Can host-range allow niche differentiation of invasive polyphagous fruit flies (Diptera: Tephritidae) in La Réunion?

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Abstract. 1. Biological invasions bring together formerly isolated insect taxa and allow the study of ecological interactions between species with no coevolutionary history. Among polyphagous insects, such species may competitively exclude each other unless some form of niche partitioning allows them to coexist.

2. In the present study, we investigate whether the ability to exploit different fruits can increase the likelihood of coexistence of four species of polyphagous Tephritidae, one endemic and three successive invaders, in the island of La Réunion. In the laboratory, we studied the performances of all four species on the four most abundant fruit resources in the island, as well as the relative abundances of fly species on these four fruit species in the field. We observe no indication of niche partitioning for any of the four abundant fruits.

3. Analyses of an extensive field data series suggest that: (i) the four fly species largely overlap in fruit exploitation, once climatic effects are accounted for; (ii) however, one species (*Ceratitis capitata*) can exploit rare fruit species that are not exploited by others present in the same climatic niche; and (iii) the endemic species *C. catoirii*, now nearly extinct in La Réunion, has no private niche with respect to either climatic range or fruit use.

4. On the whole, with the possible exception of *C. capitata*, the results point to a limited role of fruit diversity in encouraging coexistence among polyphagous tephritids recently brought into contact by accidental introductions.

Key words. Biological invasions, coexistence, fruits, host-plant, niche partitioning, Tephritidae.

Introduction

Differences in host range are often invoked to explain the coexistence of related species of phytophagous insects in the same habitat (DeBach, 1966; Rathcke, 1976; Denno *et al.*, 1995; Price, 1997). Fruit flies (Diptera: Tephritidae) are able to attack a wide range of hosts including numerous commercial fruits (White & Elson-Harris, 1992). Among the species infesting

fruits, some are specific to one host such as the olive fruit fly [*Bactrocera oleae* (Gmelin)] or the cherry fruit fly [*Rhagoletis cerasi* (L.)], while others are generalists which can develop in many host families (White & Elson-Harris, 1992). This polyphagy can be extremely large: for example, Liquido *et al.* (1991) reported 353 hosts belonging to 67 families for the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann). Although differences in fundamental niches among species are often obvious in the case of specialists, they are not so in the case of extreme polyphagy, and the coexistence of several such species therefore deserves scrutiny. Many pairs of polyphagous species have proven able to coexist in the field, many of which have been recently

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brought into contact through unintentional introductions (White & Elson-Harris, 1992; Reitz & Trumble, 2002; Duyck *et al.*, 2004a). In a general review of 120 studies of species interactions during invasions, Bruno *et al.* (2005) have concluded that, although inter-specific competition is frequent in this context, it does not often result in competitive exclusion of resident species, thus confirming the conclusions of an earlier review by Simberloff (1981) [but see possible cases of local competitive exclusions of *Aphitis* spp. on citrus in California and braconids on fruit flies in Hawaii (DeBach, 1966, 1974)]. This suggests that even two species with no coevolutionary history may often be different enough in their ecological requirements to coexist in the invaded area (Bruno *et al.*, 2005). For example, different species can be competitively dominant on different hosts although they all can exploit the same array of host plants. Our goal here is to evaluate the possibility that such differences in host use could promote coexistence within a set of polyphagous fruit fly species brought into contact by recent invasions in the tropical island of La Réunion (Indian Ocean). To this end, we combine laboratory experiments (concentrating on the four most abundant fruits exploited by tephritids in La Réunion) and the analysis of field distributions.

Invasions of polyphagous Tephritidae have occurred in areas where, most of the time, other species (being indigenous or previous invaders) were already present (Duyck *et al.*, 2004a). In such cases, modifications of the host range of certain species are sometimes observed, depending on their relative preference for one host or another. A well-documented case is the reduction in the host range of *C. capitata* in Hawaii: this species has been displaced from most cultivated hosts of the lowlands after the invasion of *Bactrocera dorsalis* (Hendel) (Reitz & Trumble, 2002). However, this competition is host dependent as *C. capitata* persists in lowlands on coffee, a host plant to which it is better adapted (Vargas *et al.*, 1995). It is assumed that such a niche restriction results from inter-specific competition leaving the resident species only on particular refuge hosts (Reitz & Trumble, 2002).

Intra-specific competition commonly occurs in tephritids (Fletcher, 1987). Numerous cases of species displacements attest for the occurrence of inter-specific competition, particularly after invasions (Duyck *et al.*, 2004a). Usually, complete exclusion did not occur after tephritid invasions but competitive displacements and niche shifts linked to climate and/or host plants were observed (Duyck *et al.*, 2004a). The main resource for which competition can plausibly occur among species of tephritid flies is the host fruit (Prokopy & Roitberg, 1984). Competition between larvae results in smaller flies, longer development times and increased mortality (Keiser *et al.*, 1974; Duyck *et al.*, 2006a).

On La Réunion (a volcanic tropical island of the Indian Ocean), four species of polyphagous Tephritidae are currently found. The Mascarene fruit fly *C. catoirii* Guérin-Méneville is endemic to Mauritius and La Réunion islands (Orian & Moutia, 1960; Etienne, 1972; White *et al.*, 2000). It used to be abundant in cultivated habitats in La Réunion before the arrival of the other species and was described on at least 16 host plants in Mauritius (Orian & Moutia, 1960). The Mediterranean fruit fly *C. capitata* was introduced in 1939 and became widespread in La Réunion (White *et al.*, 2000). The Natal fruit fly *C. rosa* Karsch was first detected in 1955 (Orian & Moutia, 1960; Etienne, 1972). In La Réunion, a few individuals of *B. zonata* (Saunders) were first detected in 1991 but its populations grew massively and spread in 2000 (Quilici *et al.*, 2005). These four species compete for fruit resources at least in a part of their ranges (Duyck *et al.*, 2006a). Among the numerous host plants of these species present in La Réunion, four are of particular importance because of their abundance on the island, namely: guava (*Psidium guajava* L.), mango (*Mangifera indica* L.), Indian almond (*Terminalia catappa* L.) and strawberry guava (*Psidium cattleianum* Sabine) (Quilici & Jeuffrault, 2001). In La Réunion, guava is found between 0 and 600 m, mostly in Creole gardens. Strawberry guava is a very abundant shrub both in open pastureland and in the understorey of many natural habitats; it is established from 0 to 1200 m, mostly in the most humid areas of the island (south and east). Indian almond trees, mainly present on the coastline, have no economic importance but are considered as a major reservoir for fruit flies. Mango is present from 0 to 400 m, predominantly on the west coast in many Creole gardens and in orchards (Quilici & Jeuffrault, 2001).

Abiotic factors such as temperature and rainfall have been demonstrated to promote the regional coexistence between some, but not all, pairs of species: *C. rosa* can live in wetter and colder climates than any of the other three species, while *B. zonata* is dominant in dry and/or warm lowlands (Duyck *et al.*, 2006b). On the other hand, Duyck *et al.* (2006b) suggested that the regional persistence of *C. capitata* and *C. catoirii* was not guaranteed by climatic niche partitioning, in the face of competition with *B. zonata* and *C. rosa*. In the present study, we focus on the possible role of differences in another component of the ecological niche, host range, in favouring coexistence among the four polyphagous tephritid species present in La Réunion. The nature of the host fruit can affect fruit fly development by direct effects on pre-imaginal survival, pre-imaginal development duration and pupal weight (Fitt, 1986) but also indirect effects on fecundity via pupal weight (Krainacker *et al.*, 1987, 1989).

