

IMPORTANCE OF COMPETITION MECHANISMS IN SUCCESSIVE INVASIONS BY POLYPHAGOUS TEPHRITIDS IN LA RÉUNION

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Abstract. Understanding the strength and modes of interspecific interactions between introduced and resident species (native or previously introduced) is necessary to predict invasion success. We evaluated different mechanisms of interspecific competition among four species of polyphagous fruit flies (Diptera: Tephritidae) from the island of La Réunion: one endemic species, *Ceratitis catotrii*, and three exotic species, *C. capitata*, *C. rosa*, and *Bactrocera zonata*, that have successively invaded the island. Larval competition experiments, i.e., co-infestations of the same fruit, and behavioral interference experiments measuring the ability of one female to displace another from a fruit, were performed among all pairs of the four species. We observed asymmetric and hierarchical interactions among species in both larval and adult interference competition. In agreement with the hypothesis that invasion is competition-limited, the competitive hierarchy coincided with the temporal sequence of establishment on the island, i.e., each newly established species tended to be competitively dominant over previously established ones.

Key words: *Bactrocera zonata*; biological invasions; *Ceratitis capitata*; *Ceratitis catotrii*; *Ceratitis rosa*; competitive asymmetry; exploitative competition; fruit flies; interference competition; Tephritidae.

INTRODUCTION

Biological invasions pose major problems for biodiversity conservation (Vitousek et al. 1996), one of which is the extirpation of indigenous species by competitive displacement (Elton 1958, Juliano and Lounibos 2005). While attempts to predict invasions based on ecological rules have had some success (Hobbs and Huenneke 1992, Kolar and Lodge 2001, Levine et al. 2004), the importance of interspecific competition in determining when and where invasions occur remains ambiguous. Clearly, competition often takes place between invaders and the recipient community (Dyer and Rice 1999, Shea and Chesson 2002, Levine et al. 2004). However this does not mean that it acts as an important sieve to retain successful invaders from a pool of candidate species. Although this hypothesis or similar ones have been repeatedly put forward (Crawley 1993, Thébaud et al. 1996, Byers 2000, Vila and Weiner 2004), in other cases the emphasis is put on *r*-selected traits and the ability of species to rapidly colonize empty space (Lodge 1993, Rejmanek and Richardson 1996). These two visions seem contradictory, unless one rejects the classical idea of a trade-off between competitive ability and colonization ability (Mac Arthur 1962, Tilman

1994), or, equivalently, envisages invasive species as the “happy few” that happen to override this trade-off. Of course, this apparent contradiction can stem from mixing together different situations: invasions into vacant niches, such as by a predator in a predator-free island (Fritts and Rodda 1998), are by definition not competition limited and should depend only on colonization ability, while invasions into occupied niches can be competition limited. However, for the latter, only empirical studies can tell whether competition is a major determinant of invasion success. Controlled experiments can be useful for this purpose. These experiments give access to competitive responses (the ability of a species to withstand competition exerted by other species) and competitive effects (the negative effects of a species on other species) (Goldberg and Barton 1992). To the extent that laboratory or experimental field results represent phenomena that also operate *in natura*, the competitive effect is expected to determine how an invader may affect established species if it succeeds, while the competitive response, if the competition limitation hypothesis is true, is expected to determine the probability that invasion succeeds. Sets of closely related species successively invading the same territory are ideal situations to test this hypothesis, because competition is expected to be more intense among similar species, especially when they are first brought into contact and have no coevolutionary history (Reitz and Trumble 2002). In addition, within homogeneous

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guilds of animals or plants, competition usually tends to be asymmetrical and organized in a hierarchical way (i.e., transitive [Keddy 2001]). This provides a simple way to test the competition limitation hypothesis: successive invaders should be at higher and higher levels of the hierarchy in competitive response, if such a hierarchy exists.

We here test this prediction in a case study on four species of fruit flies (*Tephritidae*). We are aware that this is only a case study and that many more studies of the same kind would be needed to generalize. Unfortunately, competitive hierarchies have not yet received in invasion biology the attention they have received in plant community ecology (Keddy 2001, Daehler 2003). The choice of *Tephritidae* as a model system is motivated by several important features. First, the four species studied are all highly polyphagous and show considerable diet overlap (Quilici and Jeuffrault 2001), providing large opportunities of competition. Indeed, species displacements following invasions have been repeatedly observed among *Tephritids* (Debach 1966, Duyck et al. 2004a). Second, a hierarchical mode of competition is suggested by the fact that invasion links (i.e., the ability of species A to invade in the presence of B) seem transitive but never reciprocal in a number of *Tephritid* invasions worldwide (Duyck et al. 2004a). Finally, the history of invasions is well known in our study site: the island of La Réunion (Indian Ocean). One of the species (*Ceratitis catairii*) is indigenous while the other three (*Ceratitis capitata*, *C. rosa*, and *Bactrocera zonata*) are invaders, whose chronology of introduction is precisely known. Each invader has rapidly grown in numbers once introduced, while previously established species, be they native or previous invaders, declined in at least a part of their range.

The main resource for which interspecific competition can plausibly occur among species of *Tephritid* flies is the host fruit (Prokopy and Roitberg 1984). In *Tephritids*, females search for fruit at the appropriate maturation stage and puncture the fruit skin to deposit eggs (Prokopy and Roitberg 1984, White et al. 2000). Eggs hatch and larvae develop within the fruit, then jump out of the fruit onto the ground, where they bury themselves to pupate. Competition can occur in the form of scramble competition among larvae when two species co-infest the same fruit or in the form of direct aggressive interference between females ready to lay eggs in the same fruit. In addition, some features of female behavior may influence the effects of interspecific competition in the field. The ability of a female to detect and avoid fruits that are already infected and the ability to localize available fruits faster than other species can determine how a species tolerates the presence of other, previously established species. In this study we try to compare each of these aspects among the four species in the laboratory.

A potential problem is that the laboratory necessarily represents a single environment that is not representative

of the diversity of niches exploited by the species in their natural environment. The four *Tephritids* we studied are generalist species found on many species of fruits (>350 for *C. capitata* [Liquidó et al. 1991]) and in a variety of climatic conditions throughout the island (Duyck and Quilici 2002, Duyck et al. 2004b). It is very likely that competition varies among these different niches (Duyck et al. 2004a). The study of this variation is a large subject in itself; however, if interspecific competition is to somehow limit invasions, one expects relevant patterns to be found in resources that are both numerically abundant and shared by all species. For this reason we chose to focus our study on a single fruit (guava, a very common fruit in La Réunion, on which all four species have regularly been observed) and a single temperature (25°C, the most favorable temperature for all four species [Duyck and Quilici 2002, Duyck et al. 2004b]), typical of the cultivated lowlands in La Réunion, where the largest fruit fly populations are found and where new invaders are more likely to be introduced by overseas transport).

