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Can more *K*-selected species be better invaders? A case study of fruit flies in La Réunion

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ABSTRACT

Invasive species are often said to be *r*-selected. However, invaders must sometimes compete with related resident species. In this case invaders should present combinations of life-history traits that give them higher competitive ability than residents, even at the expense of lower colonization ability. We test this prediction by comparing life-history traits among four fruit fly species, one endemic and three successive invaders, in La Réunion Island. Recent invaders tend to produce fewer, but larger, juveniles, delay the onset but increase the duration of reproduction, survive longer, and senesce more slowly than earlier ones. These traits are associated with higher ranks in a competitive hierarchy established in a previous study. However, the endemic species, now nearly extinct in the island, is inferior to the other three with respect to both competition and colonization traits, violating the trade-off assumption. Our results overall suggest that the key traits for invasion in this system were those that favoured competition rather than colonization.

Keywords

Biological invasions, competitive displacement, life-history traits, *r*–*K* trade-off, Tephritidae.

INTRODUCTION

Biological invasions are now considered one of the most important components of human-induced recent changes in the biosphere (Vitousek *et al.*, 1996), and have dramatic impacts on both species distributions and global biodiversity (Lodge, 1993; Mack *et al.*, 2000; Mooney & Cleland, 2001). Thus, the identification of biological traits typical of potential invaders (Crawley, 1986; Gray, 1986; Mack, 1996; Kolar & Lodge, 2001) and of features of invasible habitats (Lonsdale, 1999; Levine, 2000; Stachowicz *et al.*, 2002; France & Duffy, 2006; Richardson & Pysek, 2006) has become an important challenge. Despite an increasing number of studies, it has been notoriously difficult to obtain robust generalizations, both because of the heterogeneity of taxa and ecosystems affected by invasion, and because of the predominant effect of variation in propagule pressure among case studies (Lonsdale, 1999; Kolar & Lodge, 2001). A pervasive historical paradigm, although with quite ambiguous empirical support (see, e.g. Mack, 1996; Kolar & Lodge, 2001), is the assumption that invasive species should be good colonists (Elton, 1958; Lodge, 1993; Williamson, 1996). Invasive species are defined on a biogeographical basis, as those that have recently been introduced and have established viable populations far from their original distribution areas (Williamson, 1996). In contrast, colonists have been historically defined by a set of biological

traits including short generation times, short juvenile phase, high reproductive effort, production of many small, mobile offspring, and in some cases vegetative reproduction (Pianka, 1970). There has been much debate on the reality and exact nature of the 'colonist's syndrome' (MacArthur, 1962; Pianka, 1970; Grime, 1977; Stearns, 1992; Mueller, 1997; Reznick *et al.*, 2002). Because the intrinsic growth rate is positively affected by such traits, they were termed '*r*-selected traits' by Pianka (1970) and said to be advantageous in non-competitive environments such as early successional or otherwise unstable habitats (MacArthur, 1962). This theory is based on the assumption of a trade-off among traits so that competitive ability and *r* cannot be maximized at the same time (MacArthur, 1962; Tilman, 1994; Kneitel & Chase, 2004). Without questioning this principle, modern theory of life-history evolution has complexified this view, showing that a low sensitivity of early-life stages to competition, not necessarily the absence of competition, was the key condition for the evolution of the so-called '*r*-traits' (Charlesworth, 1994; Mueller, 1997; Reznick *et al.*, 2002). With this limitation in mind, the historical conception that invaders should be good colonists still must rely on two assumptions: (1) invaded habitats are often unsaturated or otherwise resemble the habitats that favour *r*-traits in native ranges, and (2) invasion is limited by the ability to rapidly spread and grow in numbers in such habitats. Both assumptions have received some empirical support, although not completely

conclusive. Indeed, disturbed habitats seem more prone to invasions (Lozon & MacIsaac, 1997; see, however, Bruno *et al.*, 2004), and some comparisons between invaders and non-invasive related taxa highlight the role of traits typical of the so-called *r*-strategy (see Rejmanek, 1996 and references below). The best-known example is found in invasive conifers, in which several large-scale comparisons have revealed higher relative growth rate, smaller seed mass, shorter juvenile phase, and more frequent seed production in comparison to non-invasive species (Rejmanek & Richardson, 1996; Grotkopp *et al.*, 2002; Richardson & Rejmanek, 2004). Similarly, invasive populations of *Spartina alterniflora* show earlier and larger reproductive effort, higher investment into vegetative reproduction, and lower self-incompatibility than their congeners from the native range in common garden experiments (Davis, 2005). Note, however, that component traits, rather than the intrinsic rate of increase itself, have been used in such studies.

