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Invasive Phytophagous Pests Arising Through a Recent Tropical Evolutionary Radiation: THE *BACTROCERA DORSALIS* COMPLEX OF FRUIT FLIES

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■ **Abstract** The *Bactrocera dorsalis* complex of tropical fruit flies (Diptera: Tephritidae: Dacinae) contains 75 described species, largely endemic to South-east Asia. Within the complex are a small number of polyphagous pests of international significance, including *B. dorsalis* s.s., *B. papayae*, *B. carambolae* and *B. philippinensis*. The majority of species within the complex were first described in 1994 and since then substantial research has been undertaken in developing morphological and molecular diagnostic techniques for their recognition. Such techniques can now resolve most taxa adequately. Genetic evidence suggests that the complex has evolved in only the last few million years and development of a phylogeny of the group is considered a high priority to provide a framework for future evolutionary and ecological studies. As model systems, mating studies on *B. dorsalis* s.s. and *B. cacuminata* have substantially advanced our understanding of insect use of plant-derived chemicals for mating, but such studies have not been applied to help resolve the limits of biological species within the complex. Although commonly regarded as major pests, we note that there is very little published evidence documenting economic losses caused by flies of the *B. dorsalis* complex. Quantification of economic losses caused by *B. dorsalis* complex species is urgently needed to prioritise research for quarantine and management. Although documented invaders, relatively little work has been done on the invasion biology of the complex and this is a further area warranting work.

CONTENTS

INTRODUCTION 3
TAXONOMY, SYSTEMATICS AND DIAGNOSTICS 6
Complex diagnosis and taxonomic history 6
Diagnostic tools 8
<i>Non-genetic diagnostic tools</i> 8
<i>Genetic diagnostic tools</i> 9
Evolutionary history12
ECOLOGY13
Adult resources and mating systems14
Larval host range16
PEST STATUS AND INVASION BIOLOGY18
Pest status in South-east Asia18
Invasion biology22
CONCLUSIONS24
Systematics and evolutionary history24
Pest status26
ACKNOWLEDGEMENTS27
REFERENCES28

INTRODUCTION

Dacine fruit flies (Diptera: Tephritidae: Dacinae) are one of the key pest groups of Asia and the Pacific (126, 127), with the larval stages being frugivorous on a wide range of fruits and vegetables (3). Direct fruit damage, fruit drop and loss of export markets through quarantine restrictions are all mechanisms by which fruit fly infestation causes economic loss. With adult traits that include high mobility and dispersive powers, high fecundity and, in some species, extreme polyphagy, dacines are well documented invaders and rank high on quarantine target lists. Reviews of the general biology, ecology and pest status of the dacine fruit flies can be found in a variety of sources (13, 18, 35, 91, 132, 136).

One decade ago, in a seminal taxonomic revision, Drew and Hancock (26) described 40 new species within the *Bactrocera dorsalis* complex of tropical fruit flies. *Bactrocera dorsalis sensu lato* had long been recognised as the most pestiferous, polyphagous and widespread species within a group of morphologically similar, but generally non-pestiferous dacine fruit flies (23, 44). However, the 1994 revision was critical in that *B. dorsalis sensu stricto* was redescribed and multiple sibling species existing under that name were recognised. Most notable among the newly described species was a small group of pest species, *B. papayae* Drew & Hancock, *B. philippinensis* Drew & Hancock and *B. carambolae* Drew & Hancock. Each of these species has a different geographic and host range to *B. dorsalis s. s.* While description of the new species was carried out using traditional morphological features (26), their recognition as separate biological units was based on a suite of evidence including allozyme, geographic, host range and pheromonal differences (26, 88, 90). These pest species, along with a number of non-pest species, form a sibling group within the *B. dorsalis* complex and their discrimination based on morphological criteria alone is extremely difficult.

Incursions of flies of the *B. dorsalis* complex into Australia, central America, mainland USA and Oceania, with resultant direct and indirect costs running into hundreds of millions of dollars, have kept the complex at the forefront of applied and quarantine research over the last decade. Because of their economic importance, much of the research on the complex has tended to be pragmatic, focusing on diagnostics (2, 50, 60, 78), quarantine (36, 56, 57, 83) and eradication (67, 101, 119, 129). Formal systematics on the complex has been limited, although new species have been described (116), or recognised based on cytogenetic grounds (10, 11). Pest management, behavioural and related work has tended, by its nature, to concentrate on individual species within the complex, with the extensive work on *B. dorsalis* in Hawaii (eg 105, 119, 120) and in Taiwan (eg 61, 62) being excellent examples.