MATERIALS AND METHODS

Fly species and strains

On La Réunion (a volcanic tropical island of the Indian Ocean), four species of polyphagous *Tephritidae* are currently found. The Mascarene fruit fly *Ceratitis catairii* is endemic to Mauritius and La Réunion islands (Orlan and Moutia 1960, Etienne 1972, White et al. 2000). The Mediterranean fruit fly *C. capitata* was introduced in 1939 and became widespread in La Réunion, while *C. catairii* became rarer (White et al. 2000). The Natal fruit fly *C. rosa* was first detected in 1955 (Orlan and Moutia 1960, Etienne 1972). A similar pattern of successive invasions has been observed in Mauritius, except that *C. catairii* is now considered extinct on this island, having not been recorded for the last 20 years (White et al. 2000). In La Réunion, the peach fruit fly *B. zonata* was first detected in 1991 but its populations grew massively and spread in 2000 (Hurtrel et al. 2000). This last species is still in the process of expansion. Among the numerous host plants of these species present in La Réunion, four are of particular importance because of their abundance, namely guava (*Psidium guajava* L.), Indian almond (*Terminalia catappa* L.), mango (*Mangifera indica* L.), and strawberry guava (*Psidium cattleianum* Sabine) (Quilici and Jeuffrault 2001). While the four *tephritids* studied do not have identical host ranges, they share these four main host fruits, as well as many less important ones (Quilici and Jeuffrault 2001). Also, the four *tephritids* do not have similar climatic niches (Duyck and Quilici 2002, Duyck et al. 2004b), but all of them are abundant in the lowlands of the island.

Experiments were conducted with recent laboratory cultures of the four fruit fly species. Techniques for maintenance of these laboratory cultures were described in previous studies (Duyck and Quilici 2002, Duyck et

al. 2004b). For experiments on adults, naïve females (with no prior ovipositional experience) were studied at their peak of fecundity (between age 20 and 25 d for the three *Ceratitis* spp. and 40–45 d for *B. zonata*). Rearing conditions were 25°C ($\pm 1^\circ$), 80% relative humidity ($\pm 10\%$), and 12:12 light : dark photoperiod for all experiments.

Larval competition

The opportunity of interspecific competition depends on the frequency of co-infestations and on the density of larvae within fruits. In order to estimate these parameters, we used a database of 3778 infested fruits of various species, including 786 fruits of guava (*Psidium guajava* L.) and 1196 fruits of Indian almond (*Terminalia catappa* L.), collected in different parts of La Réunion island from 2002 to 2005. Fruits were brought back to the laboratory, individually weighed, and placed on a grid in a closed container layered with sand or sawdust, following standard methods for fruit fly rearings (White and Elson-Harris 1992). Pupae fallen into the sand or sawdust were then counted and species were identified when adults emerged from pupae.

Manipulation trials have often been used successfully to detect asymmetrical competition and hierarchy in plant communities (Goldberg and Barton 1992, Keddy 2001). These experiments usually compare the relative yield of different competing species in the absence and in the presence of competitors (Keddy 2001). We used a similar approach with the four species of Tephritidae in order to assess whether their competitive hierarchy correlates with the ability of a species to invade in the presence of another. Larval competition experiments in the laboratory were conducted with all pairwise combinations of the four species. For each replicate, one or two noninfested guava fruits (total mass of 100 g) were washed and nicked at the surface for introduction of newly hatched larvae (<3 h old) inside the pulp. Fruits were carefully infested with a fine brush under a binocular microscope with 50 newly hatched larvae of only one species (for the control) or 50 larvae of each species (for cross infestations). Such a density of infestation has already been used in several studies on the larval development of Tephritidae (Fitt 1986, Krainacker et al. 1987) and is comparable to observed densities in the field (see *Results*). Our design is additive rather than substitutive (Keddy 2001) and therefore allows us to test the effect of the addition of competitors; this is relevant in our case because fly density in wild-caught fruits co-infested by two or more species exceeds that of mono-infested fruits (see *Results*). However, using our design, the effects of intraspecific and interspecific competition cannot be compared. Infested fruits were put in an open plastic box inside a plastic container, with its bottom covered by a layer of sand to allow for pupation of mature larvae that have jumped from the fruit. From six days after infestation, sand was sifted daily in order to collect pupae. Each pupa was

weighed and put in a separate plastic box until emergence of the adult and species determination. Three to seven replicates were done for each pair of species tested and for each control (67 boxes in total). For each parameter and each species, four treatments were used (control and competition with each of the three other species).

Net reproductive rates (R_0), i.e., the expected number of offspring per female in a lifetime, was estimated in order to integrate survival and pupal mass in a single parameter, so as to facilitate comparisons between different treatments. Original R_0 were calculated using established life tables for each species (P. F. Duyck, P. David, and S. Quilici, *unpublished manuscript*). Survival from larva to adult (measured in the experiment) was multiplied by a function of body size that represents the expected number of offspring in an adult lifetime. We used regression equations of fecundity on body size established separately for the four species ($R'_0 = R_0 e^{0.0211(p - 112)}$, $R^2 = 0.061$, $P < 0.001$; $R'_0 = R_0 e^{0.0506(p - 94)}$, $R^2 = 0.58$, $P < 0.001$; $R'_0 = R_0(0.0082p + 0.1191)$, $R^2 = 0.31$, $P < 0.001$; and $R'_0 = R_0 e^{0.0347(p - 118)}$, $R^2 = 0.29$, $P < 0.01$, respectively, for *C. catovirii*, *C. capitata*, *C. rosa*, and *B. zonata*; p = pupal mass, R_0 = original net reproductive rate [$R_0 = 18.2$, 130.6, 128.4, and 66.3, respectively]; R'_0 = estimated net reproductive rate).

In order to test for resource preemption, the relationship between pupal mass and developmental time was analyzed by analyses of covariance (ANCOVA) for each species. Pupal mass was fitted as a function of developmental time (covariate), competition treatment (presence and species of competitor), and their interaction.

Competition results are usually given in terms of relative yield (RY) for plant experiments (Wilson and Keddy 1986, Keddy 2001). As we compared interspecific competition in insects, this indicator was replaced by relative performance (RP), but we kept the same methodology as for plant experiments. Relative performance was calculated for R_0 , pupal mass, and survivorship by dividing the value of the target species reared with a competing species by the value of the target species reared alone. Relative performance distinguishes between two components of competitive interactions: the mean response and the mean effect (Goldberg and Barton 1992). For a given target species, the mean response is the mean of RP when reared with competing species, while the mean effect is the inverse of the mean RP of all competing species when reared with the target species. For each parameter (R_0 , pupal mass, survivorship), the asymmetry of competition was calculated between species pairs by dividing the RP of the target species by that of the competitor. This definition indicates the direction of asymmetry and differs slightly from the one of Keddy (2001), in which asymmetry is calculated by always dividing the highest RP by the lowest RP of the two competitors.