We first studied the influence of the four main host-fruit species mentioned above on survival, developmental duration and pupal weight of the four tephritid species to address different questions: (i) does fruit species influence the development of the four tephritid species? (ii) If so, do the different species of flies have different optimal fruits? (iii) Are the four tephritid species ordered differently, in terms of life-history performance, depending on host fruit? We then analysed an extensive dataset on field-caught samples of many different infested fruits, including the four fruit species used in the experimental study. We first asked whether the actual patterns of infestation on these four host species were consistent with laboratory results; then, generalizing to all host species sampled, tried to evaluate the prospects of fruit fly coexistence based on overall host-range differences. Note that we do not assume that the four species are currently in a stable state of coexistence; the future will tell whether some of them eventually go extinct (a very probable outcome for *C. catoirii*, see discussion). We rather examine whether fruit type could provide an axis for niche differentiation.

Methods

Insects for laboratory experiments

Experiments were conducted with laboratory cultures initiated with 50–100 individuals for *C. catoirii* and 500–1000 individuals for *C. capitata*, *C. rosa* and *B. zonata* and maintained later at several thousand per generation for 32, 5, 53, and 8 generations, respectively. Techniques for maintenance of these laboratory cultures were described in previous studies (Duyck & Quilici, 2002; Duyck *et al.*, 2004b). Rearing conditions were 25 °C (±1 °C), 80% RH ($\pm10\%$), LD 12:12 h for all laboratory experiments. In a first experiment, we established the relationship between pupal weight and fecundity. Then, we determined the effect of host fruit on survival and pupal weight which allowed us to estimate the net reproductive rate.

Relationship between pupal weight and fecundity

In order to obtain a high variability in pupal weight, fruits of guava, mango, and strawberry guava were infested with different densities (1, 2 or 4 larvae g^{-1}) of young larvae. Pupae were collected daily and individually weighed, grouped in classes of 1 mg and placed in a box containing a moist piece of sponge until emergence.

Estimations of fecundity were performed at the peak of fecundity (20 days post-emergence for the three *Ceratitis* spp. and 40 days post-emergence for *B. zonata* (Duyck *et al.*, 2007), by placing groups of five fertilized females of the same class of pupal weight in cages and letting them lay eggs. Flies had free access to a diet of sugar and enzymatic yeast hydrolysate (ICN Biomedical, Aurora, CO, U.S.A) and a wet sponge placed in a container as a water source. An orange table-tennis ball, cut in half, and pierced with 24 evenly spaced holes (418 ± 90 µm diameter), covering a piece of mango fruit (*Mangifera indica* L.) and inserted in a plastic base of suitable diameter was used as an egg-laying device. Eggs were counted daily during six successive days. Six days do not correspond to the life time fecundity but allow the estimation of daily fecundity at the peak of the fecundity curve. Six replicates were carried out for each species and pupal class.

Larval development in the four host fruits

The development of each of the four tephritid species was studied on the four following hosts: guava, mango, Indian almond and strawberry guava (see introduction for scientific names). For each replicate, fruits (total weight of 100 g which correspond to a small fruit or a piece of mango fruit, to one or several guava fruits or to several fruits in the case of strawberry guava or Indian almond) were washed and nicked randomly at the surface to allow the introduction of newly hatched larvae (<3 h old) into the pulp. Fruits were carefully infested using a fine brush under a binocular microscope with 100 newly hatched larvae of one species (eggs were randomly collected in our laboratory routine rearing cages containing a few thousand females).

Such a level of infestation can be found in the field (Duyck *et al.*, 2006a) and has already been used in several studies on tephritid larval development (Fitt, 1986; Krainacker *et al.*, 1987). Infested fruits were placed in a plastic container, the bottom of which was covered with a layer of sand to allow pupation of mature larvae. Presence of larvae appeared to be the main cause of the quick fruit decay. Sand was sifted daily in order to collect pupae. Development time, survival and pupal weight were measured. Four replicates were carried out for each combination of host fruit species and tephritid species (64 different data units).

Net reproductive rate

Net reproductive rate (R_0), i.e the expected number of offspring per female lifetime, was estimated in order to integrate larval survival and pupal weight in a single parameter, so as to facilitate comparisons between fruit types and tephritid species. R_0 is the product of survival from egg to adult (*S*) and expected number of offspring produced during adulthood ($R'_0 = R'_0 = \sum_{y=0}^{\infty} l'_y m_y$, where l'_y is the probability for a newly emerged female to survive at least *y* days, and m_y is the fecundity *y* days after emergence). In the scope of the present work, we could estimate *S* directly from the data, but we were not able to conduct a complete demographic study to get a direct estimate of R'_0, which would have been very long, given the number of treatments (fruit species, tephritid species). We therefore used an indirect estimation of fecundity based on a 6-day period around the fecundity peak of each tephritid species. We fit linear or exponential regressions to predict peak fecundity as a function of pupal weight [$m_x = f(w)$]. These regressions are given in the legend of Fig. 1. We assumed that a change in peak fecundity m_x would produce a proportional change in R'_0, and used the mean pupal weight (w_m) and R'_0 values (R'_{0m}) from our previous demographic study (Duyck *et al.*, 2007) to obtain the calibration factor [$R'_{0m}/f(wm)$] allowing us to convert predicted peak fecundities into predicted R'_0. The latter were then multiplied by *S* to get R_0 estimates for each species and treatment. In the previous study Duyck *et al.* (2007) obtained complete life-time fecundity and calculated demographic parameters: R'_{0m} and mean pupal weight (w_m) for *C. catoirii*, *C. capitata*, *C. rosa* and *B. zonata* were 18.2 (eggs/female), 112 (10^{-4} g); 130.6, 94; 128.4, 107 and 66.3, 118, respectively.