It is not our intent to review here all research undertaken on species belonging to the *B. dorsalis* complex. Compilations in recent publications (4, 5, 113, 115) offer a lead into much of the dacine literature, which in turn covers much of the *B. dorsalis* complex. Rather, this review will focus on studies which simultaneously treat multiple species within the complex (eg biogeography, systematics and diagnostics), biological studies which allow cross-species comparisons (eg mating and resource utilization studies) and areas where recognition of the complex in 1994 has significantly impacted on subsequent research aimed at managing the flies (eg invasion biology). We also include a section on the pest status of the complex within South-east Asia, its indigenous range, an issue which has received insufficient attention when trying to interpret the risk posed by the complex as potential invaders.

TAXONOMY, SYSTEMATICS AND DIAGNOSTICS

The *B. dorsalis* complex was originally defined to contain 16 species closely related to *B. dorsalis* (44). Since the early 1980's a number of additional species have been described, beginning with *B. opiliae* in 1981 (27). The *B. dorsalis* species complex was redefined (23) and expanded (26), and now contains 75 described species (Table 1), with undescribed species remaining in collections (60). The complex shows its greatest diversity in the islands of the Indonesian Archipelago. To the east of Wallace's line the diversity of *B. dorsalis* complex species rapidly declines such that Australia, with the World's second most diverse *Bactrocera* fauna, contains only three endemic *B. dorsalis* complex species. Similarly the complex becomes rapidly less diverse moving into Asia, with only two species endemic to India.

Complex diagnosis and taxonomic history

Originally defined by Hardy (44), the *B. dorsalis* complex was redefined as one of 20 species complexes in the subgenus *Bactrocera* of the genus *Bactrocera* (23, 26). A contemporary morphological diagnosis of the complex is as follows: species with a clear wing membrane except for a narrow costal band not reaching R_{4+5} and a narrow anal streak, costal cells colourless or pale yellow-brown and without dense microtrichia, lateral postsutural vittae present but medial postsutural vittae absent, scutellum mostly yellow with a narrow brown basal band, scutum mostly black, abdominal terga 3-5 with a median longitudinal dark band and variable dark patterns on lateral margins (23, 26). Male flies of the complex are attracted to methyl eugenol or cue lure, plus a significant percentage have no known lure response (Table 1).

Table 1: *Bactrocera* species currently considered as belonging to the *B. dorsalis* complex of tropical fruit flies (23, 26, 28, 60, 116).