Apart from the need for more data, a more basic criticism of the *r*-strategy hypothesis is that different contexts are expected to favour different types of invaders, and no single combination of traits can be successful everywhere (Holdgate, 1986; Lodge, 1993; Mack *et al.*, 2000; Radford & Cousens, 2000; Facon *et al.*, 2004; Richardson & Pysek, 2006). Invasion depends on an interaction between a species' traits and characteristics of the recipient ecosystem (Byers, 2002; Thuiller *et al.*, 2006; see also the 'niche opportunity' concept in Shea & Chesson, 2002), especially the resident community (Shea & Chesson, 2002). A high intrinsic rate of increase by itself cannot impede invasion; however, if *r*-traits trade-off with traits important for the interaction with resident species, the relationship between invasive ability and *r* could be negative instead of positive. For example, the *r*-selected traits in the oyster *Crassostrea ariakensis* do not make it a good invader because they come with a low investment in defence and high susceptibility to predation by blue crabs (Bishop & Peterson, 2006).

Competition is an important component of the biotic environment of invasive species (Stachowicz & Tilman, 2005). Of course, examples of invaders with traits typical of colonists are often associated with either disturbed habitats (case of woody plants, Rejmanek, 1996) or previously empty habitats (mudflats invaded by *S. alterniflora* in the US Pacific coast; Davis, 2005). However, not all invasions happen in such contexts (Byers, 2002; Daehler, 2003; Evans, 2004). In contexts where competition occurs and is an important constraint on the demography of invasive species, one expects, based on trade-off theory (Kneitel & Chase, 2004), a negative relationship between *r* and invasive success. Such a context has recently been identified in a group of four species of polyphagous fruit flies (tephritids) now inhabiting the island of La Réunion (Duyck *et al.*, 2004a).

The family Tephritidae is well known for multiple invasions that pose important economic problems in fruit or vegetable crops in tropical and subtropical areas worldwide (Duyck *et al.*, 2004a). Historical records are available because of the economic importance of these species, and they are easy to rear under laboratory conditions. Four species of ecologically very similar tephritids now inhabit La Réunion, including an endemic species *Ceratitis catoirii* Guérin-Mèneville, and three others that have

successively invaded: *Ceratitis capitata* (Wiedemann) in 1939, *Ceratitis rosa* Karsch in 1955, and *Bactrocera zonata* (Saunders) in 1991. Each newly arrived species has partially excluded and/or displaced each other, and has become largely dominant over previous ones, at least in the lowlands (< 100 m a.s.l.), where the four species now coexist. An exception to this pattern is that *C. rosa* continues to be dominant in the highlands because the climate there is unsuitable for the other species (Duyck *et al.*, 2006b). Duyck *et al.* (2006a), studying larval exploitative competition in fruits and interference between adult females for access to laying sites, concluded that competitive interactions were hierarchically organized, with recently arrived species systematically dominant on previous ones. In the same study, natural densities and co-infection rates in field-collected fruits were such that interspecific competition must occur in the field as it did in the laboratory.

This system is a good opportunity to test our hypothesis of a negative relationship between invasivity and *r*-traits, not only because competition has been a major component of invasions (Duyck *et al.*, 2006a), but also because the species are similar enough, phylogenetically and ecologically, to provide meaningful comparisons of life-history traits and document potential trade-offs. We here use experiments in a common laboratory environment to establish the life tables of all four species (including both the intrinsic rate of increase and its component traits) and to test whether successive invaders are characterized by decreasing *r* (or component traits), as predicted by our hypothesis. Our approach does not contrast invaders vs. non-invasive related species as done in previous studies of the relationship between traits and invasiveness; instead we compare invaders to their competitors (endemic and introduced) because our previous studies have shown that competition was a strong limit to invasion in this system (Duyck *et al.*, 2004a). In such a context, what matters is the relative values of traits of the invader and its competitors rather than with external non-invasive species not involved in competition in the invaded area (Daehler, 2003; Vila & Weiner, 2004).

METHODS

Source material and rearing conditions for laboratory studies

We measured life-history traits under laboratory conditions. We used laboratory strains of *C. catoirii*, C. *capitata*, *C. rosa*, and *B. zonata*, initiated from fruit samples collected in La Réunion, and subsequently reared on artificial diets optimized for each studied species [composition in Duyck & Quilici (2002) and Duyck *et al.* (2004b)], for 30, 3, 51, and 6 generations, respectively. The populations were initiated with 50–100 individuals (*C. catoirii*) or 500–1000 individuals (other species) and later all maintained at several thousands of individuals per generation. Laboratory rearings were conducted at constant temperature (25 ± 1 °C) and photoperiod (L12:D12) supplemented by natural light to maintain twilight conditions (necessary for mating). The temperature of 25 °C was previously shown to be the most favourable for the four studied species (Duyck & Quilici, 2002; Duyck *et al.*, 2004b).