Field data

Field campaigns were regularly conducted by the CIRAD to detect infested sites between 1994 and 2005. The whole island was prospected all year round looking for orchards, gardens, or secondary habitats where host species were potentially infested. Fruits were both collected on trees and on the soil, when recently fallen. Samples of infested fruits (identified by the puncture holes made by laying insects) were collected and placed onto a grid in a closed container layered with sand or sawdust. We waited for emergence of adults from pupae fallen into the sand or sawdust, and counted the adults of the different species.
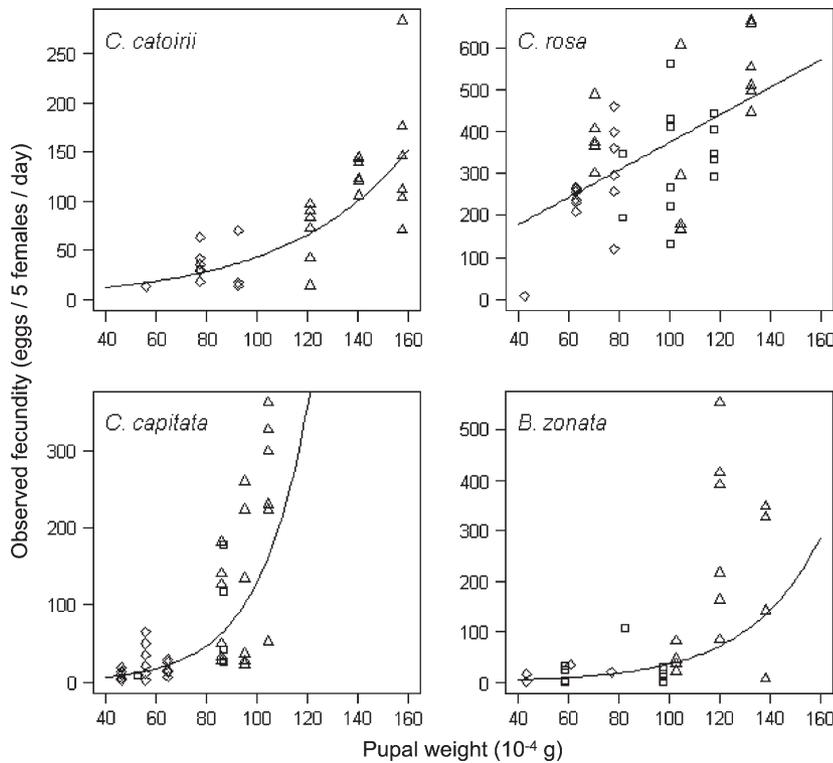
Fig. 1. Relationship between fecundity and pupal weight for four species of Tephritidae. Diamonds, squares and triangles represent samples reared from strawberry guava, guava, and mango, respectively. *Ceratitis catoirii*: $m_x = 5.23e^{0.02}w, R^2 = 0.61, P < 0.001$; *C. capitata*: $m_x = 0.82e^{0.05}w, R^2 = 0.58, P < 0.001$; *C. rosa*: $m_x = 3.27w + 47.29, R^2 = 0.31, P < 0.001$; *Bactrocera zonata*: $m_x = 1.10e^{0.04}w, R^2 = 0.29, P < 0.01$, where m_x and w correspond to peak fecundity and pupal weight respectively.

The results were expressed in relative abundance as we could not evaluate the proportion of infested fruits in the field. The entire dataset comprises 109 775 flies obtained from 866 fruit samples (108, 790 flies from 674 samples when samples < 10 flies are removed from the dataset). We created an index of resource availability (from 1 to 10) representing for each fruit species, the abundance of resource available for Tephritidae at the scale of the island. While this is only an estimate, it is necessary to compare the importance of resources. Although absolute abundance data are not available for most plants, this index is based on our field experience and ecological knowledge of the island and is expected to represent well the main contrasts in abundance among different host species.

Statistical analyses

For pupal weight, development duration, survival and net reproductive rate, statistical analyses evaluated the effect of two factors: tephritid species (T) and fruit species (F), plus their interaction (I). Data on pupal weight, development duration and net reproductive rate were analysed using analysis of variance (ANOVA) while survival data were analysed using a logistic binomial model (analyses of deviance with binomial error). For the latter, overdispersion was accounted for using F-tests instead of χ^2 to evaluate the significance of changes in deviance (Crawley, 1993). For all the above analyses, we worked on means of replicates (a replicate being a group of 100 larvae reared together on 100 g fruit) rather than on individual measures in order to avoid pseudoreplication.

Field data were analysed in two ways: firstly by a generalised linear model (GLM) and secondly by a multivariate analysis. For the generalised linear model, larval relative abundances were separated into two periods (1994–2000 and 2001–2005) and analysed separately, because *B. zonata* is present only in the second period. Species proportions first depend on climatic factors. We used a Poisson log-linear model of temperature and rainfall effects already published (Duyck *et al.*, 2006b) to which we added the factor *fruit species*. In such models, the factors *sample* and *tephritid species* are first fitted, allowing us to fix the totals per sample and per species [see Manly (1985), Crawley (1993) pp. 297–299]. The change in relative proportions of tephritid species as a result of each effect is modelled as an interaction term between this effect and the *tephritid species* factor. The significance of each term is computed using model simplification and F-tests (see above).

For the multivariate analysis, we used the canonical correspondence analysis (CCA) with three factors: temperature, rainfall, and fruit species. This method was introduced by ter Braak (1986). It has been developed to study the relationship between species composition and environment within sites. Here the basic sampling unit is a fruit sample separated in space or time from other samples. CCA is an extension of correspondence analysis (CA) in which samples are given linear weights so as to maximise the variance among species. CCA looks for coefficients of environmental variables to obtain a site score that maximises the variance of the average positions of species. We completed this analysis by a partial CCA (ter Braak, 1988) in order to eliminate the effects of temperature and rainfall. All computations and graphical displays were carried out using *R*,

with routines available in the vegan package and the ade4 package (Chessel *et al.*, 2004).

Results

Relationship between pupal weight and fecundity

Estimations of fecundity from pupal weight have been obtained from fruits of guava, mango, and strawberry guava. For each tephritid species, the effect of *fruit species* and the interaction between *fruit species* and *pupal weight* were not significant ($P > 0.05$). However, for each tephritid species, a significantly positive relationship was observed between pupal weight and fecundity (Fig. 1). For each species, the best type of relationship (linear or exponential) was determined using the highest correlation coefficient (R^2). The best relationship was exponential for *C. catoirii*, *C. capitata* and *B. zonata* and linear for *C. rosa* (regressions: $P < 0.01$ for *B. zonata* and $P < 0.001$ for the other species).

Larval development in the four host fruits

Figure 2 shows the developmental parameters of the different tephritid species in the four host fruits. Pupal weight differs markedly among tephritids and fruit species [ANOVA, tephritid species (T): $F_{3,48} = 56.0$, $P < 0.0001$, fruit species (F): $F_{3,48} = 218.9$, $P < 0.0001$, interaction (I): $F_{9,48} = 3.5$, $P < 0.002$]. *Ceratitis catoirii* had the highest pupal weight, and *C. capitata* had the lowest, in all four fruit species. The biggest pupae were obtained in mango for all four species.

Larval survival was different among tephritids and fruit species (GLM with binomial error, T: $F_{3,57} = 6.6$, $P < 0.001$, F: $F_{3,57} = 16.1$, $P < 0.0001$, I: $F_{9,48} = 4.2$, $P < 0.001$). *Bactrocera zonata* had the highest survival in all four host fruits except in guava where *C. rosa* survived better. The survival in strawberry guava was on average lower than in other fruits, especially for *C. catoirii*.

Larval duration was also different among the tephritid species and fruit species (ANOVA, T: $F_{3,48} = 29.7$, $P < 0.0001$, F: $F_{3,48} = 116.3$, $P < 0.0001$, I: $F_{9,48} = 4.3$, $P < 0.001$). *Bactrocera zonata* had the shorter larval duration in all four host fruits. *Ceratitis catoirii* had the longest larval duration except in mango where *C. rosa* had the slowest development. The larval duration in strawberry guava was longer than in any other fruit for the four tephritid species.