Species ^a	Location ^b	Host Range			Economic	Lure
		Family	Genera	Species		
<i>B. abdolonginqua</i> (Drew)	l	-				ME
<i>B. aemula</i> Drew	l	-				CUE
<i>B. affinidorsalis</i> (Hardy)	g, m	-				CUE
<i>B. arecae</i> (H&A)	a, i, n, q	1	2	3		-
<i>B. atrifemur</i> D&H	i	1	1	1		ME
<i>B. bimaculata</i> D&H	g, r	-				CUE
<i>B. cacuminata</i> (Hering)	a	6	7	8		ME
<i>B. carambolae</i> D&H	c, f, g, i, n, q, r	27	50	77	*	ME
<i>B. caryeae</i> (Kapoor)	f, o	7	8	10	*	ME
<i>B. ceylanica</i> T&W	o	-				CUE
<i>B. cibodasae</i> Drew	g, r	-				CUE
<i>B. cognata</i> (H&A)	m	1	1	1		-
<i>B. collita</i> D&H	m	-				ME
<i>B. consectorata</i> Drew	l	-				CUE
<i>B. dapsiles</i> Drew	l	1	1	1		ME
<i>B. diallagma</i> Drew	l	-				ME
<i>B. dorsalis</i> (Hendel)	b, d, e, f, j, k, n, o, p, r	42	79	124	*	ME
<i>B. dorsaloides</i> (H&A)	m	1	2	3		-
<i>B. endiandrae</i> (Perkins & May)	a, l	7	10	24		ME
<i>B. fernandoi</i> T&W	o	-				CUE
<i>B. floresiae</i> D&H	g	-				ME
<i>B. fuliginus</i> (D&H)	a, l	-				CUE
<i>B. fulvifemur</i> D&H	m	-				CUE
<i>B. fuscitibia</i> D&H	g, j, r	-				CUE
<i>B. gombokensis</i> D&H	j, r	-				CUE
<i>B. hantanae</i> T&W	o	-				CUE
<i>B. holtmanni</i> (Hardy)	j, m, r	-				CUE
<i>B. inconstans</i> Drew	l	-				CUE
<i>B. indecora</i> (Drew)	l	-				CUE
<i>B. indonesiae</i> D&H	g	-				ME
<i>B. infulata</i> D&H	g, i	-				ME
<i>B. involuta</i> (Hardy)	g	-				-
<i>B. irvingiae</i> D&H	q	3	3	3		-
<i>B. kanchanaburi</i> D&H	q, r	1	2	2		-
<i>B. kandiensis</i> D&H	o	13	16	22	*	ME
<i>B. kinabalu</i> D&H	i	1	1	1		CUE
<i>B. lateritaenia</i> D&H	i, r	-				CUE
<i>B. laticosta</i> Drew	l	-				CUE
<i>B. latilineola</i> D&H	i	-				ME
<i>B. lombokensis</i> D&H	g, i, r	-				CUE
<i>B. makilingensis</i> D&H	m	-				CUE
<i>B. malaysiensis</i> D&H	j	-				CUE
<i>B. melastomatos</i> D&H	f, i, n, q	1	1	2		CUE
<i>B. merapiensis</i> D&H	g	-				CUE
<i>B. mimulus</i> Drew	l	-				ME
<i>B. minuscula</i> D&H	g	-				ME
<i>B. muii</i> (H&A)	g	-				-

<i>B. neocognata</i> D&H	g, i	-				CUE
<i>B. neopropinqua</i> D&H	m	-				-
<i>B. nigrescens</i> (Drew)	l	-				ME
<i>B. occipitalis</i> (Bezzi)	c, i, m	3	3	3	*	ME
<i>B. opiliae</i> (Drew & Hardy)	a	4	4	4		ME
<i>B. osbeckiae</i> D&H	q, r	1	3	7		-
<i>B. papayae</i> D&H	a, g, i, l, n, q	51	117	209	*	ME
<i>B. paraverbascifoliae</i> Drew	f	-				ME
<i>B. pedestris</i> (Bezzi)	g, m	-				CUE
<i>B. penecognata</i> D&H	g	-				CUE
<i>B. philippinensis</i> D&H	m	5	5	6	*	ME
<i>B. profunda</i> T&W	o	-				CUE
<i>B. propinqua</i> (H&A)	d, g, i, n, q, r	1	1	9		CUE
<i>B. pyrifoliae</i> D&H	q, r	5	6	7	*	-
<i>B. quasipropinqua</i> D&H	m	1	2	2		-
<i>B. raiensis</i> D&H	q, r	4	4	5		-
<i>B. selenophora</i> T&W	o	-				CUE
<i>B. sembaliensis</i> D&H	g	-				CUE
<i>B. sulawesiae</i> D&H	g	-				ME
<i>B. sumbawaensis</i> D&H	g	-				CUE
<i>B. syzygii</i> T&W	o	1	1	1		-
<i>B. thailandica</i> D&H	q, r	1	1	1		-
<i>B. trivialis</i> (Drew)	a, l	4	4	4	*	CUE
<i>B. unimacula</i> D&H	g, i	-				ME
<i>B. usitata</i> D&H	i, m, n, r	-				CUE
<i>B. verbascifoliae</i> D&H	f, q, r	1	1	5		ME
<i>B. vishnu</i> D&H	f	-				CUE
<i>B. vulgaris</i> (Drew)	a, l	-				CUE
<i>B. amarambalensis</i> Drew ^c	f	-				ME
<i>B. neoarecae</i> Drew ^c	f	-				ME

^aAuthors: H&A =Hardy & Adachi; D&H = Drew & Hancock; T&W = Tsuruta & White

^bLocation only includes countries within each species' natural range. *Country Codes*: a, Australia; b, Bhutan; c, Brunei; d, Cambodia; e, China; f, India; g, Indonesia; h, Laos; i, Malaysia; j, Myanmar; k, Nepal; l, Papua New Guinea; m, Philippines; n, Singapore; o, Sri Lanka; p, Taiwan; q, Thailand; r, Vietnam

^cThese species fit the description of the *B. dorsalis* complex and are morphologically similar to other *B. dorsalis* complex species, however, they have not officially been placed within the complex (28): in this paper they are not treated as part of the complex.