Adult life-history patterns

Thirty newly emerged male–female pairs (< 2 h) of each of all four species were each confined (1 pair per cage) in separate transparent plastic cages (1 L) aerated via meshed openings, in environmental chambers (25 ± 1 °C, 80 ± 10% RH, 4000 lux, L12:D12) (Strader, Pellouailles les Vignes, France). Flies had free access to a diet of sugar and enzymatic yeast hydrolysate (ICN Biomedical, Aurora, IL, USA), and a wet sponge was placed in a container as a water source. An orange table tennis ball (diameter 4 cm), cut in half, and pierced with 24 evenly spaced holes (418 ± 90 µm), containing a piece of mango fruit (*Mangifera indica* L.) and inserted in a plastic base of suitable diameter, was used as a substrate for egg laying. Each morning, new egg cups were placed in all 120 cages to record daily fecundity. On the following day, the number of eggs was counted and each egg cup was replaced to maintain the females in constant conditions, dead males were replaced by new ones from the same cohort. The procedure was repeated until the last female died.

Calculation and analysis of demographic parameters

Daily adult survival and fecundity were combined with previously published data on developmental times and survival rates of immature stages (egg, larvae, and pupae) in the same fly strains at 25 °C [Duyck & Quilici (2002) for *Ceratitis* spp. and Duyck *et al.* (2004b) for *B. zonata*] to compute demographic parameters following standard methods (Carey, 1982; Ebert, 1999). Immature age-specific survivorship rates were interpolated as in Carey (1982). Confidence intervals for demographic parameters were estimated as the 2.5 and 97.5 percentiles of a bootstrap distribution resampled 1000 times (Efron & Tibshirani, 1993; Caswell, 2001).

Daily fecundity curves were fitted by a log linear model with a Poisson error using GLIM software (Crawley, 1993). Fecundity was fitted as a seventh-order polynomial of age (log number of eggs = $b_0 + b_1 x + b_2 x^2 ... + b_7 x^7$), within each species separately. We chose polynomial functions because they are flexible and provide smooth fitted curves while they impose no constraint on the form of the curve. We dropped the higher-order terms (> 7) because including further terms did not yield a significant increase in goodness of fit in any species. In some species, the term x^7 was non-significant but we nevertheless included it in order to treat all species the same way. We tested for significant differences among species in timing and magnitude of fecundity using the change in deviance between two models: one in which all coefficients are free to vary among species, and one with a common set of coefficients for all species (*F*-test in analysis of deviance, Crawley, 1993). This allowed us to establish that species had significantly different overall fecundity patterns, i.e. polynomial fits do uncover significant differences among species. However, differences in polynomial coefficients have no simple interpretation, so the polynomial equations were used to extract several more informative quantities of interest. All polynomial curves showed a major peak followed by a progressive decrease in fecundity. We characterized these curves using the age at the major fecundity peak, its height, and the age interval during which fecundity exceeded half the peak value. Patterns of senescence in survival were analysed by fitting the Weibull mortality model (hazard function $h(t) = \lambda \alpha t^{\alpha-1}$) (Carey, 2001) using the software GLIM (Crawley, 1993). This formulation includes, as a special case ($\alpha = 1$), the basic exponential model. The senescence parameter (α) exceeds unity when mortality increases with age. Its significance was assessed by a likelihood-ratio test that compared the Weibull model with the exponential model (i.e. with the constraint $\alpha = 1$). To help interpretation, we also provide the mean life expectancy ($\mu = \lambda^{(1-\alpha)}$) and the time interval after which estimated mortality rates are doubled ($d = 2^{1/(1-\alpha)}$).

Egg size and pupal mass

Lengths of 50 randomly chosen eggs, collected from the stock colony ($N > 1000$), were measured for each species within 2 h of oviposition with the graduated graticule of a binocular microscope (× 32). Pupal masses were determined by individually weighing 160 young pupae (< 4 h old) from one cohort of larvae of each species with a precision balance (10^{-4} g). Differences in pupal mass and egg length among species were analysed by analysis of variance, after square-root transformation to ensure normality, and *post hoc* comparisons of means were performed using the Tukey HSD test (5% level of significance).