The net reproductive rate (R_0) differs markedly among tephritid and fruit species (ANOVA: T: $F_{3,48} = 97.3$, $P < 0.0001$, F: $F_{3,48} = 46.8$, $P < 0.0001$, I: $F_{9,48} = 9.1$, $P < 0.0001$) (Fig. 3). For the four tephritid species, the highest R_0 was obtained on mango while the lowest was on strawberry guava. *Ceratitis rosa* retains a high relative R_0 on guava and Indian almond compared with the other tephritid species.

For guava, Indian almond and strawberry guava, significant linear relationships were observed between larval durations and pupal weights (Fig. 4). For these three hosts, pupal weight decreased with larval duration. However, such a relationship was not observed in mango.
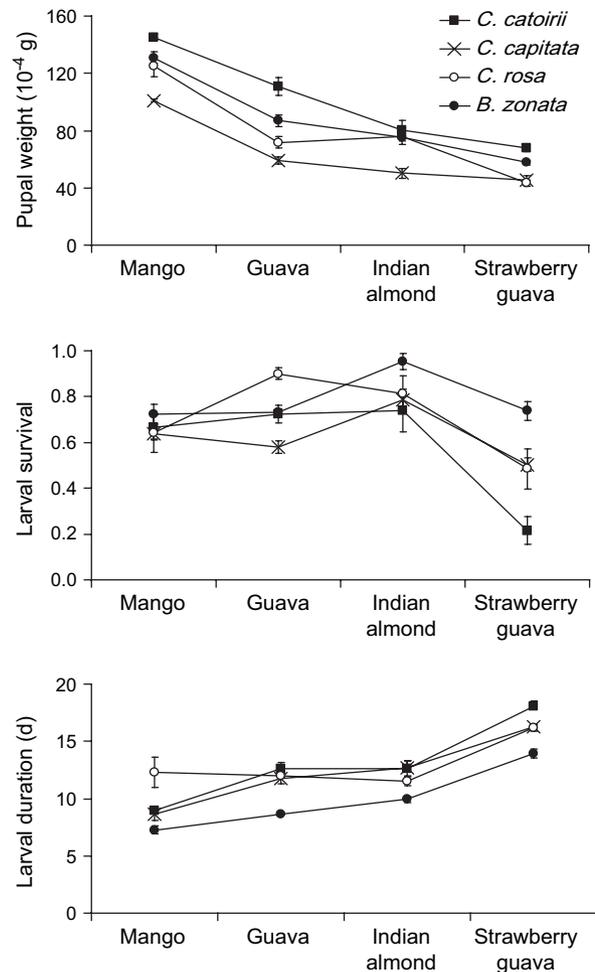
Fig. 2. Pupal weight, survival to pupation and larval duration (mean ± SE) for four tephritid species reared on four different host fruits. For the three parameters, the factors *fruit*, *tephritid species* and their interaction were significant (ANOVAs for pupal weight and larval duration, GLM with binomial error for larval survival).

Field data

All the interactions between tephritid species and rainfall, temperature and fruit species have a significant effect (GLM with Poisson error, all $P < 0.001$, Appendix 1) on larval relative abundance for both periods (before and after 2000). *Ceratitis catoirii* was always very rare in all combinations of fruit, temperature, and rainfall. Figure 5 shows the fitted relative abundances of tephritid species in the four major fruits and in all other fruit species (41 species, see list in Table 1) pooled together. This is given for two combinations of temperature and rainfall, one representative of the warm, dry lowlands in the West of the island (the preferred habitat of *C. capitata*) and one representative of more humid and colder conditions, found in either the east coast and/or in the highlands throughout the island (>300–400 m), which constitute the preferred habitat of *C. rosa*. Before 2000 (when *B. zonata* had not yet invaded the island), all fruits were infested principally by *C. capitata* and
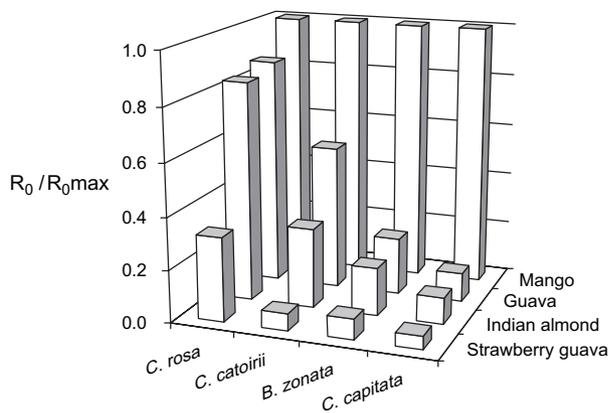
Fig. 3. Influence of larval host fruit on the net fecundity (R_0) relative to the maximum net fecundity of four tephritid species. The maximum was always obtained on mango (R_0 = 108.5 eggs per female for *Ceratitis rosa*, 37.0 for *C catoirii*, 79.8 for *Bactrocera zonata* and 123.7 for *C. capitata*); in order to make the graphics more readable, we represented all R_0 values in relative units, dividing by the R_0 obtained on mango for the same fly species. The factors fruit, species and the interaction were significant (ANOVA on log transformed data).

C. rosa with different proportions depending on the climate and fruit considered (Fig. 5). In dry and hot areas, *C. rosa* was numerically dominant on mango, while the other two *Ceratitis* species were roughly equally abundant in guava and Indian almond. In the same climatic conditions after 2000, *B. zonata* was dominant, and *C. capitata* became relatively rare, in all these fruits. However, *C. capitata* was still dominant on the other fruits, such as *Minusops elengi*, *Murraya paniculata* and *Pithecelobium dulce*. In colder and more humid areas, *C. rosa* was largely dominant in all fruits both before and after 2000.

In total, 45 different host fruits of the four tephritid species of La Réunion have been collected (Table 1). The number of hosts (from which at least 10 flies have emerged) of *C. catoirii*, *C. capitata*, *C. rosa* and *B. zonata* was 3, 30, 33 and 9 respectively. The number of specific hosts (i.e. hosts on which only one Tephritidae species among the four studied has been found) was respectively 0, 11, 12 and 1 for *C. catoirii*, *C. capitata*, *C. rosa* and *B. zonata*. While *B. zonata* has been found (up to now) on a relatively limited host range, its hosts present a high level of resource availability.

CCA with both climatic and fruit factors showed that rainfall and temperature had opposite influences on relative abundance of tephritid species (Fig. 6a, proportion of variance of axis 1: 0.59, axis 2: 0.39, axis 3: 0.02). In the same analysis many fruit species were placed along this climate axis, indicating that, as one could expect, many fruit species distributions are correlated with climatic conditions. On the partial CCA (after elimination of the effect of temperature and rainfall), most of the fruits were placed in the centre of the graph (Fig. 6b,c, proportion of variance of axis 1: 0.71, axis 2: 0.27, axis 3: 0.02), indicating that these fruits are not more correlated with any of the tephritid species than expected, based on the effect of climate. *Ceratitis catoirii* was present only in a few fruit samples (Fig. 6c). *Ceratitis capitata* and *C. rosa* shared many fruit species and sites but the

centroids of species distributions were separated (Fig. 6b,c). The presence of *C. capitata* was associated with Spanish cherry while the presence of *C. rosa* was associated with guava and pineapple guava. *Bactrocera zonata* was found in fewer fruit samples than *C. capitata* and *C. rosa* and was associated with Indian almond. Note, however, that all these associations are relatively weak and unspecific (given the large dispersion of each species and overlap among species ellipses in the first factorial plane).

