

REVIEW

A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae)

PIERRE-FRANCOIS DUYCK¹, PATRICE DAVID² and SERGE

QUILICI¹ ¹UMR “Peuplements Végétaux et Bio-agresseurs en Milieu Tropical”, CIRAD Pôle de Protection des Plantes, La Reunion island, France and ²Centre d’Ecologie Fonctionnelle et Evolutive, CNRS UMR 5175, Montpellier, France

Abstract. 1. A number of invasions in the family Tephritidae (fruit flies) have been observed worldwide despite quarantine procedures. In this review, the potential importance of interspecific competition and competitive displacement among different tephritid species is evaluated in the context of recent invasions.

2. Where polyphagous tephritid species have been introduced in areas already occupied by a polyphagous tephritid, interspecific competition has resulted in a decrease in number and niche shift of the pre-established species. No reciprocal invasions have been observed.

3. The data on tephritid invasions seem to support a hierarchical mode of competition; however, complete exclusion usually did not occur. Indeed, tephritid distribution and abundance are markedly structured by various abiotic (mostly climatic) and biotic (host plants) factors.

4. The primary determinant of competitive interactions in near-optimal conditions, such as lowlands with abundant fruit plantations, is probably the life-history strategy. The r - K gradient could be used as a predictor of potential invaders, because K traits (such as large adult size) may favour both exploitation and interference competition.

5. For future research, a better understanding of competition mechanisms seems essential. Different species competing in the same area should be compared with respect to: (i) demographic parameters, (ii) the outcome of experimental co-infestations on the same fruit, and (iii) behavioural and chemical interference mechanisms.

Key words. Competitive displacement, demographic strategies, ecological niche, exploitation, life history.

Introduction

The importance of interspecific competition for community structure has been discussed at length by ecologists, especially with respect to plant-eating insects (Wiens, 1977; Connell, 1980, 1983; Lawton & Hassell, 1981; Schoener, 1982). Recent reviews have shown that interspecific compe-

titition is widespread among insects (Denno *et al.*, 1995; Stewart, 1996; Reitz & Trumble, 2002). In their review on competitive displacement among insects and arachnids, Reitz and Trumble (2002) showed that displacement is generally observed between very closely related species, and often in relation to invasion phenomena, in which an exotic species displaces a native one (33% of cases) or another already established exotic species (55% of cases). After analysing 193 pairs of competitor species, Denno *et al.* (1995) concluded that interspecific competition markedly affected the distribution and abundance of plant-eating insect populations. Thus, plant-eating insect population

Correspondence: Pierre-François Duyck, CIRAD 3P, 7, chemin de l'IRAT, 97410, St Pierre, La Reunion island, France. E-mail: duyck@cirad.fr

structure is affected by competition as well as by natural enemies or host plants

The family Tephritidae (fruit flies) is of major economic importance because many species in this family attack important fruit crops in tropical and subtropical regions (White *et al.*, 2000). A number of recent invasions by tephritids have been observed, despite quarantine procedures (White *et al.*, 2000; Allwood *et al.*, 2002; Duyck *et al.*, 2004). The potential importance of interspecific competition and competitive displacement among different tephritid species is reviewed here in the context of recent invasions.

The main objectives of this review are to list the best known cases of invasions by polyphagous Tephritidae, highlighting the possible involvement of competition among species, and to put forward the potential mechanisms of these invasions. Firstly a clarification of the terminology and conceptual framework is established, followed by reviewing the case studies and potential mechanisms underlying invasion and competition in tephritids.

Competition, invasions, and life-history strategies in insects: the conceptual framework

Competition and coexistence

Interspecific competition is defined as a reduction in individual fecundity, survival, or growth as a result of exploitation of resources or by interference with individuals of another species (Begon *et al.*, 1996). Two types are usually recognised. Exploitation competition does not involve behaviour (Dajoz, 1976; Pianka, 1976; Begon *et al.*, 1996), and occurs when resources are insufficient for the individuals of both species. Resource use by one species then reduces availability to others. In interference competition, one species behaviourally denies access to food or target sites to another. This may occur even when there is a surplus of the resource. The simplest interspecific competition models (Lotka–Volterra) produce two possible equilibria: either the elimination of one of the species or a stable equilibrium in which the two species coexist. There may also be an unstable equilibrium, in which the advantage depends on the initial densities of the two competing populations (Balasubramanian, 1990; Begon *et al.*, 1996). In short, stable coexistence occurs when interspecific competition is weak compared with intraspecific competition. According to conventional niche theory, the primary determinant of interspecific competition is the overlap in the resources used (or niche overlap). Two species with highly similar fundamental niches (i.e. the niches potentially occupied in the absence of competitors) will therefore often compete strongly with each other when they first meet. This situation is particularly relevant for members of a given family or guild, that come into contact following accidental introductions, such as the polyphagous fruit-eating tephritids. The competitive interaction may result either in ecological displacement, by which one or both species shifts or reduces its

niche until coexistence becomes possible, or in competitive exclusion of one of the species. This poses the practical problem that interspecific competition tends to destroy itself: strong interspecific competition may be observed during transient dynamics of species interactions, though not between two stably coexisting species. In this respect, non-equilibrium situations such as invasions provide a unique opportunity to observe interspecific competition in action.