As defined by Drew (23), in addition to *B. dorsalis*, the complex in 1989 contained the following eight species from the Australasian and Oceanian regions: *B. abdolonginqua* (Drew), *B. cacuminata* (Hering), *B. dapsiles* (Drew), *B. diallagma* (Drew), *B. endiandrae* (Perkins and May), *B. mimulus* (Drew), *B. nigrescens* (Drew), *B. opiliae* (Drew and Hardy), all responding to methyl eugenol. When the *B. dorsalis* complex from Asia was revised a few years later (26), the definition of the group was expanded to include eight species from the *B. aemula* species complex of Drew (23), and numerous new species were described from Asia bringing the total to 68 species in Asia and Oceania. Concurrent with the addition of new species to the complex, a number of species originally included in

the complex by Hardy (44) were removed (*B. bryoniae*, *B. breviaculeus*, *B. mayi*, *B. moluccensis*, *B. rutilus* (23); *B. limbifera*, *B. luzonae* (26)) as the taxonomic scope of the complex was narrowed. Within the last four years, six new species belonging to the complex have been described from Sri Lanka (116) and one from India (28), bringing the total number of species to 75 (Table 1). Thirty-five species respond to cue lure, 26 species respond to methyl eugenol and 14 species have no known lure response. Identification of species in the complex is complicated because not all species are treated within a single key (26). This complication has been partly overcome with the development of an interactive, computer-based key to 68 species in the complex (60), while a similar key has been produced for the identification of Indo-Australasian dacine fruit flies as a whole (133). However, the six Sri Lankan members of the complex and *B. paraverbascifoliae* (from India) are still keyed separately (28, 116).

Diagnostic tools

Uncertainty in species limits based on the traditionally used adult morphological features, together with overlapping host and geographic ranges, impacts significantly on quarantine, pest management and general biological study. Accurate identification is essential for species found in fruit destined for export, for distinguishing exotic from native fauna and for providing crucial data on risk and invasion pathways. Frequently such identifications involve immature life stages, for which there are few morphologically distinguishable characters (132). Given these problems, significant effort has been spent in developing diagnostic tools for species within the complex since 1994.

Non-genetic diagnostic tools

Species belonging to the *B. dorsalis* complex are morphologically very similar, with species-specific diagnostic characters found in relatively minor variation in the colour patterns on the wings, thorax, legs and abdominal tergites (60). Large samples of flies, available from surveys using male lure traps or fruit rearing, reveal that many of these diagnostic characters are variable at species level and intermediates that span the morphological space between distinct species are found at non-trivial frequencies.

Discriminant analyses using wing morphometrics can reliably distinguish (90% or greater correct) between small subsets of species from Sri Lanka and Thailand (2), although the performance of these diagnostics is likely to be reduced when discrimination is attempted between a larger number of species in the complex. Increasingly the shape and ornamentation of the ovipositor is used as a taxonomic character system for distinguishing species of the complex (23, 26, 27). More recently the length of the male aedeagus has also been used as a diagnostic feature at species level in this group (50, 54). Aedeagal length and length of the female ovipositor are significantly correlated in many *Bactrocera* species (53, 54, 131), due to the mechanics of mating, and these data provide a useful diagnostic for sympatric pest species of the *B. dorsalis* complex in Asia (50-52). Cuticular hydrocarbon analysis has also been found useful for distinguishing between two species of the complex from Malaysia (37).

Computer-based, multi-access keys (60, 133) have gone a substantial way to resolving the problems of traditional dichotomous keys for flies of the *B. dorsalis* complex, as they have for many other taxa. Decision paths can be optimised dynamically, allowing the most discriminative character to be used at each step and thus minimising the number of decisions needed to reach an identification. Additionally, variation in character states can be accounted for in key development and can be more completely illustrated. However,

the available keys are still only suitable for identification of adult specimens in good condition. This has driven the exploration of other character systems for more reliable diagnostics, particularly of the larval stages.