Discussion

Host plants have a marked influence on fruit fly development, through effects on development duration, larval survival, and pupal weight. As a consequence, the net reproductive rate R_0 is largely dependent on the host fruit. This has already been shown in laboratory studies for *C. capitata* (Krainacker *et al.*, 1987) and other Tephritidae such as *B. dorsalis* and *Rhagoletis pomonella* (Walsh) (Averill & Prokopy, 1987; Krainacker *et al.*, 1989). In the *C. capitata* study (Krainacker *et al.*, 1987), mango was classified as one of the best out of 30 host species studied, in agreement with our results. We observed strong negative linear relationships between pupal weight and larval duration for the four studied Tephritidae in guava, Indian almond, and strawberry guava. As the quantity of food available for larvae was probably limiting (but in accordance with quantities observed in field studies; Duyck *et al.*, 2006a) this pattern might be explained by competitive pre-emption of resources, i.e. the first larvae to develop benefit from more resource than later ones (Blanckenhorn, 1999; Krijger *et al.*, 2001). Moreover, the first larvae to develop could damage the fruit and have an indirect effect on other larvae through excretion of metabolic wastes (Fitt, 1989). The observed relationship can also be explained by the heterogeneity in nutritive value within the same fruit; indeed tephritid larvae are able to detect and consume preferentially the most nutritive part of a fruit (Zucoloto, 1991). This relationship was not observed on mango, where the last larvae to pupate show no reduction in pupal weight compared with preceding larvae. Resources were apparently still available after the development of all the larvae, indicating a relatively high nutritive value of mango for fruit fly larvae. Chemical analyses reveal that mango contains a very high proportion of sugar (14%) compared with guava (5%) and strawberry guava (5%) (Favier *et al.*, 1993; Normand, 1994).

Overall, our study did not reveal any significant degree of differential specialization of the fly species to the four host fruit studied in the laboratory. By differential specialization we mean a difference in profitability ratios among species, so that, for example, different fly species would have different optimal hosts. Although the interaction between host plant species and tephritid species was significant for all the studied parameters, all tephritids show qualitatively the same order of fruit profitability, reflecting a gradient of nutritive value of the fruit species. The four fly species show the highest net reproductive rate on mango and the lowest on strawberry guava. For all four species, approximately the same (or slightly higher) R_0 values are obtained in guava as in Indian almond, and these values are intermediate
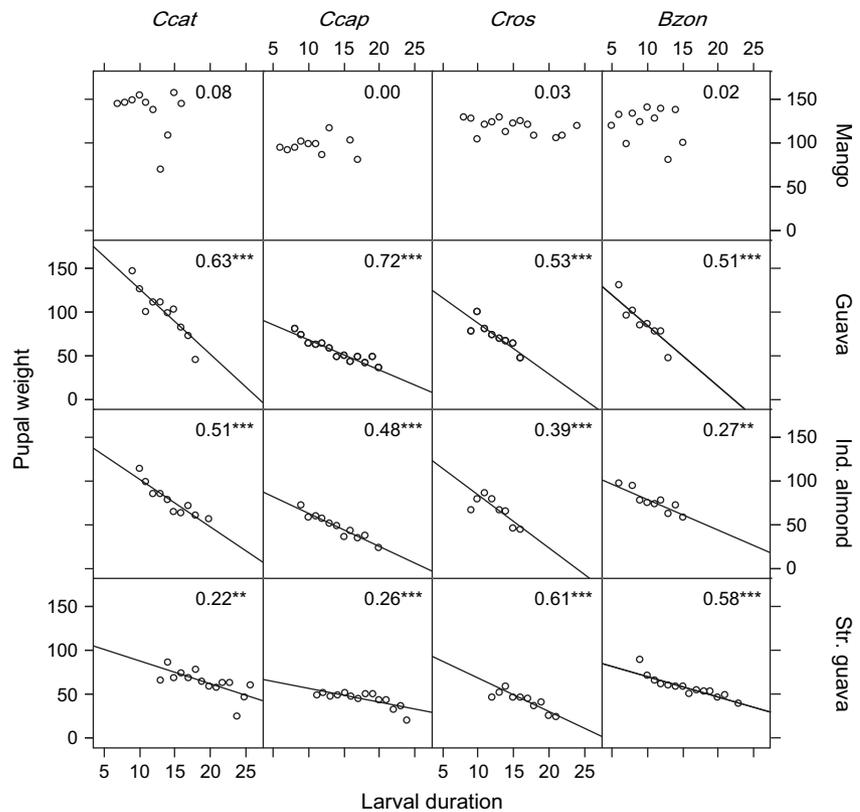
Fig. 4. Relationship between development duration (days) and pupal weight (10^{-4} g) for four tephritid species reared on four different host fruits. Correlation coefficients (R^2) are given on graphs. Means per time interval are represented together with regression lines (**$P < 0.01$ and ***$P < 0.001$). *Ccat, Ceratitis catoirii*; *Ccap, C. capitata*; *Cros, C. rosa*; *Bzon, Bactrocera zonata*.

between those obtained on mango and strawberry guava. However, compared with other tephritid species, *C. rosa* loses less of its net reproductive rate when raised in fruits with relatively low nutritive value (guava, Indian almond, and strawberry guava, see Fig. 3); at the other extreme *C. capitata* is extremely sensitive, as its R_0 on these fruits is reduced 10-fold compared with that on mango. The same tendencies can be seen by examining how host fruit affects fly species ranks for life history traits. On all fruits except mango, *C. rosa* has by far the highest R_0. On mango, *C. capitata* shows a slightly higher R_0 value than *C. rosa*. On the whole, all species have their maximal performance in the same and most nutritive fruit, i.e. mango; however, fly species seem to differ in their ability to tolerate suboptimal or less nutritive fruit: *C. rosa* is relatively tolerant while *C. capitata* is very sensitive.

According to a previous study, some pairs of species can coexist in La Réunion through differences in climatic niches (Duyck *et al.*, 2006b). The coexistence between *B. zonata*/*C. rosa* and between *C. rosa*/*C. capitata* is allowed by a different response to temperature and temperature plus humidity, respectively. However, such differences in response were not sufficient to promote the coexistence of *C. capitata* and *B. zonata*, and the persistence of *C. catoirii* in the presence of any of the other three species. Could host range further divide ecological niches and allow for coexistence of all species? Clearly, the relative abundances of the different tephritid species differ among fruit species (Figs 5 and 6). A part of these differences is confounded with climate as these two variables are not independent (Fig. 6a) but there remains an effect of fruit differences even after remov-

ing the effect of climate (Figs 5 and 6b). However, these species are far from being specialized: they all exploit the most common fruits and their realised niches largely overlap in the partial canonical correspondence analysis.