Competition mechanisms, life-history strategies, and behaviour

Most studies of competition are descriptive: an increase in the population density of one species co-occurs with a decrease in another. Numerous experiments have also measured the impact of competition by modifying population levels (Connell, 1983; Schoener, 1983, 1985). The mechanisms underlying competition are little known and may be specific to each pair of competing species. A more tractable, though indirect, approach is to identify species traits that can be used as predictors of competitive displacement. Two classical determinants of competition in insects are focused on: life-history strategies and behavioural traits.

Some studies highlighted the links between life-history traits and competitive ability. A classical dichotomy was introduced by MacArthur and Wilson (1967) between so-called *r*- and *K*-selected species. In their view, *r* species display a suite of traits that favour rapid population growth and colonisation of new habitats, while *K* species are adapted to competition in saturated habitats. Although later studies have shown that the conditions of selection for *r* vs. *K* traits are much more complex than just density-independent vs. density-dependent population regulation (Reznick *et al.*, 2002), species often fall into *r* or *K* syndromes. Some species tend to mature early, have small size, high growth rates, little resistance to competitors, and efficient dispersal; while others present long lifespan, low fecundity, large sizes, and little mobility. Of course, these are extremes of a continuous gradient, along which species may be classified. A modern theory that is reminiscent of *r* and *K* is the coexistence theory developed by Tilman (1994). This theory states that coexistence of several species can be promoted in a structured habitat by (i) a perturbation regime that constantly regenerates new empty sites, and (ii) competition–colonisation trade-offs among different species (Tilman, 1994). The bad competitors must be good colonisers because their maintenance depends on their being first in colonising empty sites.

Using life-history or demographic traits to characterise the competitor (or *K*) strategy implies that competition is mainly related to exploitation of resources; however behavioural traits may be involved in competition through interference. In insects, according to Case and Gilpin (1974), interference is common, despite its high costs, because it can provide very rapid benefits. Interference competition implies the anticipated use and often defence of resources, enabling a more aggressive species to gain access to a

resource to the detriment of another species (Huffaker & Gutierrez, 1999). As a result, many species avoid resources that are chemically marked or have already been exploited in some way (Schowalter, 2000). Intraguild predation is an advanced form of interference that is particularly effective when it concerns the eggs of another species, since the cost of this type of interference is low (Case & Gilpin, 1974).

Interspecific competition and invasions

Biological invasions are increasingly being seen as one of the components of global change (Vitousek *et al.*, 1996). Most of them result from human activity. Once an exotic species is established, it often cannot be eradicated, and its management is often problematic, if not impossible (Kolar & Lodge, 2001). Forecasting invasions is therefore a major issue (Williamson, 1996; Williamson & Fitter, 1996; Kolar & Lodge, 2001; Sakai *et al.*, 2001). The import fluxes (Lonsdale, 1999) and the lack of natural enemies (Simberloff & Wilson, 1970) have traditionally been put forward as the primary determinants of invasion, especially in islands. Less attention was paid to the competitive abilities of the invaders themselves, due to the importance given to the lack of natural enemies (Pimm, 1987; Byers, 2000). However, except for a few cases, the niches invaded by exotic species are not entirely vacant, and they usually displace established species, be they native or themselves exotic (Reitz & Trumble, 2002). The ambiguity of the role of competition in invasions must partly result from the difficulties of demonstrating competition unequivocally (Byers, 2000). An understanding of invasion phenomena therefore necessarily involves a study of interspecific competition and the related species traits. Invaders are generally assumed to have a type *r* demographic strategy, but this idea was not confirmed by correlation analyses (Lodge, 1993). It is true that during the colonisation phase, species with the traits typical of colonisers may be at an advantage (Sakai *et al.*, 2001). However, as mentioned above, most of them have to compete later to establish a permanent, large population. Studies have already shown that in the case of two species, the exotic invader species tends to be more competitive by a better conversion efficiency of resources (Byers, 2000) or a superior harvesting ability (Petren & Case, 1996). Because the traits required for rapid colonisation may not be the same as for long-term persistence (Sakai *et al.*, 2001), successive invasions in a given region may be analogous to ecological successions, though at a very different scale. A logical order of strategies ranging from coloniser (or *r*-like) to competitor (or *K*-like) species could therefore be expected.