Genetic diagnostic tools

Exploitation of genetic markers has been prompted largely through the frustration of not being able to confidently distinguish, morphologically, between the pest species *B. dorsalis*, *B. carambolae*, *B. papayae* and *B. philippinensis*. Genetic approaches also provide stable characters for the identification of immature life stages and an alternative tool for routine identifications that avoids adding to the strain on expert taxonomists (130). Larval polytene chromosome differences (38) and metaphase karyotypes (10-12) have been used to distinguish *Bactrocera* species, including *B. dorsalis*. Electrophoretic data was used initially with limited success to distinguish between five species of the *dorsalis* complex, with *B. dorsalis*, *B. carambolae* and *B. papayae* lacking any species-specific alleles or loci (134). However, more success in finding species-specific differences has been subsequently reported between these species and *B. occipitalis* and *B. philippinensis* (65). Neither karyotyping nor allozyme electrophoresis are suitable for routine diagnostic testing, being compromised by the need for reasonable amounts of good quality tissue and allozyme analyses being vulnerable to differential expression of enzymes at different life stages and under different environmental conditions. DNA markers, however, are not restricted in this way and a number of diagnostic procedures have emerged.

The first report of DNA markers used probes from genomic extracts to hybridise to anonymous repetitive DNA of *B. dorsalis*, *B. cucurbitae* and *Ceratitidis capitata* (47). As a squash blot method it was proposed to be a simple, rapid and reliable method of distinguishing any life stage of these species and ideal for border quarantine application. However, it would be complicated to use for distinction of any more than a few species and has not been developed further.

Polymerase chain reaction (PCR) based technologies offer more flexibility and a number of tests using PCR-RFLP (restriction fragment length polymorphism) analysis have been described for the most pestiferous species. Early methods targeting nuclear ribosomal DNA regions, 18S+ITS1 (8, 9) and ITS1 and ITS2 (68), are still used routinely within quarantine procedures to identify larvae and eggs of tephritids intercepted at the New Zealand and Australian borders, respectively. Both methods can reliably distinguish *B. carambolae* from *B. dorsalis* s.s. The latter method (ITS1 and ITS2) uses a more complicated series of primer sets with restriction analyses, but has the added benefit of being able to distinguish *B. dorsalis* s.s. from *B. papayae* and *B. philippinensis* as well as the Australian *B. dorsalis* complex species, *B. opiliae*, *B. cacuminata* and *B. endiandrae*. Neither of the two approaches can distinguish *B. papayae* and *B. philippinensis*. No population-level variation in the restriction patterns for 18S+ITS1 has been observed for morphologically confirmed species (8).

Other DNA based methods targeting mitochondrial DNA D-loop+12S (80, 82) and 16S (77, 78, 81) gene regions appear to have greater resolution, such that the species *B. dorsalis*, *B. papayae*, *B. philippinensis*, *B. carambolae*, *B. occipitalis* and *B. kandiensis*, can all be distinguished. This was validated using 83 individuals across 18 *Bactrocera* species, but, in contrast to the nuclear DNA methods above, population-level variation was observed for four of those species (78). As restriction pattern variation occurs in only some of the 16S sections (I-IV) amplified, incorrect identification can be avoided through

choice of amplicon and restriction enzyme. Of note, however, was a difficulty discriminating between *B. papayae* and the majority of *B. carambolae* individuals, although PCR-RFLP of the nuclear ITS region found the haplotype to be specific for *B. carambolae* (78).

Most recently, an original test based on EPIC (exon primed intron crossing)-RFLP of muscle actin to differentiate *B. dorsalis* s.s. populations (48) has been developed into a microarray-based test that can distinguish *B. dorsalis*, *B. papayae* and *B. carambolae* (79). Allele-specific 50-mer oligonucleotides, designed from the intron sequences of each species, are hybridised to the EPIC PCR product. The detection of heterozygote individuals and intra-specific variation suggest that this is a rapid and reliable means of documenting both the species and population genotype. However, the test is anticipated to be unable to discriminate species where alleles are shared and, as in all the other tests, highlights the need for several loci to be incorporated into any one diagnostic procedure.

There is no molecular test to date that is designed to identify each of the nine Asian pest species, with *B. caryae* and *B. pyrifoliae* not included in any studies. A more comprehensive test, comprising more than one gene region and more taxa within the complex, is clearly required. Further development of the oligonucleotide microarray format (79) could go some way towards this. Nonetheless, a reference nucleotide sequence database is essential to underpin this or any other advance in diagnostic capability for the complex. The collation of such data is currently underway to support an internet-based tool for New Zealand quarantine (6) and promises to provide a more flexible means of diagnosis.