RESULTS

Data regarding immature development and survival have been obtained from earlier studies on the same strains [Duyck & Quilici (2002) for the three *Ceratitis* species and Duyck *et al.* (2004b) for *B. zonata*]. Pre-imaginal developmental times were significantly different among all species (ANOVA $F_{3,44} = 1799.5$, $P < 0.0001$, Table 1). However, the probability to survive to adulthood was much lower in *C. catoirii* than in the three invading species (ANOVA $F_{3,44} = 528.4$, $P < 0.0001$, Table 1). The four species had significantly different age–fecundity curves ($F_{24,4670} = 64.3$, $P < 0.0001$ by model simplification; all pairs of species are significantly different at $P < 0.0001$, Fig. 1). Knowing that our polynomials capture significant differences among species, and that all of them had a major fecundity peak early in reproductive life, we could use polynomial equations to extract the height, time, and duration of the fecundity peak. The three *Ceratitis* species began to oviposit 5–10 days after emergence, while *B. zonata* began oviposition 20 days after emergence but of the four, oviposited over a longer duration (Fig. 1 and Table 1). *Ceratitis capitata* and *C. rosa* showed similar egg-laying patterns, but the fecundity peak was higher and of shorter duration for *C. capitata* (Table 1). Temporal variation in fecundity of *C. catoirii* was similar to the two other *Ceratitis* spp. but with a very low maximum. Female survival curves decreased in a similar fashion for the four species until *c.* 40 days after emergence, after which, survivorship appeared to be higher in *B. zonata* (Fig. 1). The last females died after 82, 80, 95, and 126 days, respectively, for *C. catoirii*, *C. capitata*, *C. rosa*, and *B. zonata*. Weibull survival parameters were very similar for the three *Ceratitis* species. These three species senesce faster than
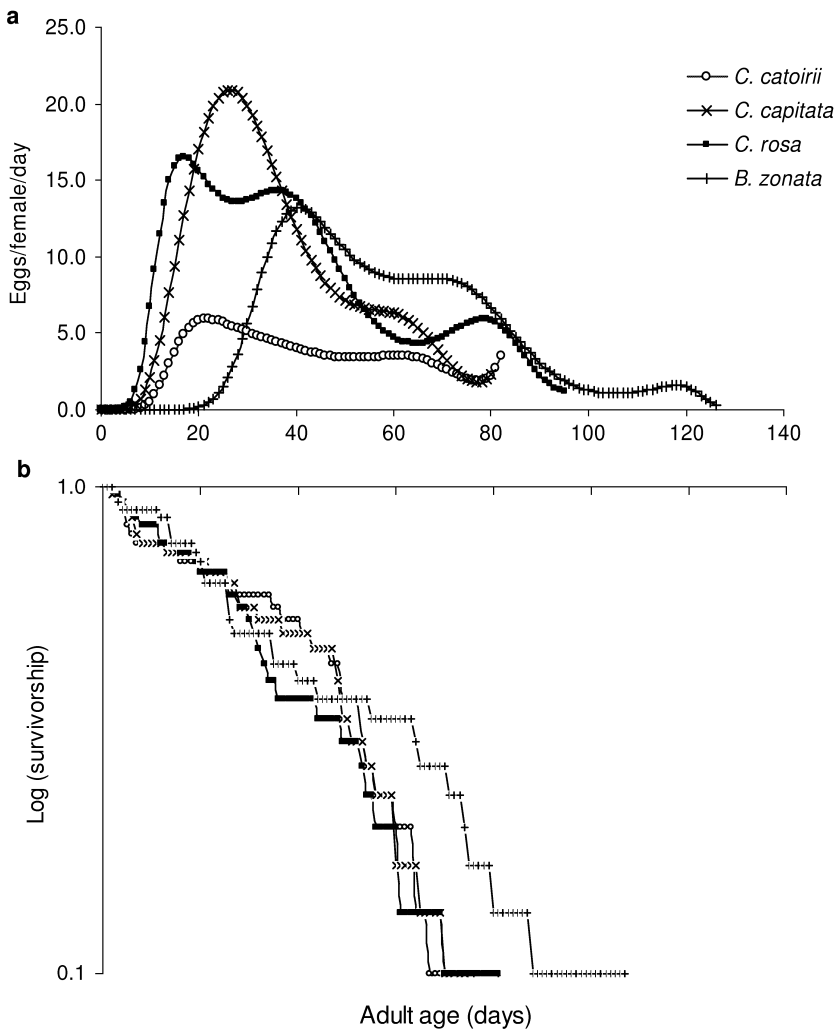
Figure 1 Fecundity and survival patterns in the four species. (a) Number of eggs laid per female per day. Fitted polynomial curves are given. In order to avoid extrapolation, each curve is stopped at the maximum age reached by experimental individuals. (b) Female survivorship of *Ceratitis catoirii*, *C. capitata*, *C. rosa* and *Bactrocera zonata*.

Table 1 Life tables of *Ceratitis catoirii*, *Ceratitis capitata*, *Ceratitis rosa*, and *Bactrocera zonata*. The *P*-value for the Weibull model is the significance of the senescence parameter (H0: $\alpha = 1$) tested by likelihood ratio. The doubling time of mortality is the age at which the death rate is twice its initial value. Cross at max/2 is defined as the two dates when the fecundity curve crosses the value of half maximum fecundity. Data regarding immature development and survival have been obtained from earlier studies on the same strains [Duyck & Quilici (2002) for the three *Ceratitis* species and Duyck *et al.* (2004b) for *B. zonata*] *Means in the same line with the same superscript letter are not significantly different at the 5% level (Tukey HSD).