The four fly species do not show large differences in their exploitation of mango, guava, Indian almond, and strawberry guava in the field, and the differences observed do not correspond to their relative performance in the laboratory. Indeed, in the climatic conditions where all species can be found (24 °C, 750 mm), and before the invasion of *B. zonata*, one would expect, on the basis of laboratory performances, a higher relative abundance of *C. capitata* in mango and of *C. rosa* in guava and Indian almond, while the reverse is found (Fig. 5). Moreover, the invasion of *B. zonata* seems more influenced by climate than by the four dominant host fruits. Indeed this species has become dominant in all these fruits in the lowlands (24 °C, 750 mm) although its relative abundance is still low in the highlands (22 °C, 2000 mm). Neither *C. catoirii*, nor *C. capitata*, seem to be protected from competition by *B. zonata* through differential specialisation on any of these four fruits. Field data may differ from laboratory performances for a number of reasons. Habitat variation in the field is not restricted to host plants, as illustrated by the effect of climate. Moreover field patterns are not necessarily in equilibrium, especially as the invasion of *B. zonata* is recent. For these reasons, we do not expect a strict correspondence between field and laboratory data. However, we did expect field and laboratory data to be consistent in the following sense: if laboratory data suggest that the four studied hosts have similar effects on relative performances of the four fly species, relative
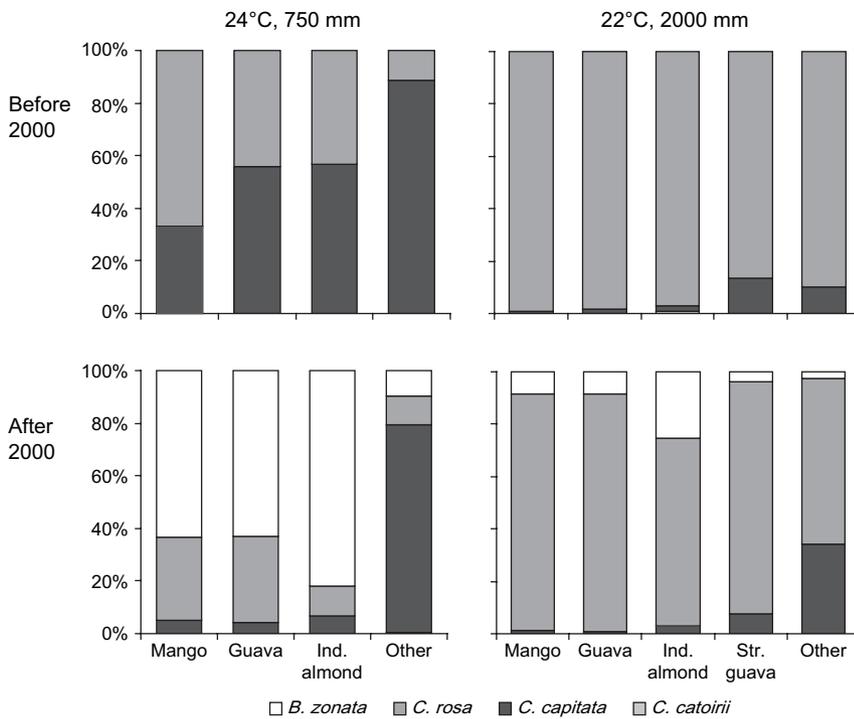
Fig. 5. Relative abundance (fitted from the generalised linear model) of larvae from the field in the four host species studied in the laboratory and in all other fruits collected before and after 2000. The results are presented for two contrasting climates. Strawberry guava is not presented for 24 °C, 750 mm as it is not found under this climate.

abundances in the field should not vary dramatically among these hosts, within given climatic conditions, i.e. none of the four host plants can be a refuge host for any fly species. This is essentially what we found.

However, a niche differentiation based on other fruits than the four dominant species could occur. Indeed, *C. capitata* is proportionally much more abundant, even after the establishment of *B. zonata*, in the *other fruits* category than in mango, guava or Indian almond. It seems that *C. capitata* has a number of specific fruits belonging to different families: Apocynaceae, Flacourtiaceae, Passifloraceae, Polygonaceae, Rutaceae and Solanaceae. It seems hard to find any common characteristic to all these fruits. However, some of them, like *Thevetia peruviana* or *Capsicum* spp. are known to contain toxic compounds and many of them are small in size. In further studies, it would be interesting to test the relative tolerance of the different tephritids to these particular fruits. Note that extrinsic factors (the ability of tephritid species to localize the fruit) could also be a possible cause of dominance of one species (here *C. capitata*) on particular hosts.

A common characteristic of these specific hosts of *C. capitata* is their low abundance on the island, which leads to two possible outcomes. Either these host fruits are sufficient in quantity and continuous availability throughout the year to maintain viable populations of *C. capitata*, or the populations of the latter may carry on decreasing, because of the competition with *B. zonata* which flourishes in other, more abundant fruits in the same climatic niche (Duyck *et al.*, 2006a,b). However, with respect to the latter scenario, it must be mentioned that spatial and temporal aggregation of populations within each species may alleviate the effect of inter-specific competition, and even allow coexistence of different species in the same niche

(Shorrocks *et al.*, 1984). An interesting perspective would therefore be to study the distribution of *C. capitata* and *B. zonata* populations in the field.

Remaining native forest habitats are present in mountain areas and also in the lowlands of the south-eastern (and most humid) part of La Réunion. Regarding climatic conditions, these habitats could be considered suitable respectively for *C. rosa* and *C. catoirii*. However, no fruits from these habitats are currently known to be the host of any of the different tephritid species. *Ceratitis catoirii* does not seem to have any private niche, either in terms of climate (Duyck *et al.*, 2006b) or in terms of host fruits. Although the low number of fruit species where *C. catoirii* was found leaves the impression that its fruit range is restricted, this is mainly a sampling effect owing to a very low overall abundance (see sample sizes in Table 1). A possible drawback of this study is that no fruit from the native forest habitat has been sampled. Such fruit could provide a refuge to the endemic *C. catoirii* if this species has acquired specific adaptations to them during its evolutionary history in La Réunion prior to human establishment. However, native forest habitats are now extremely restricted and *C. catoirii* used to be abundant in cultivated habitats before the establishment of the other species (Orian & Moutia, 1960). This suggests that the persistence of this species is unlikely to rely on native habitats only. We believe that this species is on the way to extinction in La Réunion, as has apparently already occurred in Mauritius (White *et al.*, 2000).

A potential limitation of this study is that all possible dimensions of the niche have not been explored. For example, natural enemies may differ among fruits and tephritids species (Sivinski *et al.*, 2001). Generalist predators such as ants likely have

Table 1. Recorded host plants of four species of Tephritidae in La Réunion from 1991 to 2004 and species relative abundance in samples corresponding to one to nine adults emerged. (+) corresponds to 10 or more emerged flies. Numbers of hosts, specific hosts (= exclusively used by a particular tephritid) and sums of resource availabilities are calculated using only fruit species in which more than 10 individuals have been caught [without (+)]; numbers in brackets take into account all samples [including (+)]. Each sample represents a set of attacked fruit of a given host species collected at a given place and time.