Evolutionary history

Because of their pest and quarantine importance, species-level taxonomic work and diagnostics is relatively well advanced in the *B. dorsalis* complex, however, few authors have addressed the evolutionary relationships of the group, or addressed to what extent the contemporary classification reflects the phylogeny of the group. None have tackled the *B. dorsalis* complex *per se* and there is no phylogeny (either morphological or molecular) for the complex upon which to develop an evolutionary history. Species from the complex have been included in higher taxonomic analyses, sometimes though with *B. dorsalis* s.s. being the sole representative (17, 40, 41, 66).

Studies enabling direct phylogenetic comparison of species within the complex are limited, but where done all have used nucleotide sequence data. An early study of the nuclear genes encoding the 18S rDNA, Cu/Zn superoxide dismutase enzyme and mitochondrial 12S rDNA gene, found those loci too conserved to differentiate *B. dorsalis*, *B. carambolae* and *B. papayae* (130). However, differences between the group and *B. (B.) correcta* (5% in Cu, Zn superoxide dismutase) and *B. (Austrodacus) cucumis* (1.5%, 7% and 18% at the respective loci) led to the proposal that the complex had diverged within *Bactrocera* less than a million years ago. This was consistent with another estimation of 87,000 years since divergence of the complexes *B. (B.) dorsalis* and *B. (Zeugodacus) tau* (55).

Monophyly of the complex (n=3 to 6 species) within *Bactrocera* has been supported in analyses using 1,680 bp of the 16S+12S rDNA (77), 1,391 bases and combined trees for 16S, 12S and COII+tRNA_{Lys}+tRNA_{Asp} (111) and 841 bases from combined trees for 16S and COII+tRNA_{Lys}+tRNA_{Asp} (110). However, in a study of five *Bactrocera* subgenera, monophyly of the complex was questioned with *B. (B.) musae*, from outside the complex,

appearing within the clade (78). Clearly a more comprehensive phylogenetic analysis requires the inclusion of additional nucleotide characters and more taxa. Additional loci to consider may be those already examined in *B. dorsalis* s.s., such as the introns of muscle actin (48) and EF1-A (99) nuclear genes, plus the mitochondrial COI gene that successfully resolved relationships within the *B. (Z.) tau* complex and in which *B. dorsalis* and *B. pyrifoliae* formed the anticipated clade (55).

ECOLOGY

Few ecological studies have dealt concurrently with multiple species within the *B. dorsalis* complex and thus the known ecology of the complex is actually the ecology of a few select species, commonly pests, which have been studied in the context of pest management. Given this limitation, the following section is highly selective in the ecological areas covered and focuses on only two areas where research during the past decade has led theoretical developments in a wider field (*Adult resources and mating systems*), or where compilation of species specific research offers insights into studying and management of flies of the *B. dorsalis* complex (*Larval host range*).

Adult resources & mating systems

Dacine fruit flies are anautogenous, i.e. they emerge from puparia as sexually immature adults that need to forage for resources to facilitate survival and reproduction (93). Key resources include moisture for metabolism, sugars to fuel flight, protein to attain sexual maturity and, in conjunction with lipids, for egg production (35). Sugar sources include honeydew and other plant exudates. Protein is derived from sources such as phylloplane bacteria (21, 25) and bird faeces (13, 35), while moisture is derived from dew and rain (70). Adult flies forage for these resources in the environment, although lipids are probably synthesized *de novo* (97). In addition, adults may also actively seek out certain plant-derived phenyl propanoids (e.g. methyl eugenol and raspberry ketone) (72, 73) that are hypothesized to play a role in the mating behaviour of dacine species (33, 34, 84-86, 94, 95, 103, 104, 106, 108, 114). With respect to frequency of mating, female flies are considered monandrous, while male flies are polygynous (93). Within the *B. dorsalis* complex, mating behaviour of some of the major pest species (85, 103, 104, 106, 108, 114) and one non-pest species (93-96) has received considerable attention. Mating behaviour in dacine fruit flies has been explored from two main perspectives, though both rely on the functional significance of plant-derived chemicals to which dacine flies respond.