Interspecific competition in tephritids

Among the family Tephritidae, numerous species are polyphagous fruit-eating flies that have become a major concern in agriculture. Through fruit trade, they have been introduced into various countries where they behaved as invasive

pests. Most of the time, the invaded countries were previously occupied by other tephritid species, either local species or originating in a previous invasion. Invasions bring into contact a number of previously isolated species and in a way provide natural experiments on interspecific competition. Here an attempt will be made to list the known cases of invasion of a fruit-infesting tephritid species in an area already occupied by another tephritid. This list can be used to answer some basic questions on interspecific competition. The cases presented in Table 1 have been included on the basis of two criteria: (i) the invasive species must be a polyphagous tephritid, and (ii) another polyphagous tephritid was initially present in the invaded area and during the invasion process. These criteria were selected in order to ensure that the ecological niches of the two species largely overlap.

First, one can distinguish two dominant modes of interaction between pairs of species. In the first mode (*hierarchical competition*), one of the species always dominates and excludes the other. A second mode leads to stable coexistence, triggered either by niche differentiation (see above) or by a colonisation–competition trade-off, i.e. the fact that the less competitive species can occupy a fraction of empty sites not yet colonised by the more competitive species. If the dominant mode is hierarchical competition, then (i) invasions should generally lead to exclusion of the pre-existing species by the invasive species, and (ii) reciprocal invasions should not be observed, i.e. if A invades a territory occupied by B, then B should never invade a territory previously occupied by A. These two predictions should be violated if the dominant mode is niche differentiation or colonisation–competition trade-off.

In addition, and especially if a hierarchical order of competition can be established among species, is it possible to relate the competition rank to species-specific demographic or life-history traits? In particular, when A invades over B, is A usually characterised by a relatively *K*-selected lifestyle compared with B? Does A possess interference behaviours more efficient than B?

Examples of competitive interactions

Most examples of interspecific competition among tephritids derive from situations in which a new species has been introduced into a given environment (Fitt, 1989). Although tephritids commonly invade new zones (Fletcher, 1986), relatively few cases are described in any detail in the literature. Table 1 summarises the known situations in which a polyphagous tephritid has become established in the presence of one or more other polyphagous tephritid species. The best-known cases are described below.

The Queensland fruit fly in Australia. The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), was introduced from Europe into Australia in 1897 or thereabouts (Hooper & Drew, 1989; Vera *et al.*, 2002). It was then gradually displaced around the Sydney area by the

Table 1. Major cases of polyphagous tephritid species introduced in areas where other polyphagous species of the family were pre-established.

Invasive species	Pre-established species	Colonised areas	Date or period	References
<i>Bactrocera carambolae</i> Drew & Hancock	<i>Anastrepha fraterculus</i> (Wiedemann)	French Guyana, Guyana,	1975–	1, 2
	<i>Anastrepha obliqua</i> (Wiedemann)	Surinam	1993	
<i>Bactrocera dorsalis</i> (Hendel)	<i>Ceratitidis capitata</i>	Hawaii	1945	3–5
<i>B. dorsalis</i>	<i>Ceratitidis rosa</i> Karsch	Kenya	2003	6
	<i>C. capitata</i>			
	<i>Ceratitidis cosyra</i> (Walker)			
<i>B. dorsalis</i>	<i>Bactrocera kirki</i> (Froggatt)	Tahiti (French Polynesia)	1996	7, 8
	<i>Bactrocera perpusca</i> (Aubertin)			
	<i>Bactrocera tryoni</i> (Froggatt)			
<i>B. kirki</i>	<i>B. perpusca</i>	Tahiti (French Polynesia)	1928	7
<i>B. kirki</i>	<i>Bactrocera luteola</i> (Malloch)	Bora Bora, Ha (French Polynesia)	Before 2000	7
<i>B. kirki</i>	<i>Bactrocera setinervis</i> (Malloch)	Henderson, Pitcairn islands	Before 2000	7
<i>B. tryoni</i>	<i>C. capitata</i>	Sydney (Australia)	Early 1900s	3
<i>B. tryoni</i>	<i>B. kirki</i>	Tahiti	1970s	7
	<i>B. perpusca</i>			
<i>B. tryoni</i>	<i>Bactrocera curvipennis</i> (Froggatt)	New Caledonia	1969	7, 8
	<i>Bactrocera psidii</i> (Froggatt)			
<i>Bactrocera xanthodes</i> (Broun)	<i>Bactrocera melanota</i> (Coquillett)	Cook Islands	1970s	8
<i>B. xanthodes</i>	<i>Bactrocera atra</i> (Malloch)	Raivavae (Îles Australes, French Polynesia)	1998	7
<i>Bactrocera zonata</i> (Saunders)	<i>C. rosa</i>	Reunion island, Mauritius	1987–	9
	<i>C. capitata</i>		1991	
	<i>Ceratitidis catoirii</i> Guérin-Mèneville			
<i>B. zonata</i>	<i>C. capitata</i>	Egypt	1998	10
<i>C. capitata</i>	<i>C. catoirii</i>	Reunion island, Mauritius	1939–1942	9, 11, 12
<i>C. capitata</i>	<i>Anastrepha suspensa</i> (Loew)	West Indies	1950s	1, 13
<i>C. capitata</i>	<i>Anastrepha ludens</i> (Loew)	Central America	1950s	1, 13
<i>C. capitata</i>	<i>A. fraterculus</i>	Central and South America	1950s	1, 13
	<i>A. obliqua</i>			
<i>C. rosa</i>	<i>C. capitata</i>	Reunion island, Mauritius	1953–	9, 11, 12
	<i>C. catoirii</i>		1955	