Behavioral observations

A first assay was carried out to assess the outcome of interference competition for laying sites, i.e., direct interactions between the females of the different species on the same fruit. One half of a strawberry guava (*Psidium cattleianum* Sabine) fruit, cut lengthwise and placed with the skin side exposed, was presented to two females of different species (cage size, $7 \times 12 \times 15$ cm). The number of takeovers, i.e., aggressions by species A leading to the departure of species B from the fruit, was recorded during 30 min. We performed 30–33 replicate assays for each pair of species. Data were analyzed using a Poisson log-linear model (analysis of deviance with Poisson error). Overdispersion was accounted for by using F tests instead of chi-squares to evaluate the significance of changes in deviance (Crawley 1993). The asymmetry of female interference was calculated between each pair of species by dividing the number of takeovers of the target species by that of the competitor.

Other behavioral traits may allow a species to avoid fruit already infested by other species or to localize noninfested fruits faster than other species. Two types of signals may reveal that a fruit is infected: signals from puncture holes made by laying females and host-marking pheromones. In order to determine whether females prefer to lay their eggs in already punctured fruits, we presented two halves of strawberry guava to individual females. One half was intact while the other was artificially punctured 30 times (0.50 ± 0.04 mm) with a needle through the skin to mimic oviposition holes. During 30 min, we recorded the number of landings on each half-fruit and the number of egg-layings in the fruit as well as the occurrence of an “ovipositor dragging” behavior following an egg-laying, previously described as typical of flies depositing host-marking pheromones (HMPs; Prokopy et al. 1978, Papaj et al. 1989). This procedure was repeated with 30 different females for each species.

A second (independent) assay was carried out to test whether females were influenced by prior infestation by females of the same species or of any of the other species. The same procedure as in the previous experiment was employed except that the “treated” half-fruits were not punctured but exposed (in series of 10) to 30 females of the same species or other species during 24 h, while the “control” half-fruits were not. The number of landings and egg-layings were recorded on each half-fruit during 30 min. First, we tested for an intraspecific effect, i.e., whether the behavior of the target species was affected by previous visits by conspecific females. We considered that species with no significant intraspecific response and little ovipositor-dragging behavior did not leave detectable chemical signals or HMPs and used only species with a significant intraspecific effect and a frequent marking behavior (i.e., *C. capitata* and *C. rosa*) to assess interspecific effects. The same experiment as for intraspecific effects was carried out, except that the fruit was first exposed to females of another species (either *C.*

capitata or *C. rosa*) and then to the target species. Each test was replicated 30–33 times.

The abilities of females of the four species to localize host fruits were compared using a cylindrical mesh-screened field cage (2.5 m tall \times 3 m diameter). Within the cage, four plants of the non-host *Ficus benjamina* were placed in front of three noninfested washed guava fruits hanging from a metallic support. Twenty females of each species (80 females in total) were released in the cage at the opposite side of the hanging guava fruits. The observer stood behind the *Ficus* plants during 45 min and recorded for each species the number of landings on and egg-layings in the fruits. The procedure was replicated 13 times. The number of landings and egg-layings were analyzed using a Poisson log-linear model. Cumulative time spent on fruits was transformed into percentage of total potential time spent by the 20 females (20×45 min) on fruit prior to angular transformation (arcsine square-root transformed x) and analyzed by one-way ANOVA.

RESULTS

Larval competition

The mean final larval density per fruit in the laboratory experiment measured by the total number of pupae across species was 0.33 ± 0.17 pupae/g (mean \pm SD; range 0.050–0.740). In the field, infested guava fruit produced on average 0.22 ± 0.21 pupae/g (range 0.001–1.661). Irrespective of fruit species, the mean infestation in the field was 0.43 ± 1.07 pupae/g (range 0.001–20.0). The pupal density increased significantly when two (and furthermore three) species were present in a guava fruit ($N = 786$; one species, 73%, 0.16 ± 0.17 pupae/g [mean \pm SD]; two species, 23%, 0.33 ± 0.24 pupae/g; three species, 4%, 0.47 ± 0.33 pupae/g; ANOVA on log-transformed data, $F_{2,283} = 77.45$, $P < 0.0001$) and in an Indian almond fruit ($N = 1196$; one species, 72%, 0.26 ± 0.28 pupae/g; two species, 26%, 0.44 ± 0.32 pupae/g; three species, 2%, 0.50 ± 0.27 pupae/g; ANOVA on log-transformed data, $F_{2,1196} = 88.49$, $P < 0.0001$). The final density ratios observed in our experiments and in the field for pairs of species co-infesting the same fruit are given in the Appendix.

Table 1 shows the relative performance of each species reared in all possible pairwise combinations. For most or all species, there is a significant effect of the competition treatment on R_0 (ANOVA, $P < 0.05$ for all species, complete statistics in Table 1), survivorship (ANOVA, $P < 0.05$ except for *C. capitata*), and pupal mass (ANOVA, $P < 0.05$ except for *C. rosa*). Species differed significantly in mean response with respect to R_0 (ANOVA, $F_{3,44} = 8.51$, $P < 0.0005$), survivorship (ANOVA, $F_{3,44} = 6.92$, $P < 0.001$), and pupal mass (ANOVA, $F_{3,40} = 8.45$, $P < 0.005$). However, the mean effect for these three attributes was not significantly different among the species (ANOVAs, $F_{3,44} = 1.22$, $P = 0.31$; $F_{3,44} = 1.55$, $P = 0.21$; $F_{3,40} = 0.88$, $P = 0.46$, respectively for R_0 , survivorship, and pupal mass). The

TABLE 1. Relative performance of four species of Tephritidae in all pairwise combinations.