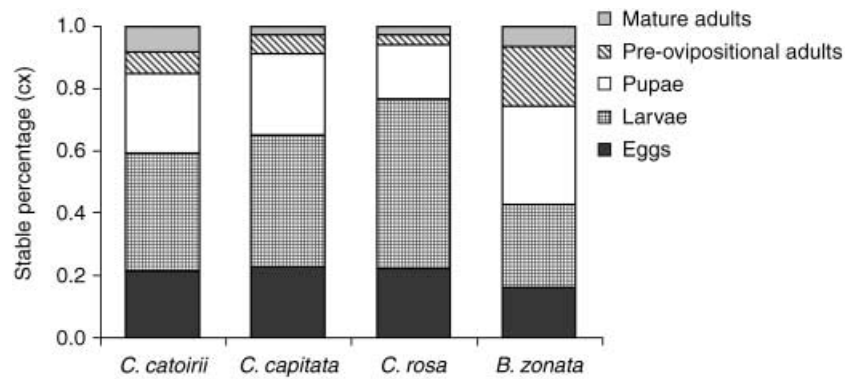| Parameters	C. catoirii	C. capitata	C. rosa	B. zonata
Date of invasion	Resident	1939	1955	1991
Probability to survive from egg to adult*	0.30[c]	0.73[ab]	0.75[a]	0.70[b]
Mean age at emergence (*d*)*	21.7[b]	18.4[c]	23.6[a]	17.1[d]
Fecundity parameters:				
Maximum fecundity (eggs/*d*)	5.9	20.9	16.6	13.2
Date of the maximum fecundity (*d*)	21.7	26.5	16.8	40.5
Cross at max/2 (*d*)	[13.9, 50.5]	[15.7, 41.9]	[10.6, 50.5]	[30.9, 80.2]
Parameters of the Weibull model:				
λ	0.006	0.004	0.005	0.008
α	1.366	1.485	1.422	1.265
μ	41.5	42.6	40.0	47.6
Doubling time of mortality (*d*)	6.6	4.2	5.2	13.7
Test: *P*-value	0.02	0.06	0.03	0.12

Figure 2 Expected stable age distribution of *Ceratitis catoirii*, *Ceratitis capitata*, *Ceratitis rosa* and *Bactrocera zonata*.

Table 2 Population parameters of *Ceratitis catoirii*, *Ceratitis capitata*, *Ceratitis rosa*, and *Bactrocera zonata*. 95% confidence intervals were obtained by bootstrap (see Methods). *Means in the same line with the same superscript letter are not significantly different at the 5% level (Tukey HSD).

Parameters	Units	*C. catoirii* value [95% CI]	*C. capitata* value [95% CI]	*C. rosa* value [95% CI]	*B. zonata* value [95% CI]
Gross reproductive rate (GRR)	Eggs/female	137.1 [85.2, 174.7]	344.5 [283.3, 405.7]	389.3 [222.6, 536.1]	303.0 [228.3, 367.9]
Net reproductive rate (R_0)	Eggs/female	18.2 [10.6, 25.8]	130.6 [87.5, 162.5]	128.4 [76.1, 177.7]	66.3 [33.7, 101.2]
Intrinsic rate of increase (r)		0.059 [0.048, 0.066]	0.115 [0.104, 0.123]	0.110 [0.097, 0.119]	0.069 [0.057, 0.077]
Intrinsic birth rate (b)		0.128 [0.117, 0.137]	0.121 [0.113, 0.128]	0.120 [0.109, 0.128]	0.096 [0.084, 0.104]
Intrinsic death rate (d)		−0.069 [−0.071, −0.067]	−0.006 [−0.009, −0.004]	−0.010 [−0.012, −0.009]	−0.027 [−0.030, −0.025]
Mean generation time (T)	Days	48.8 [46.3, 51.5]	42.3 [39.9, 44.9]	44.2 [41.8, 47.3]	60.6 [57.7, 64.8]
Average age in stable population ($\bar{a}$)	Days	9.8 [9.0, 10.9]	7.1 [6.6, 7.6]	7.6 [7.1, 8.4]	11.4 [10.5, 12.6]
Mean egg size ± SD*	mm	1.026 ± 0.032[a]	0.783 ± 0.025[c]	0.866 ± 0.038[b]	1.036 ± 0.041[a]
Pupal weight ± SD*	10^{-4} g	112 ± 14[b]	94 ± 9[d]	107 ± 12[c]	118 ± 13[a]

B. zonata, for which the senescence parameter is non-significant (Table 1). Similarly, the estimated doubling time of mortality was more than twice as long in *B. zonata* as in the other species.