Sources: 1, White and Elson-Harris (1992); 2, Allwood *et al.* (2002); 3, Debach (1966); 4, Keiser *et al.* (1974); 5, Reitz and Trumble (2002); 6, Lux *et al.* (2003); 7, Leblanc and Putoa (2000); 8, Allwood and Drew (1997); 9, White *et al.* (2000); 10, J. P. Cayol, pers. comm.; 11, Orian and Moutia (1960); 12, Etienne (1972); 13, Fletcher (1989).

Queensland fruit fly, *Bactrocera tryoni* (Froggatt), which invaded Australia from the north in the early 20th century (Debach, 1966).

The Oriental fruit fly in Hawaii. A similar phenomenon occurred in Hawaii in 1945, when the Oriental fruit fly *Bactrocera dorsalis* (Hendel) largely displaced *C. capitata* from coastal zones. *Ceratitidis capitata* had itself been introduced in 1910 and had become a major pest throughout Hawaii. Since the invasion by *B. dorsalis*, *C. capitata* has generally been restricted to cooler climates at high altitudes, where *B. dorsalis* is not found. However, the ecological segregation between the two species is modulated by the host fruit: *C. capitata* is found at low altitudes on coffee, to which it seems to be more suited than *B. dorsalis* while it is only rarely found on guava and mango, although they were by far its preferred hosts before the establishment of *B. dorsalis* (Debach, 1966; Keiser *et al.*, 1974; Reitz & Trumble, 2002).

The situation in the Mascarene Islands. In the Mascarene Islands, *C. capitata* apparently became established in Reunion island in 1939 and Mauritius in 1942, whereas the Mascarene fruit fly *Ceratitidis catoirii* Guérin-Mèneville was an indigenous species on both islands (Orian & Moutia, 1960; Etienne, 1972). A further invasion by the Natal fruit fly *Ceratitidis rosa* (Karsch) was seen in Mauritius in 1953 and Reunion island in 1955 (Orian & Moutia, 1960; Etienne, 1972). More recently, the peach fruit fly *Bactrocera zonata* (Saunders) was found in Mauritius in 1987 and Reunion island in 1991 (White *et al.*, 2000). In Reunion island, *C. catoirii* is now only found in small numbers on the east and south coast of the island, while it seems to have disappeared completely from Mauritius (White *et al.*, 2000). *Ceratitidis rosa* is generally dominant at high altitudes in Reunion island, while *B. zonata* is continuing to spread and has already colonised a large proportion of the niches used by the other three species at low altitudes.

Other important cases. *Bactrocera zonata* has been seen for several years in Egypt, where *C. capitata* is also found (J.P. Cayol, IAEA, pers. comm.). A species of the complex *Bactrocera dorsalis* has also apparently been recorded recently in Kenya (Lux *et al.*, 2003), where *C. capitata*, *C. rosa*, and *Ceratitis cosyra* (Walker) are also found. In these last two cases, the effects on the species found beforehand are not yet known.