Target species	Control	Competing species (relative performance)				Mean response	ANOVAs for competitive effect		
		<i>Bzon</i>	<i>Cros</i>	<i>Ccat</i>	<i>Ccap</i>		df	<i>F</i>	<i>P</i>
<i>R</i> ₀ (no. eggs/female)									
<i>Bzon</i>	19.41		0.79	0.30	0.71	0.59 ^a	3,13	5.1	0.015
<i>Cros</i>	124.27	0.55		0.36	0.50	0.44 ^{ab}	3,15	4.4	0.020
<i>Ccat</i>	10.22	0.02	0.22		0.29	0.15 ^{bc}	3,12	6.8	0.006
<i>Ccap</i>	20.33	0.10	0.04	0.16		0.10 ^c	3,11	4.2	0.032
Mean effect		4.00	2.41	3.66	2.00				
Survivorship (rate)									
<i>Bzon</i>	0.70		0.89	0.78	1.03	0.90 ^a	3,13	4.0	0.032
<i>Cros</i>	0.82	0.62		0.43	0.64	0.56 ^{ab}	3,15	3.6	0.039
<i>Ccat</i>	0.30	0.05	0.38		0.52	0.32 ^b	3,12	4.6	0.023
<i>Ccap</i>	0.39	0.49	0.22	0.60		0.46 ^b	3,11	1.7	0.216
Mean effect		2.50	1.79	1.67	1.35				
Pupal mass (10 ⁻⁴ g)									
<i>Bzon</i>	91.01		0.95	0.70	0.89	0.85 ^a	3,13	5.2	0.014
<i>Cros</i>	102.75	0.84		0.76	0.78	0.80 ^a	3,15	2.7	0.085
<i>Ccat</i>	104.89	0.56	0.57		0.72	0.63 ^b	3,10	13.0	0.001
<i>Ccap</i>	66.03	0.60	0.56	0.64		0.61 ^b	3,9	6.7	0.011
Mean effect		1.43	1.32	1.43	1.25				

Notes: Species whose competitive responses do not significantly differ (Tukey's studentized test, $P < 0.05$) are denoted by common superscript letters. Abbreviations are: *R*₀, net reproductive rate; *Bzon*, *Bactrocera zonata*; *Cros*, *Ceratitidis rosa*; *Ccat*, *C. catoirii*; *Ccap*, *C. capitata*. The study was conducted on fruit fly species found on La Réunion, a volcanic tropical island of the Indian Ocean.

hierarchy in competitive response was *B. zonata* > *C. rosa* > *C. catoirii* > *C. capitata* except for survivorship, in which the ranks of *C. catoirii* and *C. capitata* were reversed. Note, however, that although the four means are statistically different for all traits, not all pairs of species are, so the hierarchy indicated should be only considered as an overall pattern. The asymmetry of competition and its direction are overall decreasing functions of competitive response ranks (Fig. 1).

For each species, pupal mass decreased with developmental duration and competition treatment (Fig. 2; ANCOVA, $P < 0.05$; see legend for complete statistics), and the interaction was not significant.

Interference competition in the laboratory

Recordings of aggression were strongly asymmetric (Table 2, Fig. 1). The mean number of takeovers (aggressions towards females of other species ending in effective displacement) varied among species (generalized linear model [GLM] with Poisson error, $F_{3,386} = 16.18$, $P < 0.0001$) following the order: *B. zonata* = *C. rosa* > *C. capitata* > *C. catoirii*. Compared with other species, *B. zonata* was overall the species least often driven from fruits by another species (GLM with Poisson error, $F_{3,386} = 3.05$, $P = 0.029$).

Fruit choice experiments

For *C. capitata*, the percentage of visits to artificially punctured fruits was significantly higher (62.4% of all visits, $N = 30$, pairwise *t* tests, $P < 0.05$) than on intact fruits, while for the three other species this percentage did not differ between the two half-fruits (52.5, 50.6, and 47.7% of all visits respectively for *C. catoirii*, *C. rosa*,

and *B. zonata*; $N = 30$ for each species, pairwise *t* tests, $P > 0.05$). For all species, the mean percentage of egg-layings was not significantly different between the wounded fruit and the control (45.8, 57.5, 44.0, and 37.8% of all egg-layings, respectively, for *C. catoirii*, *C. capitata*, *C. rosa*, and *B. zonata*; $N = 30$ for each species, pairwise *t* tests, $P > 0.05$).

During our experiments, a behavior of "ovipositor dragging" (as described by Prokopy et al. [1978]) was observed, and its frequency varied among species: it was much higher in *C. capitata* and *C. rosa* than in the two other species (18.2, 72.3, 75.5, and 12.9%, respectively, for *C. catoirii*, *C. capitata*, *C. rosa*, and *B. zonata*). The behavior also differed qualitatively between genera: for the three *Ceratitidis* spp. the whole ovipositor was dragged on the fruit surface while for *B. zonata*, only the tip of the extended ovipositor was dragged on the fruit. During this behavior, the four species completed circles on the fruit and repeatedly touched the fruit with their mouthparts. At this stage, *B. zonata* females also stroke the fruit surface with their ovipositors.

Females of *C. rosa* laid significantly less in fruits previously exposed to conspecifics than in control fruits, while the reverse was observed for *C. capitata*, and no significant effect was recorded for *C. catoirii* and *B. zonata* (Table 3a). *Bactrocera zonata* laid less in fruits previously exposed to *C. capitata* or *C. rosa* (Table 3b). The percentage of visits of *B. zonata* was lower on fruits exposed to *C. capitata* than on control fruits, while no difference was observed with fruits exposed to *C. rosa*. No significant effect of interspecific recognition of previous egg-laying was observed between *C. capitata* and *C. rosa*.