Ceratitis capitata had the highest net reproductive rate followed by *C. rosa*, *B. zonata*, and *C. catoirii*, respectively (Table 2). Note that demographic parameters previously measured on *C. capitata* (Carey, 1982; Vargas *et al.*, 2000) were similar to our estimates. In our data, the intrinsic rate of increase was similar for *C. capitata* and *C. rosa*, both of which were significantly higher than that of *C. catoirii* and *B. zonata*. The latter species has a significantly longer mean generation time than the other species: 60.6 days compared to 48.8, 42.3, and 44.2 for *C. catoirii*, *C. capitata*, and *C. rosa*, respectively. Immature stages represent the largest part of the theoretical stable age distributions in all species (Fig. 2). However, while the expected proportion of adults was 8% and 6%, respectively, for *C. capitata* and *C. rosa*, it reached 15% in *C. catoirii* and 25% in *B. zonata* (mostly immature adults in the latter). Egg size (ANOVA $F_{3,196} = 665.3$, $P < 0.0001$) and pupal mass (ANOVA $F_{3,636} = 40.3$, $P < 0.0001$) were significantly different among the four species (Table 2). Egg size of *B. zonata* was similar to that of *C. catoirii* and significantly bigger than that of *C. rosa*, itself significantly bigger than that of *C. capitata* (Table 2; Fig. 3). Pupal mass followed the same pattern (except that pupae of *C. catoirii* were significantly lighter than those of *B. zonata*).
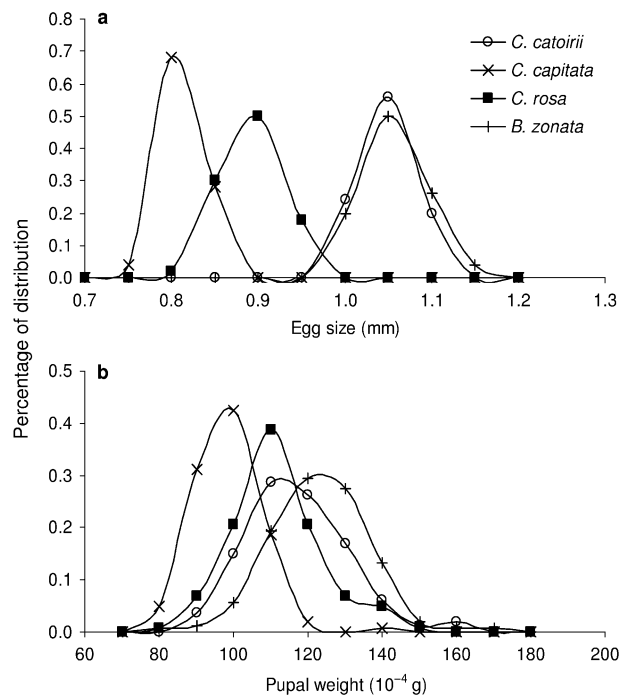

Figure 3 (a) Distributions of egg size (classes of 0.05 mm) and (b) pupal weight (classes of 1 mg) of *Ceratitis catoirii*, *C. capitata*, *C. rosa* and *Bactrocera zonata*.

DISCUSSION

Life histories of tephritid species and trade-offs

The life-history profiles of the three species *B. zonata*, *C. capitata*, and *C. rosa* seem consistent with the idea of a trade-off between traits favouring biomass accumulation and persistence and traits favouring the rapid production of many offspring. The major contrast lies between *B. zonata* and the *Ceratitis* spp., as the former has higher survival and longer duration of the reproductive period, while the other two have higher fecundity and earlier (but shorter) reproduction. Other trade-offs are apparent between the number of offspring on one hand, and both the investment per offspring (as measured by egg size) and the growth (reflected by pupal mass) on the other. These trade-offs are consistent not only with the comparison between *Bactrocera* and *Ceratitis*, but also, to a lesser extent, between *C. capitata* and *C. rosa*. Indeed, *C. capitata* has higher maximum fecundity and shorter pre-imaginal development, but smaller eggs and smaller pupae than *C. rosa*. The latter invests more in each offspring (larger egg size) and pre-imaginal growth, reaching larger pupal masses at the expense of a longer pre-imaginal development. As expected, the intrinsic rates of increase (r) under optimal laboratory conditions are in the order *B. zonata* < *C. rosa* < *C. capitata*, the most pronounced contrast (and the only significant one, i.e. non-overlapping confidence intervals in Table 2) being between the first two. In consistency with the competition–colonization and/or r–K trade-off theory (Pianka, 1970; Tilman, 1994), this pattern is the opposite of the competitive hierarchy for these three species (*B. zonata* > *C. rosa* > *C. capitata*, in which, again, the largest contrast occurred between *B. zonata* and the other two; Duyck *et al.*, 2006a).

In contrast, the combination of traits of *C. catoirii*, compared to the other three species, does not support the hypothesis of an interspecific trade-off. Basically *C. catoirii* does not counterbalance its low fecundity by a high survivorship. Although the decreased fecundity and large eggs of *C. catoirii* (as in *B. zonata*) are consistent with a trade-off between quantity and quality of offspring, this large investment per offspring does not seem to provide any advantage, as its mortality during the pre-adult stages is extremely high compared to the other three species. As a consequence, its intrinsic rate of increase under laboratory conditions (r) is approximately half that of the other *Ceratitis* species. Competition experiments have shown that this species is also the poorest competitor of all four species studied (Duyck *et al.*, 2006a). In short, this species is neither a good competitor nor a good colonist.