In all the cases listed in Table 1 reciprocal invasions were never observed. Indeed, in apparent agreement with the hypothesis of hierarchical competition the diagram of invasion links among the studied species (Fig. 1) is strongly directional. In all the cases of confrontation between two genera, a species of the genus *Bactrocera* has always invaded in the presence of, and ultimately dominated numerically, one or more species of the genus *Ceratitis*, while the reverse was never observed. Similarly the genus *Anastrepha* has been dominated in all the cases presented. Note that interspecific competition may also occur with species of other pest groups. For instance, certain lepidopterans may share the same resource and thus come into competition with tephritids (Feder *et al.*, 1995).

Although invasions links seem, at first glance, to support the hierarchical mode of competition, it is striking that complete competitive exclusion usually did not occur (in contradiction with the assumptions underlying the hierarchical hypothesis). Indeed, among all the documented cases,

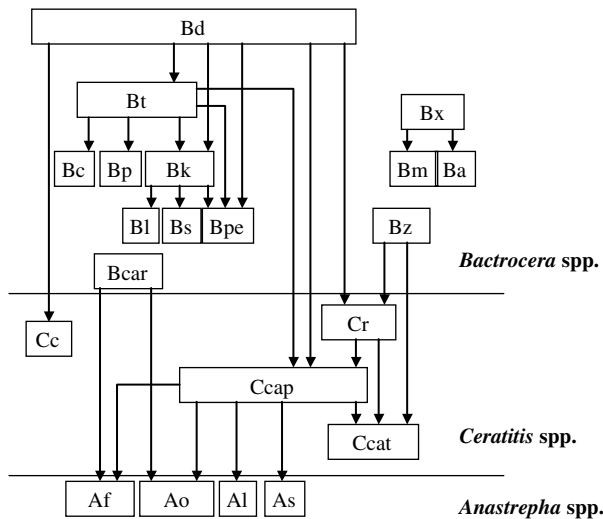


Fig. 1. Diagram of the invasion links among polyphagous tephritids from Table 1. Each arrow represents the direction of invasion and competitive displacement of a tephritid species by another one. A single link may represent two or several independent occurrences of the same invasion history (such as Hawaii 1945 and Kenya 2003 for *Bactrocera dorsalis* on *Ceratitis capitata*). Af = *Anastrepha fraterculus*, Al = *A. ludens*, Ao = *A. obliqua*, As = *A. suspensa*, Ba = *Bactrocera atra*, Bc = *B. curvipennis*, Bcar = *B. carambolae*, Bd = *B. dorsalis*, Bk = *B. kirki*, Bl = *B. luteola*, Bm = *B. melanota*, Bp = *B. psidii*, Bpe = *B. perpusca*, Bs = *B. setinervis*, Bt = *B. tryoni*, Bx = *B. xanthodes*, Bz = *B. zonata*, Cc = *Ceratitis cosyra*, Ccap = *C. capitata*, Ccat = *C. catoirii*, Cr = *C. rosa*.

competitive displacements and niche shifts are more frequent than exclusions (see above). Actually, the only case in which exclusion is certain is that of *C. catoirii* in Mauritius, which was driven extinct by the invasion of the different invasive species. Anyway, in all cases, environmental factors should affect the invasion process.

Influence of biotic and abiotic factors on competition

In exploitation competition, the species that makes best use of its environment will have a competitive advantage. The environment should therefore have a considerable impact on exploitation by swinging the balance in favour of one species or the other.

For instance, tephritid distribution and abundance are markedly structured by various abiotic and biotic factors, which have a direct effect on species distribution but also an indirect effect, by modulating interspecific competition. Several factors might affect fruit fly distribution and/or competition, including temperature, humidity, host fruit, and natural enemies.

Temperature. Temperature has a marked influence on tephritid development and survival. Many comparative studies have been carried out to determine the minimum development thresholds and thermal constants for different species (Messenger & Flitters, 1958; Crovetti *et al.*, 1986; Delrio *et al.*, 1986; Kasana & Aliniaze, 1994; Yang *et al.*, 1994b; Vargas *et al.*, 1996, 1997, 2000; Brévault & Quilici, 2000; Duyck & Quilici, 2002). These studies showed that the dominant species may differ depending on temperature, particularly as a function of latitude or altitude. For instance, in Reunion island, *C. capitata* dominates *C. rosa* in the lowland areas of the west, where temperatures are highest, while *C. rosa* is dominant in the uplands (Etienne, 1972), which tallies with the minimum development thresholds for the species (Duyck & Quilici, 2002; Duyck *et al.*, 2004). Similarly, in Hawaii, while *B. dorsalis* is dominant almost throughout the island, *C. capitata* subsists in the uplands. It is to be noted that, in this latter case, old records exist that mention the abundance of *C. capitata* in the lowlands before the establishment of *B. dorsalis* (Debach, 1966), which supports the hypothesis of a modulation of the result of interspecific competition by temperature.