Family		Scientific name	Common name	Resource availability (index from 1 to 10)	Number of samples	Number of flies	Species relative abundance			
							C. catoirii	C. capitata	C. rosa	B. zonata
Anacardiaceae	1	*Mangifera indica*	Mango	8	13	1174		0.06	0.76	0.18
Annonaceae	2	*Annona reticulata* L.	Bullock's heart	4	3	1001		(+)	0.99	0.01
Apocynaceae	3	*Carissa carandas* L.	Mahakaranda	1	2	107		1.00	(+)	
	4	*Carissa macrocarpa* (Ecklon) A. DC.	Natal plum	1	5	464		0.95	0.05	
	5	*Thevetia peruviana* (Persoon) K. Schumann	Yellow oleander	1	1	66		1.00	(+)	
Combretaceae	6	*Terminalia catappa* L.	Indian almond	8	85	177 47	0.01	0.07	0.30	0.62
Ebenaceae	7	*Diospyros kaki* L.f.	Persimmon	1	1	51		1.00	1.00	
Flacourtiaceae	8	*Dovyalis hebecarpa* (Gardner) Warburg	Ceylon gooseberry	3	1	34		(+)	1.00	
	9	*Flacourtia indica* (Burman f.) Merrill	Governor's plum	1	2	196		1.00	(+)	
Guttiferae	10	*Calophyllum tacamahaca* Willd.		1	1	16		(+)	1.00	
Lauraceae	11	*Persea americana* Miller	Avocado	4	4	269			0.59	0.41
Mimosaceae	12	*Inga laurina* (Sw.) Willd.	Sackycac	1	4	1834		0.02	0.98	
	13	*Pithecelobium dulce* (Roxb.) Benth	Guamuchil apes-earring	4	23	1849		0.87	0.13	
Moraceae	14	*Ficus carica* L.	Fig	1	4	114		0.01	0.99	
Myrtaceae	15	*Eugenia uniflora* L.	Brasilian cherry	1	24	4234		0.81	0.19	
	16	*Feijoa sellowiana* (O. Berg.) O. Berg.	Pineapple guava	1	1	7424		1.00	1.00	
	17	*Psidium araca* Raddi.		1	1	34			1.00	
	18	*Psidium cattleianum* Sabine	Strawberry guava	10	129	8561	0.01	0.03	0.95	0.01
	19	*Psidium guajava* L.	Guava	8	61	12 097	(+)	0.03	0.70	0.27
	20	*Syzygium jambos* (L.) Alston	Rose-apple	6	52	3525	0.04	0.03	0.90	0.02
	21	*Syzygium malaccense* (L.) Merr & Perry	Malay apple	3	1	15		1.00	1.00	
	22	*Syzygium samarangense* (Blume) Merr. & L.M. Perry	Java apple	3	6	2789		0.05	0.95	(+)
Oxalidaceae	23	*Averrhoa carambola* L.	Star fruit	1	3	292		1.00	(+)	
Passifloraceae	24	*Passiflora edulis* Sims	Passion fruit	2	1	131		1.00	1.00	
	25	*Passiflora molissima* (Kunth) Bailey	Banana passion fruit	1	2	227			1.00	
	26	*Passiflora suberosa* L.		1	4	182		1.00	1.00	

continued

Table 1. Continued

Family		Scientific name	Common name	Resource availability (index from 1 to 10)	Number of samples	Number of files	Species relative abundance			
							C. catoirii	C. capitata	C. rosa	B. zonata
Polygonaceae	27	*Coccoloba uvifera* (L.) L.	Seagrape	1	1	36		1.00	(+)	
Rhamnaceae	28	*Ziziphus mauritiana* Lamarck	Indian jujube	1	2	57				1.00
Rosaceae	29	*Eriobotrya japonica* (Thumb.) Lindley	Loquat	4	42	6372		0.01	0.99	(+)
	30	*Malus communis* Poir.	Apple tree	1	6	168		(+)	1.00	(+)
	31	*Prunus domestica* L.	Plum tree	1	1	541			1.00	
	32	*Prunus persica* (L.) Batsch	Peach tree	6	35	4503		0.02	0.98	(+)
	33	*Pyrus communis* L.	Pear tree	1	4	656			1.00	
Rubiaceae	34	*Coffea arabica* L.	Coffee	4	59	6505		0.71	0.29	
Rutaceae	35	*Citrus reticulata* Blanco	Mandarin tree	4	7	1123		0.86	0.12	0.02
	36	*Citrus x paradisi* Macfad.	Grapefruit	1	1	138			1.00	
	37	*Murraya paniculata* (L.) Jacq.	Orange jessamine	1	7	1844		1.00	(+)	
Sapotaceae	38	*Chrysophyllum cainito* L.	Common Star Apple	1	27	3986	(+)	0.33	0.67	
	39	*Chysophyllum carpussum* L.	Chysophyllum	1	2	3116		0.43	0.57	
	40	*Mimusops elengi* L.	Spanish cherry	1	20	13 925	(+)	1.00	(+)	(+)
	41	*Richardella campechiana* (Kunth) Pierre	Ties	1	1	34		1.00	(+)	
	42	*Synsepalum dulciferum* (Schumacher & Thonn.) Daniell	Miraculous fruit	1	1	68		1.00		
Solanaceae	43	*Capsicum* sp.	Chilli	4	18	1092		1.00	(+)	
	44	*Solanum mauritianum* Scop.	Bugweed	7	5	81		0.35	0.65	
Sterculiaceae	45	*Theobroma cacao* L.	Cocoa	1	1	103			1.00	
			Number of hosts				3 (6)	30 (34)	33 (41)	9 (14)
			Number of specific hosts				0 (0)	11 (3)	12 (9)	1 (1)
			Sum of resource availability				24 (34)	96 (105)	103 (116)	53 (68)
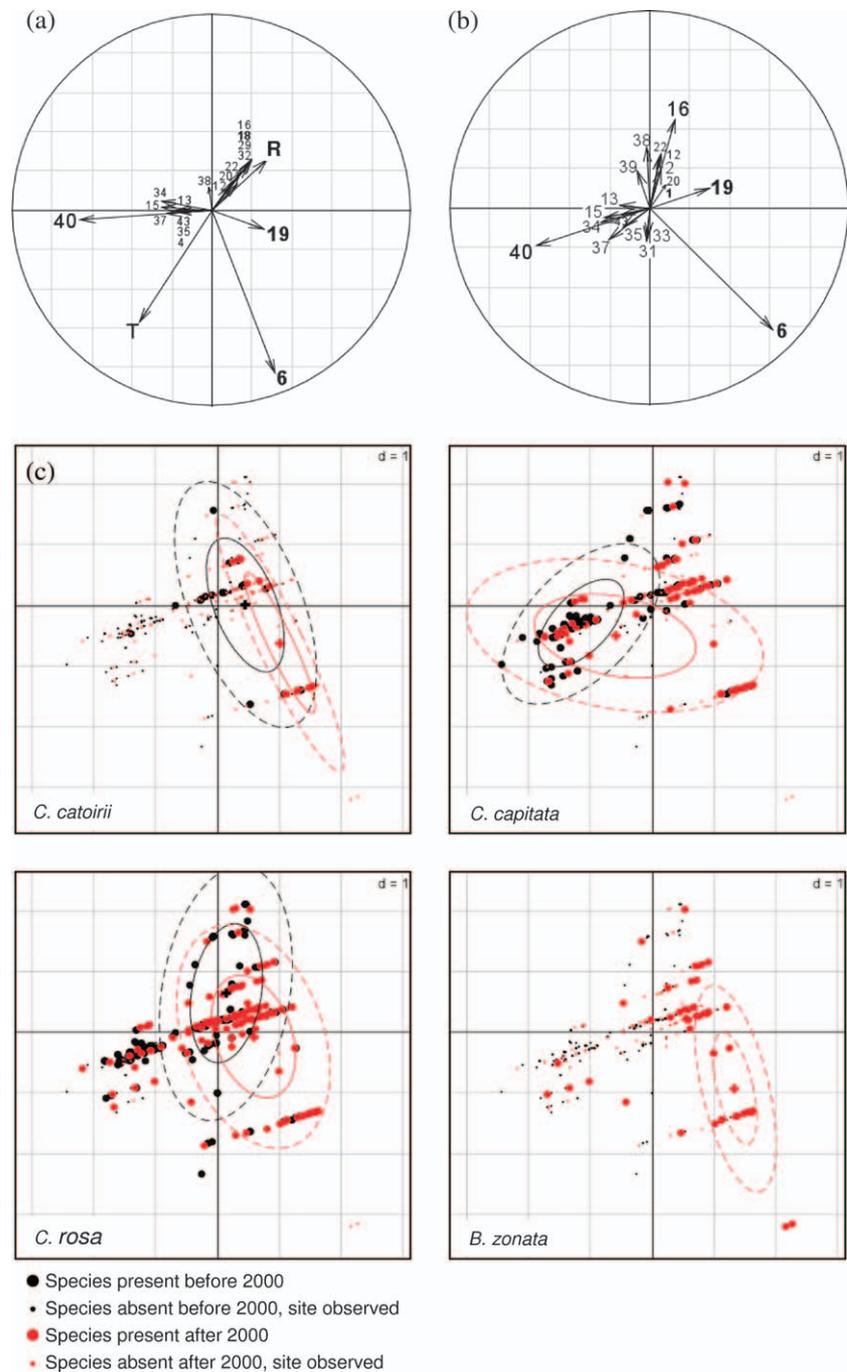
Fig. 6. Canonical correspondence analysis (CCA) of the relationship between tephritid species and fruit species. The first two figures display the correlations (excluding those < 0.1) between variables and the first two axes of the CCA for the first plot (a), and the partial CCA removing the effects of temperature and rainfall for the second plot (b). The four small figures (c) are biplots of the normalized coordinates of the sites, constrained by the fruit species, and the coordinates of the fly species. In each figure, a grid indicates the scale; the length of a square side is one. In each plot, the small circles indicate the samples and the ellipses surround the position of the fly species providing an index of the dispersion around the species centroid (continuous line: 50% of the biomass is expected to be in the ellipse; broken line: 90%). These ellipses are representations of the diversity of the fruit species used by the flies. Numbers correspond to fruit species presented in Table 1. T, temperature; R, rainfall; numbers in bold correspond to the fruits studied in the laboratory experiments (1 = Mango, 6 = Indian almond, 18 = Strawberry guava, 19 = Guava).