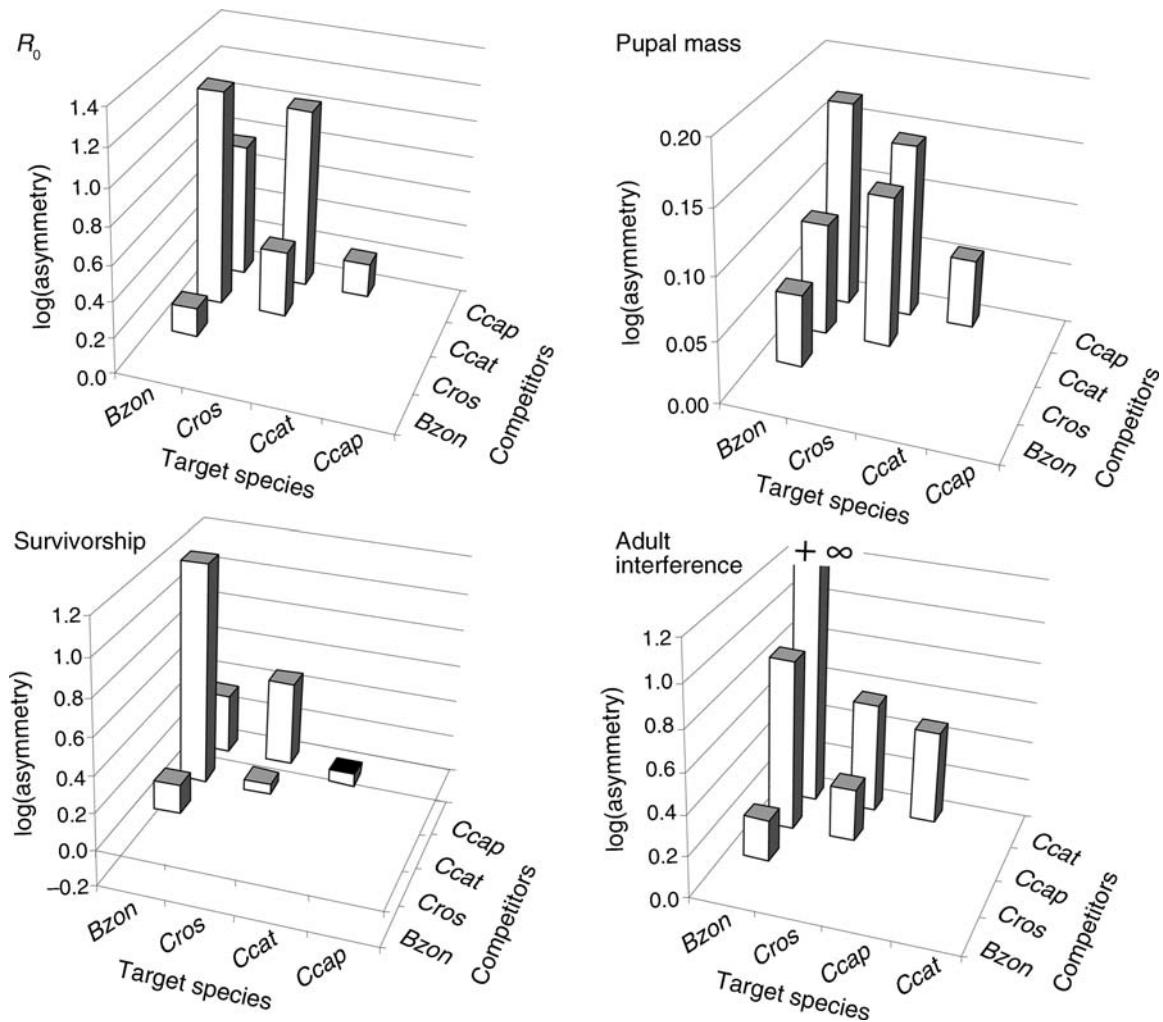


FIG. 1. Competitive asymmetry revealed by pairwise cross-infestation (net reproductive rate [R_0], larval survivorship, and pupal mass) and in adult female interference among the four species of Tephritidae. (See *Methods* for definitions.) Fruit fly species names are abbreviated as in Table 1. For adult interference, the log(asymmetry) *Bzon/Ccat* tend to infinity because no displacement of *Bactrocera zonata* by *Ceratitidis catoirii* has been observed in any trial. The study was conducted on species found on La Réunion, a volcanic tropical island of the Indian Ocean.

Host location by females

The mean number of landings on fruit (GLM with Poisson error, $F_{3,48} = 12.17$, $P < 0.0001$), layings in a fruit (GLM with Poisson error, $F_{3,48} = 11.28$, $P < 0.0001$), and the mean cumulative time spent on the fruit (ANOVA, $F_{3,48} = 7.37$, $P < 0.001$) varied significantly among species (Fig. 3). *Ceratitidis capitata* and *B. zonata* landed significantly more on the fruits than did the two other species. However, the number of egg-layings followed another order: *B. zonata* and *C. rosa* laid more than *C. capitata* and *C. catoirii*. The cumulative time spent on the fruit was longer for *B. zonata* than for the other species.

DISCUSSION

Interspecific competition reduces larval survival, pupal mass, and the potential rate of population

increase. Overall, within each species, larval development time and pupal mass are negatively correlated, with late pupae being smaller, with or without allospecific competitors. If all larvae of a given species grew at the same rate, we would expect the opposite pattern, i.e., longer developmental times associated with larger pupae. The observed pattern suggests a competitive preemption of resources within species, i.e., the first larvae to develop benefit from more resource than later ones (Blanckenhorn 1999, Krijger et al. 2001). Adding interspecific competitors does not change the slope of the mass–developmental time relationship but shifts it downward to a variable degree depending on the species involved. Thus, the presence of interspecific competitors has the same effect as having less available resources to begin with. As our experimental densities are comparable to those found *in natura* (especially when two species