Humidity. As regards egg development, Tsitsipis and Abatzis (1980) observed that in *Bactrocera oleae* (Gmelin), the development time at 20 °C could increase from 84 to 102 h if relative humidity decreased from 100 to 75%. In the wild, the effect of humidity on the embryo stage and larval instars is undoubtedly modulated more by the host fruit than by the climatic conditions. Only a few studies (Neilson, 1964; Shoukry & Hafez, 1979; Eskafi & Fernandez, 1990; Teruya, 1990) have looked at the impact of relative humidity on pupal development, despite the fact that it may be a major factor in species distribution. For example, in Reunion island, *C. catoirii* is dominated by other species but subsists in a narrow coastal strip in the east and south of the island, where there is more rainfall. A recent study on

the impact of humidity on the pupal survival confirmed the susceptibility to dryness of this species (P. F. Duyck, P. David and S. Quilici, unpubl. data).

Host plant. Host fruit species and quality both affect immature instars development (with possible repercussions on adult fecundity) and adult behaviour. In a study of five species of Dacini fruit flies, Fitt (1986) showed that the abundance of species on different host fruits was due more to the choices made by females than to larval specialisation. However, while many host plants can sustain the full development of different tephritid species, host quality governs major differences in survival rate, larval development, and adult fecundity. The nutritive value of the fruit has a major impact on larval development (Fernandes-Da-Silva & Zucoloto, 1993). Carey (1984) showed that the larval development time of *C. capitata* at 25°C could increase from around a week on a favourable host such as mango (*Mangifera indica* L.) to over 3 weeks on quince (*Cydonia oblonga* Miller). In Hawaii, the greater competitiveness of larvae on certain host fruits was shown at least partly to account for the competitive displacement of *C. capitata* by *B. dorsalis* (Keiser *et al.*, 1974).

The choice of egg-laying site by adult females is determined by visual and olfactory stimuli from the fruit (Prokopy & Roitberg, 1984; Aluja & Prokopy, 1993; Quilici *et al.*, 1994; Brévault & Quilici, 1999). In relation to interspecific competition, Berube (1980) studied the selection of egg-laying sites by two species of the genus *Urophora*. The two studied species appeared to have separate niches (they attack two different sizes of flower head); however, the species attacking the smaller flower heads can reduce the population of the second by suppression of the flower heads growth. Other studies have also shown that the outcome of direct interactions between females (Camargo *et al.*, 1996) or the ability to discriminate already occupied flower heads (Angermann, 1986) was dependent on the host plants. Although *Urophora* is not a polyphagous fruit-eating tephritid, this example illustrates a type of mechanism that could well work also in polyphagous tephritids.

Natural enemies. In a few cases, natural enemies have been shown to play a key role in the population dynamics of some tephritid species, such as *Rhagoletis cerasi* (Boller & Remund, 1989). In this species a high mortality of pupae in the soil caused by predators was demonstrated. It is, however, probable that the impact of generalist predators such as ants would affect more or less equally different tephritid species in a given biotope.

Among natural enemies, parasitoids are generally more specific and could affect differentially the tephritid species coexisting in a given biotope. However, in most instances their impact on tephritid populations appears rather limited, with the exception of a few ovo-pupal species (Vargas *et al.*, 1993).

Competition mechanisms

In tephritids, exploitation competition, when present, undoubtedly occurs at fruit level, and fruit quantity may

be a limiting factor. In this context, the demographic or life-history strategies should be an important component of relative competitive success of different species. Different types of interference competition could also be involved.

Biotic potential. There have been many studies of tephritid demographics (Carey, 1982, 1984; Carey *et al.*, 1988; Vargas & Carey, 1989, 1990; Yang *et al.*, 1994a,b; Vargas *et al.*, 1997, 2000). A very comprehensive study of *C. capitata* demographics was carried out by Carey (1982), while Yang *et al.* (1994a) compared the demographics of two species of the genus *Bactrocera* that live on Cucurbitaceae. Other studies (Vargas *et al.*, 1984, 2000) have shown that the competitive advantage of *C. capitata* at high altitudes is apparently due to its type *r* demographic strategy, which is better suited to temperate climates.