The differential age of the colonies of the different species may have affected the recorded life-history traits. However, genetic drift and inbreeding have been minimized in all colonies as they were maintained from the beginning using many individuals. Differential adaptation to laboratory conditions could also affect life-history traits. However, this hypothesis predicts that fitness traits would be higher in species cultured in the laboratory for more generations, which is not observed. For example, *C. catoirii* has distinctly lower values for many fitness traits although it is the oldest colony in our laboratory. Finally, another study on

C. capitata (Muniz, 1987) showed no significant differences in demographic parameters between an old laboratory colony (reared for 19 years) and a field population, suggesting limited effects of adaptation to laboratory conditions.

The imperfect trade-off observed in this study, even between phylogenetically closely related species, is not surprising since perfect trade-offs are the exception rather than the rule in the literature (Stearns, 1992; Reznick *et al.*, 2002; Kneitel & Chase, 2004). Two main causes are traditionally cited for imperfect trade-offs between two traits (Van Noordwijk & Dejong, 1986; Stearns, 1992): first, species may differ by the total amount of resources they are able to extract from the environment rather than by relative allocation to different traits; second, energy may be diverted towards a third trait rather than shared among the two considered. Why the Mascarenes endemic *C. catoirii* does not follow the trade-off common to the three recent invaders remains hypothetical. Anthropogenic influences are relatively recent in La Réunion (four centuries), and populations of *C. catoirii* used to depend on resources from the natural forest habitat in pre-human times. It could invest in some form of specialization to this natural habitat that confers no benefit under 'optimal' laboratory conditions and secondary habitats. This is a mere hypothesis that remains to be tested. More generally, an important caveat for laboratory experiments is that life-history traits and competitive ranks may change depending on conditions, and that actual laboratory conditions may not be optimal for all species. In our case, however, laboratory diets have been optimized for each species, and larval development rates in these diets are better than in the best natural fruits tested to date (P. F. Duyck, unpublished data). Laboratory temperature (25 °C) is also optimal for all four species although *C. rosa* is clearly more cold-tolerant (see Duyck & Quilici, 2002; Duyck *et al.*, 2004b). We are therefore confident that our laboratory conditions are at least very favourable — if not truly optimal — for all species studied.

However, whatever the causes, *C. catoirii* is inferior to the other three species in terms of both colonizing and competitive ability. *Ceratitis catoirii* used to be abundant in cultivated habitats in La Réunion before the arrival of the other species (Orian & Moutia, 1960). Following invasions of *C. capitata*, *C. rosa*, and *B. zonata*, *C. catoirii* has declined and is now very rare in La Réunion, and it has completely disappeared from Mauritius, where the same invasive tephritids have been introduced (Duyck *et al.*, 2006a). All this strongly suggests a case of competitive exclusion.

Competitive ability, traits, and invasion ranks

Based on comparisons between life-history data (this study) and competition data (Duyck *et al.*, 2006a), we can try to identify traits associated with competitive ability. Among the three exotic invasive species, size seems to be a major determinant of competition. Egg size influences larval competition: bigger eggs can reduce larval developmental times and thus confer a resource consumption advantage. This classical pre-emptive effect (Krijger *et al.*, 2001) was observed in our previous work (Duyck *et al.*, 2006a) in the form of relationships between pupal mass and developmental time, both at the interspecific and at the intraspecific

levels: late-emerging pupae were smaller because faster-developing ones had already depleted the resource. Among the three invasive species, a larger adult size also seems to confer an advantage in females competing for ovipositional sites in the same fruit, as pupal size ranks correspond to dominance ranks in interspecific contests among such females (Duyck *et al.*, 2006a). However, size is certainly not the only determinant of competition when considering the endemic species *C. catoirii*. This species lays large eggs, but is dominated by all others in larval competition, owing to a much higher larval mortality. Similarly, its large adult size is not associated to aggressive behaviour in interference contests, during which this species is systematically displaced by all others (Duyck *et al.*, 2006a).

The common hypothesis that successful invaders are often *r*-strategists (Lodge, 1993; Rejmanek & Richardson, 1996) depends on the assumption that competition is not a limiting factor for invasion. This is probably true in many — if not a majority — of cases, when invasions occur in disturbed habitats (Rejmanek, 1996; Lozon & MacIsaac, 1997; Lonsdale, 1999) or habitats devoid of species phylogenetically and/or ecologically similar to the invader. However, with the worldwide increase in the frequency of invasions, the probability that related taxa be introduced successively in the same place increases (Mack *et al.*, 2000; Mooney & Cleland, 2001). In this case, invasion may ultimately depend on the ability to outcompete, or at least to resist competition exerted by, resident species. In line with this hypothesis, in our system, as a result of trade-offs, the intrinsic rate of increase (*r*) decreases in successive invaders, while competition ability increases. In contradiction with this trend, the endemic *C. catoirii*, a species with very low *r*, was excluded by the three other species. This is not inconsistent with the hypothesis that invasions were competition-limited, as this species has the lowest competitive ability. However, it illustrates the fact that our hypothesis will only apply as far as trade-offs are respected, as the decrease in *r* is entirely dependent on its negative correlation with competitive ability.

