific encounter rate, mitigating effects of reproductive interference and fostering coexistence with a more generalist leafhopper. Coexistence is also often impacted by trade-offs at regional scales, such as the trade-off between competition and colonization (reviewed by Kneitel & Chase 2004). Mouquet and Loreau (2002, 2003) also showed that variation between species in resource acquisition (i.e., a local trait) and dispersal (i.e., a regional trait) could promote coexistence. Our results suggest that similar trade-offs between mating behaviour and habitat use can promote coexistence.

Our findings are in accord with the idea that niche partitioning is more likely to govern community structure than neutral stochastic processes (i.e., Kneitel & Chase 2004; Levine & HilleRisLambers 2009; Harrison et al. 2010). Yet, as predicted by stochastic niche theory (Tilman 2004), there appears to be a role for both niche partitioning and stochastic processes in our system. Indeed, our field survey data showed that while species coexistence occurred in most habitat patches, in line with predictions of coexistence driven by niche partitioning, many fields contained only one species



(Fig. 2B). Because niche partitioning only promoted coexistence if large fitness differences were present (Fig. 3), these results suggest that stochastic processes drove exclusion of one species in patches that did not support broad niche partitioning. Thus, in our system, stochastic processes and niche-based processes are not dichotomous elements of communities, but rather operate concurrently to determine community structure (see also Tilman 2004; Leibold & McPeck 2006; Adler et al. 2007).

Our study highlights the utility of combining stochastic, spatially explicit models with long-term field studies to investigate mechanisms that promote coexistence or drive exclusion between species. Model results and field data suggest that strong trade-offs between species traits in shared habitats and the ability to exploit habitats across landscapes can promote coexistence between native and invasive species, while stochastic processes play an important role in determining whether rare invasive species can become established. Similar studies in other systems can further clarify the patterns and processes that govern species interactions and distributions following invasions. More generally, our results provide strong support for the role of both stochastic and niche-based processes on determining community structure.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2011.09.007.

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