Vargas *et al.* (2000) compared the demographic parameters for *Ceratitidis capitata*, *Bactrocera dorsalis*, and *Bactrocera cucurbitae* (Coquillett) under several fluctuating temperature regimes. *Ceratitidis capitata* had a high intrinsic growth rate (type *r* demographic strategy) compared with the two *Bactrocera* species (type *K* demographic strategy). They did not draw any conclusions as to the impact of this difference in strategy on the competition between *C. capitata* and *B. dorsalis*. However, as mentioned earlier, it is remarkable that *B. dorsalis* has over-invaded and dominated established *C. capitata* in at least two independent occasions, while the reverse was never observed. This suggests that a relatively *K*-like strategy may underlie the apparent directionality of interactions between the genus *Bactrocera* and the genus *Ceratitidis*, although further confirmations are certainly needed. *Bactrocera cucurbitae* was not included in Table 1 because it is not a polyphagous species (mainly attacking cucurbits).

Interference between adults. There have been cases of females being disturbed by other adult tephritids during egg laying. However, Fitt (1989) felt that this competition mechanism was largely insignificant, given that the time lapse between a female's arrival on a fruit and egg laying is generally very short. Females have been seen to defend their egg-laying sites against females of the same species in *B. dorsalis* (Shelly, 1999), and it is likely that this type of behaviour may also affect interspecific competition.

Interference competition may also occur via marking pheromones. Host-marking pheromones are chemicals that are deposited by many tephritid species after egg laying, which help to regulate interspecific competition between larvae (Roitberg & Prokopy, 1987). Most studies suggest that host-marking pheromones are only effective against individuals of the same species (Fitt, 1989; Nufio & Papaj, 2001), but it has also been demonstrated in the genus *Rhagoletis* that there may be some form of cross-recognition between species of a given group (Prokopy *et al.*, 1976). No host-marking pheromones have yet been found in species of the genus *Bactrocera*, but in two species of the genus, *Bactrocera tryoni* and *Bactrocera jarvisi* (Tryon), females can recognise fruits containing developing larvae, no doubt as a result of chemical modifications in the fruit (Fitt, 1986, 1989). This recognition is not affected by

the species of the larvae, and may therefore play a role in interspecific competition.

Interactions between larvae. In terms of tephritid larvae, the two types of competition – interference and exploitation – undoubtedly both occur, but it is difficult to distinguish between them. Interference between larvae may take the form of physical attacks, cannibalism, or elimination by fruit deterioration. Whatever the mechanism, the first larvae to hatch in a given fruit will have an advantage over subsequent larvae (Fitt, 1989). The impact of cross-infestation on larva development has been demonstrated in two species that live on the Cucurbitaceae *B. cucurbitae* and *Dacus ciliatus* Loew (Qureshi *et al.*, 1987), and in *Ceratitis capitata* and *Bactrocera dorsalis* (Keiser *et al.*, 1974). These experiments have shown that the competitive advantage observed in the wild can partly be predicted by a better survival of larvae in laboratory conditions.

The biology of most of the species listed in the Table 1 has not been studied in details; however, the few results suggest that the *K* strategy species dominate the *r* strategy species in controlled environments. The importance of interference in competition is not clear. However both types of competition (exploitation and interference) could work in the same direction provided the species that have superior interference skills also have a *K* strategy. For instance, a bigger adult size could increase the ability to compete by both exploitation and interference.

Conclusion and prospects for future research

Is interspecific competition an important component of the many recent invasions by polyphagous Tephritidae? On one hand, there has been no experimental study directly demonstrating the action of competition during the invasion process, for example by manipulating species densities in the field. This is because of the well-known intrinsic difficulty of such studies. On the other hand, two arguments are, it is believed, sufficient to establish that strong interspecific competition did occur during invasions. First, several studies in controlled environments have documented interspecific competition for the fruit resource, predominantly by exploitation at the larval stage, but also by interference at the adult, and possibly at the larval stage, although the precise mechanisms are far from being well understood. Second, recent invasions by tephritids are systematically followed by regional extinction or large changes in numbers and local distribution of established species, when present. These changes can parsimoniously be interpreted as competitive exclusions or displacements. A striking aspect of the invasion history of polyphagous tephritids is their apparent directionality. This means that (i) reciprocal invasions do not occur (when A invades in the presence of B, the reverse is never observed elsewhere), and (ii) invasion ability is transitive (when A invades in the presence of B, and B in the presence of C, there can be instances of A invading in the presence of C but not the reverse). If confirmed by later

studies, this would open the possibility to rank species according to a single invasion scale. If some species-specific traits can be used as predictors of the position of a given species on that scale, this would allow the prediction of its invasion potential in a given community. The classification along the *r*–*K* gradient is a good candidate trait in tephritids. Indeed, in the few known instances, it seems to correlate with the direction of invasion links (e.g. the relationships between *Bactrocera* spp. and *Ceratitis* spp.), possibly because *K* traits (such as a large adult size) favour both exploitation and interference competition. More data are needed to confirm this correlation, though.