Could our hypothesis apply to other cases of invasion in the presence of related or similar resident species? In Hawaii, the introduced *Bactrocera dorsalis* (Hendel) largely displaced *C. capitata*, a previously established invader (Debach, 1966). Vargas *et al.* (2000) found that despite a relatively high fecundity, *B. dorsalis* shows a lower intrinsic rate of increase, a bigger size, a delayed onset of oviposition, and a longer life span compared to *C. capitata*. These authors conclude that *B. dorsalis* is less *r*-strategist than *C. capitata*, in agreement with our results. In general, the whole genus *Bactrocera* has a more *K*-orientated profile than *Ceratitis*, which would explain why the former has often displaced the latter during recent invasions, but not the reverse (Duyck *et al.*, 2004a). Such situations are not restricted to tephritid flies however: studying inter-tidal snails, Byers (2000) suggested that competitive ability could be an important characteristic of biological invaders, as did Evans (2004) studying ladybirds, and Vila & Weiner (2004) reached the same conclusion based on a review of competition experiments between resident and invasive plants. Facon *et al.* (2006) also predicted successive waves of invasions by ever-better competitors into the same niche.

Fruit flies in La Réunion are an example of a system in which life-history traits can confer competitive advantages for invading species, though we are not attempting to express a general paradigm applicable to any other system. Yet we believe that these observations should serve as a motivating example of how details of natural history can influence species invasiveness. Obviously, studying four species cannot provide evidence for a general negative relationship between *r* and invasiveness. However, the limits of our data themselves suggest interesting ways of treating data sets so as to tackle the heterogeneity of invasion cases, frequently cited as the main cause of the scarcity of conclusive results in studies of relationships between traits and invasiveness (Holdgate, 1986; Lodge, 1993; Lonsdale, 1999; Kolar & Lodge, 2001; Facon *et al.*, 2004; Richardson & Pysek, 2006). First, invasions in the absence of likely strong competitors, for example, a predator in an island devoid of predators (Fritts & Rodda, 1998), or *Spartina* in bare mudflats (Davis, 2005), should be distinguished from invasions in the presence of competitors. A possible surrogate, in the absence of competition data, could be the absence or presence of related resident species with similar ecology. Rejmanek (1996) mentioned the fact that 'alien species belonging to exotic genera are more likely to be invasive than alien species from genera represented in the native flora'. This suggests that related residents pose a competitive limit to invasion, and that different mechanisms may underlie invasions in which exotics have to overcome this limit, and those in which they do no have to do so. An important caveat, however, is that the degree of phylogenetic conservation of niche traits seem rather variable among taxa (see the review of Webb *et al.*, 2002) and that other conserved aspects (for example, parasite or enemy assemblages) may be more important than resource overlap and competition in shaping interactions between newly co-occurring congeneric species.

Second, in the case of invasion in the presence of resident competitors, both invasiveness and traits should be considered relative to residents rather than in absolute terms (see Daehler, 2003). For example, *C. capitata* was once invasive in the presence of *C. catoirii* alone, but is no longer invasive in La Réunion since the better competitors *B. zonata* and *C. rosa* arrived. Similarly, in our case, the trait values of the invader are less relevant than the differences between invader and previously established species (e.g. larger pupae or larger eggs relative to residents provide higher competitive ability and trigger invasion).

The last suggestion from our work is to distinguish direct predictions (e.g. *r*-traits are favourable to colonization in non-competitive contexts) from predictions mediated by a trade-off (*r*-traits should be negatively correlated with invasion in competitive contexts); the latter, not the former, will depend on how well the assumed trade-off applies to the set of taxa studied, which can be measured directly, as in our Tephritid example.

In conclusion, neither *r* nor *K* strategies are likely to be important for invasions in general. In some groups, such as conifers (Rejmanek & Richardson, 1996), invaders have more *r*-orientated traits than non-invaders. It would be interesting to see whether the majority of conifer invasions happened in the absence of related species and/or in relatively non-competitive habitats, as suggested by the fact that many *Pinus* invasive species are

opportunistic and abundant in disturbed habitats rather than in mature forest (Grotkopp *et al.*, 2002). In addition, for invasions that happen in the presence of competitors, invaders may be at the same time better competitors (and worse colonists) than resident species, and better colonists than other potential invaders. Among those candidate invasive species that can overcome competition with residents, the first to invade may indeed be the better colonists. If our conclusions are confirmed by further studies, this framework could provide an important tool in Pest Risk Analysis for the prediction of potential invaders as a function of established regional communities, in addition to the use of measures of environmental suitability of regions to target species (e.g. climatic matching).

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