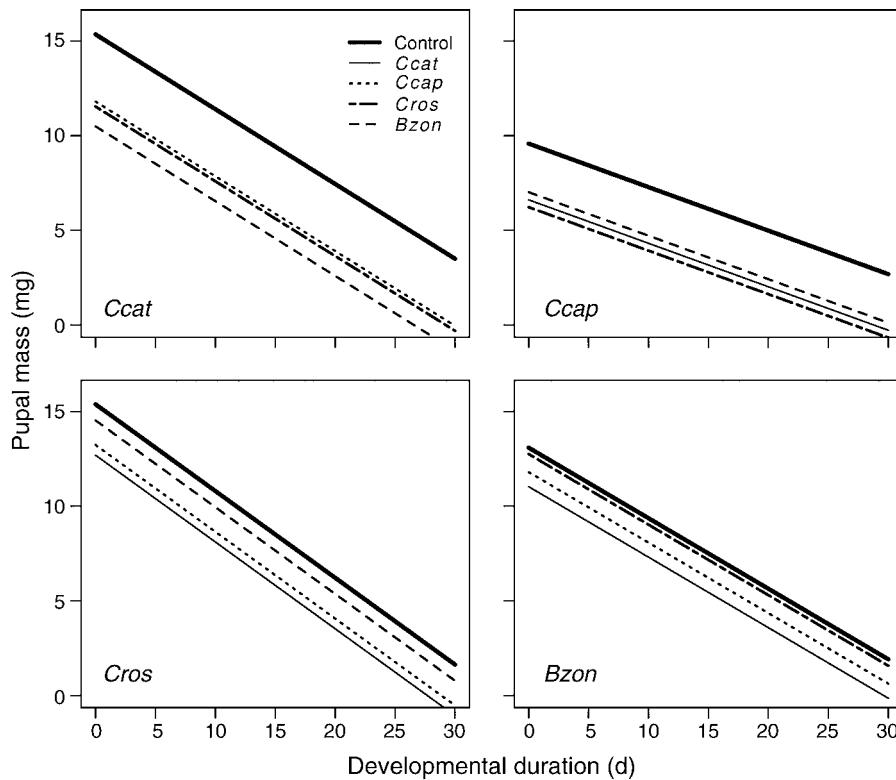


FIG. 2. Relationship between pupal mass and developmental duration for four species of Tephritidae reared alone (control) or in pairwise competition trials (names of competing species are abbreviated as in Table 1). Only regression lines are presented, estimated in the model without interaction. *Ccat*: ANCOVA, developmental duration, $F_{1,5} = 7.0$, $P = 0.04$; treatment, $F_{3,5} = 12.0$, $P = 0.01$; interaction, $F_{3,5} = 1.3$, $P = 0.36$. *Ccap*: ANCOVA, developmental duration, $F_{1,6} = 6.7$, $P = 0.04$; treatment, $F_{3,6} = 28.6$, $P < 0.001$; interaction, $F_{3,6} = 3.4$, $P = 0.09$. *Cros*: ANCOVA, developmental duration, $F_{1,11} = 15.6$, $P < 0.01$; treatment, $F_{3,11} = 6.4$, $P < 0.01$; interaction, $F_{3,11} = 2.8$, $P = 0.09$. *Bzon*: ANCOVA, developmental duration, $F_{1,9} = 17.8$, $P < 0.01$; treatment, $F_{3,9} = 13.5$, $P < 0.01$; interaction, $F_{3,9} = 2.9$, $P = 0.10$.

co-infest the same fruit) in guava or other host fruits, the same kind of competition could occur in the field. The density ratios observed in the field essentially cover all the possible range (0, 1), while we used only a single density ratio (1:1) to measure interspecific competition.

TABLE 2. Mean number of cases where species A was driven out of the fruit by species B during 30 min ($n = 30-36$ replicates).

Species B (aggressive)	Species A (driven out)				Mean
	<i>Bzon</i>	<i>Cros</i>	<i>Ccap</i>	<i>Ccat</i>	
<i>Bzon</i>		1.61	1.27	0.42	1.10 ^a
<i>Cros</i>	1.00		0.92	1.07	0.99 ^a
<i>Ccap</i>	0.18	0.50		0.67	0.45 ^b
<i>Ccat</i>	0.00	0.30	0.23		0.18 ^c
Mean	0.39 ^A	0.80 ^B	0.81 ^B	0.72 ^B	

Notes: For each pairwise combination means are significantly different (generalized linear model [GLM] with Poisson error, $P < 0.05$) between the two species except for the pairs *Bzon/Cros* and *Cros/Ccap* ($P > 0.05$). Means followed by different letters are significantly different (GLM with Poisson error, $P < 0.05$). Species names are abbreviated as in Table 1.

TABLE 3. Response of four species of Tephritidae to fruits previously exposed to egg-laying by females of (a) the same species or (b) other Tephritidae species.

Tested species	Sp. to which fruit was previously exposed	Visiting (%)	Laying (%)
a) Egg-laying by same species			
<i>Ccap</i>	<i>Ccap</i>	55.2	63.9*
<i>Cros</i>	<i>Cros</i>	49.4	29.6*
<i>Ccat</i>	<i>Ccat</i>	54.3	49.2
<i>Bzon</i>	<i>Bzon</i>	47.6	44.8
b) Egg-laying by other species			
<i>Ccap</i>	<i>Cros</i>	48.8	56.5
<i>Cros</i>	<i>Ccap</i>	54.6	38.8
<i>Ccat</i>	<i>Ccap</i>	44.8	56.3
	<i>Cros</i>	48.2	47.1
<i>Bzon</i>	<i>Ccap</i>	31.5**	26.8*
	<i>Cros</i>	44.6	32.9*

Notes: For a given species, percentages followed by one or more asterisks differ significantly from 50% ($n = 30-33$; pairwise t tests: * $P < 0.05$ and ** $P < 0.01$). Species names are abbreviated as in Table 1.

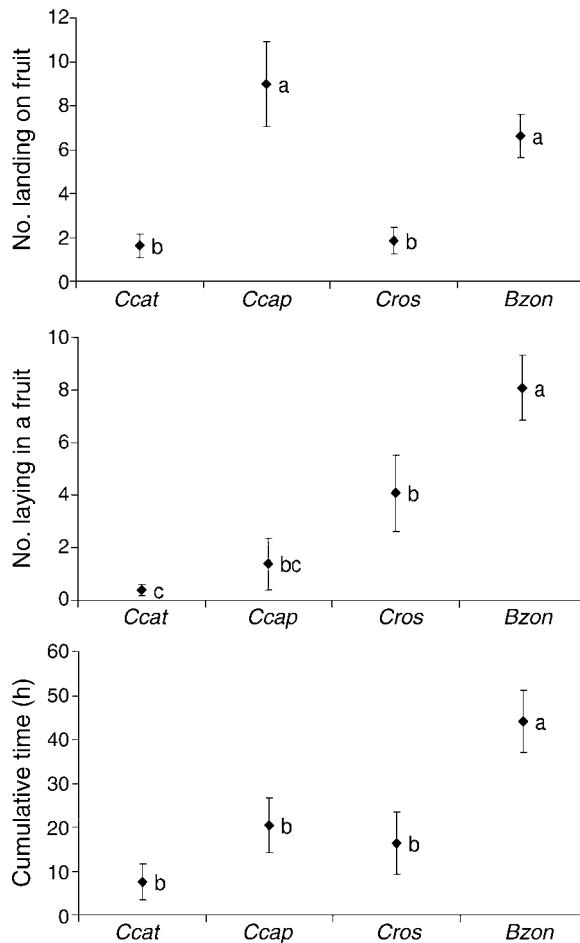


FIG. 3. Comparison of number of landings on fruit, egg-laying on fruit, and cumulative time spent on the fruit per trial by 20 females of each of four species of Tephritidae during a 45-min field cage trial (means \pm SE; $n = 13$ replicates). Different lowercase letters indicate significant differences ($P < 0.05$) using a generalized linear model with Poisson error for landings and layings and ANOVA followed by Tukey's studentized test for cumulative time ($P < 0.05$). Species names are abbreviated as in Table 1.

However the final species frequencies we obtained experimentally do not seem unrealistic: for the pair *B. zonata*–*C. rosa*, the field distribution is roughly symmetric, while experimental ratios lie between 40% and 60%; while for the two pairs involving *C. capitata*, both field and experimental distributions are skewed towards low frequencies of *C. capitata*.

The four species differ in susceptibility to larval competition. Competitive asymmetry is a dominant feature of our data set. As shown in Fig. 1, species can be ordered in a hierarchy whereby competitive asymmetry is always in favor of higher-ranking species. Species have been ordered according to this hierarchy in Fig. 1, *B. zonata* > *C. rosa* > *C. catoirii* > *C. capitata*, so that log-transformed pairwise asymmetries above the diagonal appear positive. The hierarchy is the same for

the different components of performance. Only one species pair for one trait (*C. catoirii*/*C. capitata* for survivorship) was inconsistent, as the log asymmetry was slightly negative in this combination (Fig. 1). Competitive responses differ significantly among the four species and overall follow the hierarchy above, although not all pairs of species are significantly different. On the other hand, competitive effect did not vary significantly among species in our experiments, and species ranks were not the same as for competitive responses, although *B. zonata* always came first.