In addition to using correlated traits, a direct knowledge of competition mechanisms could help predicting the outcome of interspecific interactions in tephritids; however, little is yet known about the mechanisms involved. It seems important to conduct a detailed study of all the mechanisms that give one species a comparative advantage, in order to rank them in order of importance. In terms of its application to quarantine measures, such a study could be used to classify species in relation to the risk of invasion, depending on their aptitude for competition, as part of a phytosanitary risk analysis (PRA). In short, the capacity of a species to invade (or re-invade) could be estimated by studying the potential mechanisms of competition with the species already occupying the same niche. Studying the life patterns and behaviour of invasive species from a taxon closely related to the indigenous species would therefore be an interesting way of predicting future invasive species.

Although the directionality of invasion links is consistent with the hypothesis that tephritid species exclude one another in a hierarchical way, the details of invasion histories, when available, are generally not. In most cases, established species are displaced along a geographical (restriction of distribution area) and ecological (niche shift) axis. The latter can be either climatic (temperature, humidity) or related to host plants. Indeed, the few experimental studies available suggest that such factors can greatly modulate the outcome of competition, especially at the larval stage. How can this finding be reconciled with the directionality of invasions? In other terms, if each species can dominate in its preferred niche or habitat, why don't reciprocal invasions occur? For example, in Hawaii, *Ceratitis capitata* has found an ecological refuge in high altitudes and coffee fields following the invasion by *Bactrocera dorsalis*. It could logically be expected for *C. capitata* to be able to invade high altitudes and coffee fields in another island where *B. dorsalis* is initially present; however, no such case has ever been observed. Species of the genus *Ceratitis* never invaded in the presence of established *Bactrocera* spp.

A possible solution lies with the probability of successful invasions. As a first approximation, most species of polyphagous tephritids find their optimal ecological conditions in lowland, relatively warm, areas with abundant cultivated or sub-spontaneous fruits like mango, Citrus, Indian almond, etc. The primary determinant of competitive

interactions in such near-optimal conditions is probably the life-history strategy, *K* species being favoured (see above). Thus, *K* species (such as *Bactrocera* spp.) can invade over *r* species (such as *Ceratitidis* spp.), taking over the most productive niche, while the *r* species become restricted to the limited set of habitats they can tolerate better, such as highlands (as for *C. rosa* in Reunion island) or particular host fruits (as for *C. capitata* in Hawaii). These habitats would then act as a private niche. Two things make the probability of reciprocal invasion low in such a scenario. First, the *r* strategy may favour migration and colonisation, so that *K* species tend to arrive after *r* species in a given region. Indeed, many invasions by *Ceratitidis* occurred in the 1940s and 1950s, while a number of invasions by *Bactrocera* are relatively recent (see Table 1). However, some regions have been invaded by *Bactrocera* as early as the 1920s or 1940s and have never, since then, been invaded by a *Ceratitidis* sp., in contrast with other regions devoid of *Bactrocera*. The second reason for reciprocal invasions to be improbable is ecological. Suppose that an introduced species A can only dominate the established species B in a relatively limited habitat. In order to have the opportunity to establish permanent populations, species A has to be introduced into that particular habitat. The probability of such introductions is low if such habitats are rare, or located far from the places where introduced species are expected to arrive (such as harbours or airports). To summarise, the scenario here states that *K* species invade over *r* species and not the reverse because they are competitively dominant in the most productive and most accessible ecological niche, while the *r* species can dominate only in restricted, suboptimal, and/or less accessible habitats. This, of course, has to be considered as a mere working hypothesis awaiting further data.

This documentation on interspecific competition among invasive and native polyphagous tephritid species remains fragmentary. In future research, it will be important to compare the different demographic parameters of various species known to coexist or displace each other in a given region, under the same experimental conditions, as has already been done with *Bactrocera dorsalis* and *Ceratitidis capitata* (Vargas *et al.*, 2000). This type of study would demonstrate whether it is possible to correlate life patterns and aptitude for competition. Infestations and co-infestations of host fruits by several different species should also be tested, to establish their impact on adult development time, survival, and fecundity (for instance, there could be a reduction in the size of adults that have been subject to competition during their development as larvae). The role of ecological factors other than the host fruits, especially those that seem to be important determinants of species distributions (temperature and humidity), should also be examined.

Lastly, various aspects of the influence of adult behaviour are barely known (interspecific recognition of marked fruits or fruits containing larvae, disturbance during egg laying, fruit protection after egg laying). Such studies would help to quantify the role played by interference competition.

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