similar effects on different tephritid species. Although more specific natural enemies, such as parasitoid wasps, are present, they have (unfortunately) had a very limited impact (S. Quilici, unpubl. data). *Fopius arisanus* (Sonan), which may be a more efficient parasitoid, has been released only in 2004 (Rousse *et al.*, 2005). Further studies will be needed to measure its impact on the fruit fly community. Parts of the study sites (in particular orchards) have been sprayed with insecticides. While the population levels of all tephritid species has probably been reduced in

these sites, no resistance has been documented in La Réunion, and therefore we suppose that the relative abundance of the different species has not been greatly modified by this factor.

In conclusion, the present study, combined with previous results on the effects of climatic factors (Duyck *et al.*, 2006b), suggests that climate overall plays a more important role than host-plant diversity in allowing coexistence between introduced fruit fly species in La Réunion. Further studies should clarify the role of the specific host fruits of *C. capitata* and look for

potential specific hosts of *C. catoirii* in the remaining native forest habitats. Niche partitioning is one of the basic mechanisms by which resident and introduced species may coexist (Denno *et al.*, 1995; Juliano *et al.*, 2002; Reitz & Trumble, 2002), a consequence of which is the accumulation of species diversity after successive invasions (Sax *et al.*, 2002; Bruno *et al.*, 2005). Polyphagous species – such as the fruit flies studied here – may have larger opportunities of invasion (in terms of fundamental niche) because they do not require specific hosts; however, they are also more exposed to inter-specific competition. In other words, if coexistence among polyphagous species must rely mostly on climatic rather than trophic factors (as suggested by our tephritid example), less diversity is expected to build up in the long term after invasions, because newcomers more often either fail to invade or competitively exclude resident species, in comparison to specialist species. More studies on invasions by both specialist and generalist taxa are needed to test this general prediction. In addition, other mechanisms (not depending on a potential niche partitioning) could promote co-existence, such as aggregative spatial and temporal distribution (Shorrocks *et al.*, 1984; Wertheim *et al.*, 2000) and competition–colonisation tradeoffs (Tilman, 1994).

Acknowledgements

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Appendix 1. Results of the analysis of deviance on relative abundance of larvae in fruit collections. All the effects retained in the final model (see methods) are given and their significance is indicated (*F*-tests and corresponding *P*-values). Δdev corresponds to changes in deviance as a result of the suppression of the *effect* term from the reference model (indicated in the second column). The residual deviance and d.f. relate to the reference model. *F*-tests and corresponding *P*-values test the significance of the effect. Codes for effects: f = fruit species, t = mean annual temperature, r = mean annual rainfall, s = tephritid species. Before 2000, the final model (after model simplification) included, in addition to the fly species factor s, the climatic variables r, t, r^2, t^2, $r.t$ and the fruit factor f; and all interactions with s ($s.r$, $s.t$, $s.r^2$, $s.t^2$, $s.r.t$ and $s.f$). After 2000 the simplified model included s, r, t, f and interactions $s.r$, $s.t$ and $s.f$.

Effect	Terms included in reference model	ΔDev	Δd.f.	Residual *Dev*	Residual d.f.	*F*	*P*
Before 2000							
$f.s$	All	2408	8	41 521	1068	7.74	<0.0001
$r^2.s$	All	726	2	41 521	1068	9.34	<0.0001
$t^2.s$	All	333	2	41 521	1068	4.28	0.014
$r.t.s$	All	355	2	41 521	1068	4.57	0.011
$r.s$	$r.s + t.s + f.s$	5205	2	42 672	1074	65.50	<0.0001
$t.s$	$r.s + t.s + f.s$	20 208	2	42 672	1074	254.30	<0.0001
After 2000							
$f.s$	All	11 215	12	18 179	945	48.58	<0.0001
$r.s$	All	2121	3	18 179	945	36.75	<0.0001
$t.s$	All	8335	3	18 179	945	144.43	<0.0001