Krijger et al. (2001) showed that short developmental times are associated with superior competitive ability among *Drosophila* species. This trait might confer to *B. zonata* its superior competitive response, as it has a shorter larval development time (mean \pm SE: 10.7 ± 1.2 d in the controls) compared to all *Ceratit*s spp. (12.3 ± 1.0 d, 13 ± 0.1 d, and 11.2 ± 0.9 d, respectively, for *C. catoirii*, *C. capitata*, and *C. rosa*) and may therefore preempt resources within the fruit. This also suggests that a different hierarchy may arise at other temperatures as species react differently to temperature. For example at 15°C, the larval developmental time of *B. zonata* becomes longer compared to the three *Ceratit*s spp. (Duyck and Quilici 2002, Duyck et al. 2004b).

Aggressive interactions between females at laying sites are highly asymmetrical: of two species, one almost always displaces the other much more than the reverse. As for larval competition, there is a hierarchical arrangement of pairwise interactions between adult females: *B. zonata* > *C. rosa* > *C. capitata* > *C. catoirii* (Fig. 1). A higher-ranking species always displaces a lower-ranking species at higher frequencies than it is displaced. This hierarchy is similar, though not exactly the same, as that observed in larval competition experiments (*C. capitata* and *C. catoirii* have switched positions).

Even with a strict competitive hierarchy for larval competition and adult interference, behavioral strategies could modulate the effects of competition, for example, by allowing weak competitors to lower the probability of being in competition with other species. As suggested by the performance–developmental time relationships discussed above and by the fact that old Tephritid larvae have more severe impacts on young larvae than vice versa (Averill and Prokopy 1987, Dukas et al. 2001), the temporal aspects of resource preemption are important and a species benefits from arriving first at the resource. Two strategies can be envisaged in this context: increased effectiveness in localizing resources or avoidance of previously infested fruits. Our data do not suggest that weak competitors have a better ability to localize the host fruit. On the contrary, in our experimental enclosure (Fig. 3), *Bactrocera zonata*, the best competitor, tended to occupy fruits (and lay on them) for more time than other species. Interestingly, *C. capitata* made more contacts with fruits than other *Ceratit*s species; however it didn't spend more time on it (and didn't lay more often) than *C. rosa*, probably because it was often displaced by *B. zonata*

and *C. rosa* females (Fig. 1). Overall, among the species studied, good competitors (*B. zonata* and *C. rosa*) end up more effective at laying on the resource than poor competitors (*C. capitata* and *C. catoirii*). Our data do not suggest either that poor competitors could limit the adverse effects of competition by avoiding fruits previously infested by other species. None of the species seems to be influenced by the presence of puncture holes on the fruit. However, two of them (*C. capitata* and *C. rosa*) seem to leave detectable chemical signals that influence the laying behavior of conspecifics. These two species display a high frequency of the “dragging ovipositor” behavior, classically associated with host-marking tephritids (Prokopy et al. 1978). Inhibition of oviposition by previous exposure of fruits to conspecifics, here observed in *C. rosa*, has been shown in several tephritids (Prokopy et al. 1978, Diaz-Fleischer and Aluja 2003, Nufio and Papaj 2004) and proved to be caused by host-marking pheromones (Roitberg and Prokopy 1987, Nufio and Papaj 2001). Surprisingly, *C. capitata* seems slightly attracted rather than inhibited by exposed fruits in our study. However, this species is known to show context-dependent attraction or avoidance behavior (Papaj et al. 1992, Prokopy and Roitberg 2001). Although we have no direct evidence that HMPs are involved in the attraction (*C. capitata*) or avoidance (*C. rosa*) of exposed fruits, HMPs are likely candidates. On the other hand, neither *B. zonata* nor *C. catoirii* seem to discriminate fruits previously exposed to conspecifics. The low frequency of “ovipositor-dragging” behavior has already been observed in other species of the subfamily *Dacini* that do not produce HMPs and interpreted as a remnant of ancestral marking behavior (Prokopy and Koyama 1982, Fitt 1984). Interestingly, *B. zonata* detects and avoids signals left by *C. capitata* and *C. rosa*, while the response of *Ceratitis* species to each other’s signals is nonsignificant. Again, this behavior is expected, if anything, to increase the resistance of *B. zonata* to competition exerted by other species rather than the reverse. We acknowledge, however, that these experiments conducted in artificial settings may not necessarily represent field conditions.

Each newly arrived species successfully invaded La Réunion in the presence of the previously established native or exotic species (Orion and Moutia 1960, Etienne 1972, White et al. 2000). This can be summarized as follows: $B. zonata > C. rosa > C. capitata > C. catoirii$ where the “more than” sign denotes the ability of a species to establish new populations, grow in numbers, and spread in territories occupied by another species. A previous review on invasions by fruit flies (Duyck et al. 2004a) has already shown that such links tend to be directional, not reciprocal, within this family, suggesting some deterministic mechanisms behind invasion sequences. In La Réunion, these ranks also reflect the current relative abundance of the species on several important host fruits in the lowlands where they coexist, *B. zonata* being generally dominant while *C. catoirii* has become

very rare (Duyck et al. 2004a). We should mention, however, that *C. rosa* is currently the only species with important populations in the highlands.

The results of our competition experiments together support the view that the ability to withstand interspecific competition exerted by resident species has been a major limiting factor for invasions in the Tephritid system studied here. Indeed, invasive species tend to have higher ranks than previously established species in the hierarchy for one or both forms of competition (scramble and interference). *Bactrocera zonata*, the most recently established species, appears dominant in most of the forms of competition studied. Its large body size may be an advantage in exploitative as well as in interference competition. At the other end, the endemic species, *C. catoirii*, also has a large size but gains no advantages from it, either in exploitative or interference competition. Although it can exert strong competitive effects on other species at the larval stage, it does not resist well against allospecific competitors. This might doom this species to extinction in the presence of invasive tephritids, as suggested by its currently extreme rarity in the island of La Réunion and its reported extinction in the nearby island of Mauritius (White et al. 2000). Based on this study, a future invasive polyphagous Tephritidae in La Réunion should have a better performance in larval competition and/or a more efficient, aggressive behavior than the four resident species. Both traits could be enhanced by a larger body size and a shorter larval developmental period, which can be obtained via a higher investment per offspring (larger egg size).

Other studies have already shown that invasive species can have superior competitive ability than native species (Juliano 1998, Byers 2000, Vila and Weiner 2004). Our study confirms and extends these results, showing that these mechanisms are repeatable and consistent in a group of phylogenetically and ecologically close species in the same habitat. As reported in experimental (Case et al. 1994, Holway 1999) and theoretical (Amarasekare 2002) works, our study suggests an important role of interference in the invasion success. Recently, Yasuda et al. (2004) demonstrated that intraguild predation, an extreme form of interference, contributes to the invasion success of ladybirds. Our study also suggests that interference and scramble competition abilities are not necessarily in trade-off, as illustrated by invasive ants (Holway 1999).

Finally, one important limitation of competition experiments is to ignore niche differentiation between species. In essence, we have established a clear competitive hierarchy in guava at 25°C, which would logically allow the prediction of sequential invasion and exclusion in a homogeneous landscape containing only this niche. The natural environment in La Réunion (or in any invaded country) is certainly not like this, and patterns of niche differentiation among species must be studied to get a full view of possible events in terms of invasions and coexistence or exclusion of species. For example, the large

populations of *C. rosa* found in the highlands of La Réunion, where no other species are found, are suggestive of a climate-dependent change in competitive hierarchy. Host fruit, although less well known, might have similar effects. Generalization to other conditions will be needed in future studies. To a certain extent it is even surprising that competitive abilities in an environment only chosen to be nutrient-rich (guava) and thermally optimal (25°C) for all species adequately predict the invasion sequence. Why couldn't a species directly invade the environment where it can be dominant, irrespective of its competitive ability in optimal conditions? We suggest that in the case of Tephritid flies in La Réunion, and possibly many other invasion cases, propagule pressure is concentrated into a particular habitat. In La Réunion this habitat consists of anthropized, cultivated lowlands (a rich and warm niche relatively similar to our experimental conditions). This habitat may act as a filter niche, in which any candidate invader must be able to establish a viable population (and therefore to resist competition by residents) before spreading to other habitats. Further studies are needed to test this hypothesis.

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APPENDIX

A figure showing the distributions of final density ratios when two species were present in a fruit (*Ecological Archives* E087-104-A1).

Ecological Archives E087-104-A1

Pierre-François Duyck, Patrice David, Guillemette Junod, Caroline Brunel, Raphaël Dupont, and Serge Quilici. 2006. Importance of competition mechanisms in successive invasions by polyphagous tephritids in La Réunion. *Ecology* 87:1770–1780.

Appendix A. A figure showing the distributions of final density ratios when two species were present in a fruit.

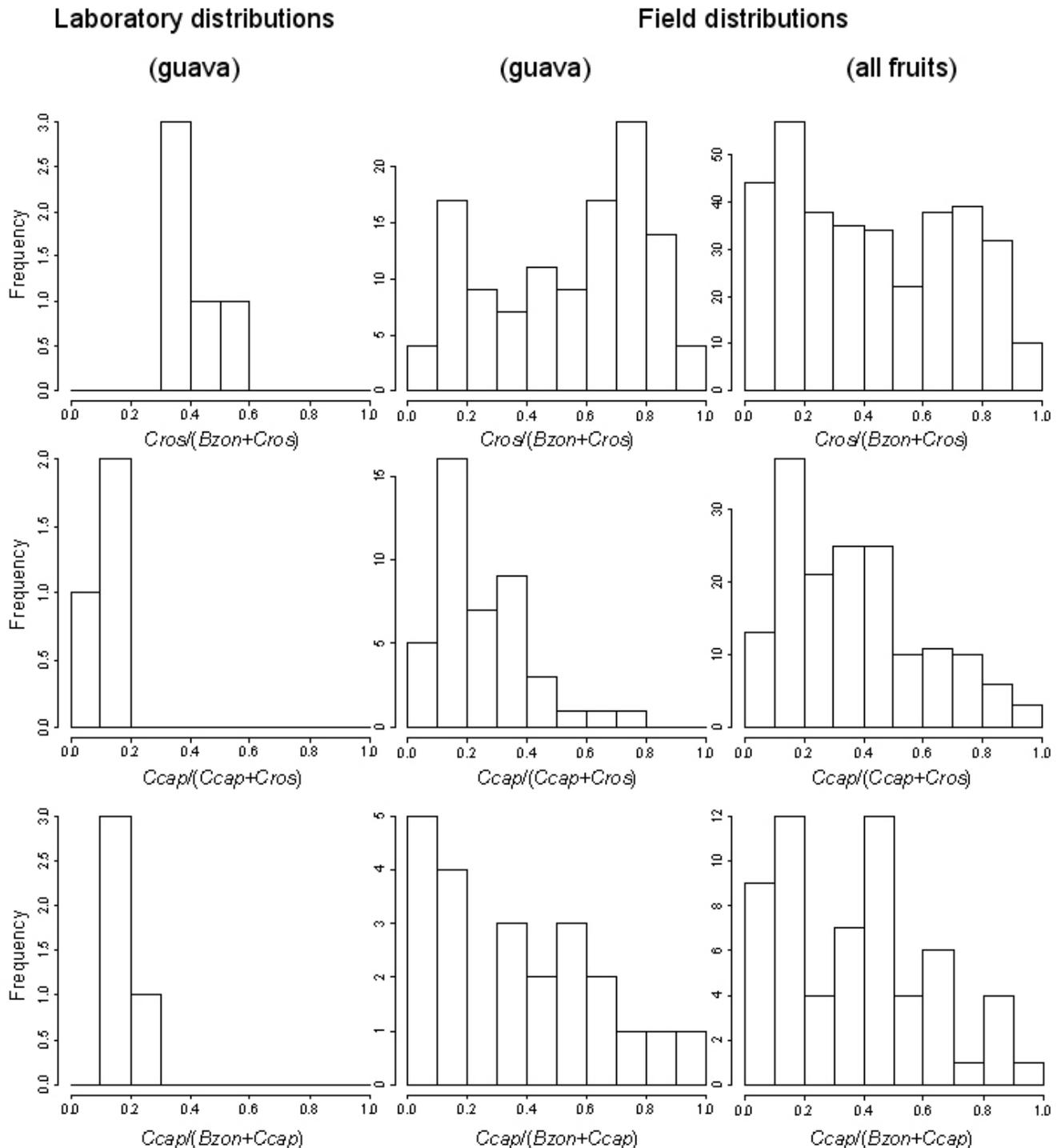


FIG. A1. Distributions of final density ratios per fruit (i.e., based on the number of emerged adults per gram fruit for each species) when two species were present in a fruit for the laboratory experiments and for fruits collected in the field. No data are presented for *Ceratitis catoirii* as this species was very rare in our samples. Species names are abbreviated as in Table 1.