The most common model of mating systems within those species of the complex studied suggests that mating occurs within a defined spatial arena ("lek" *sensu lato*) where resources for adult flies are absent (103, 107). Within these arenas sexual selection, driven by female mate choice for males that have fed on plant-derived phenyl propanoids, is hypothesized to operate. The ingested plant chemicals are integrated into the male fly's sex pheromone (33, 34) and this subsequently makes them more attractive to female flies (84-86, 103, 104, 106, 108). The mating behaviour of *B. dorsalis* s.s. most strongly supports this view of dacine mating behaviour. Male and female *B. dorsalis* aggregate on the larval host plant at dusk and females appear to choose among males that "call" to them, with males that have had prior exposure to methyl eugenol acquiring more mates than males that have not (106, 107). Contrary observations have been recorded for *B. cacuminata*, a non-pest species of the complex, where exposure to methyl eugenol appeared to confer no

advantage in mate acquisition (94). This suggests that the physiological usage of plant derived chemicals may vary between species.

A second model of mating behavior observed for species within the complex hypothesizes that plant derived phenyl propanoids serve as a mate rendezvous stimulus that both male and female flies respond to for mate location (73). This hypothesis has been considered unlikely in the past, as these chemicals have not been found to be common among larval host plant species to which mating was thought to be restricted (33, 34, 106). However, unmated female flies are known to respond to lures (1, 34, 95), and with evidence indicating that mating need not be restricted to the larval host plant (95), direct experimentation has shown that natural phenyl propanoids, such as methyl eugenol, can serve as mate aggregation stimuli when resources are spatially separated (1, 34, 95).

Research on mating systems for species within the *B. dorsalis* complex is still in its infancy, with the two most studied cases (*B. dorsalis* s.s. and *B. cacuminata*) giving quite different insights. Because species within the complex are thought to be quite recently evolved, with a high degree of genetic relatedness, the complex offers an ideal model system to study rapid speciation and the role of mate recognition, larval host plant use and the availability of other environmental resources in limiting gene pools. Such research will not only enable us to better understand the ecology and evolution of dacine fruit flies, but may also aid in the development of sustainable management strategies, relying on mating disruption, for the pest species within the complex.

Larval host range

Understanding larval host range in the complex is hampered by the fact that larval rearing records are known for only 28 species (38% of the complex): where records are known they are to be found in a variety of sources (3, 23, 26, 42, 117), but have been collated (60). Of those species with rearing records, six have only one known larval host (Table 1) and it is unclear if this is because they are truly monophagous, or simply under-sampled. Where two or more larval hosts have been recorded for a fly, only three species are restricted to a single plant genus (*B. melastomatos* on two species of *Melastoma*; *B. propinqua* on nine species of *Garcinia*; *B. verbascifoliae* on five species of *Solanum*) and can be regarded as narrowly oligophagous. In contrast, the more general pattern of larval host use by flies of the complex appears to be multiple plant species across genera and families (Table 1). The key plant families containing *B. dorsalis* complex hosts include the Anacardiaceae, Annonaceae, Clusiaceae, Lauraceae, Moraceae, Myrtaceae, Rutaceae, Sapotaceae and Solanaceae, each with 15 or more known fruit fly host species. Excluding the three highly polyphagous species within the complex (see next paragraph), less than 5% of host plants (16/369) are shared by two or more fly species. *Psidium guajava* (common guava, exotic to South-east Asia) is the host most utilised by flies of the *B. dorsalis* complex, with eight species having been being reared (*B. carambolae*, *B. caryeae*, *B. dorsalis*, *B. kandiensis*, *B. occipitalis*, *B. papayae*, *B. pyriformiae*, *B. trivialis*). It should be noted, however, that guava is an exceptionally common fruit fly host plant, being a known host for at least 20 *Bactrocera* species (3, 42). The host range for the majority of species for which larval hosts are not known can only be guessed. It is probably safe to assume that they are non-commercial, wild fruits, but whether the flies are monophagous or oligophagous is not known.

Three species within the complex are known for their extreme polyphagy: *B. papayae* with 209 recorded larval hosts across 51 plant families; *B. dorsalis*, 124 host species across 42

families; and *B. carambolae*, 77 host species across 27 families (Table 1). Detailed examination of host use by these species is in its infancy, but what is available strongly suggests that while large numbers of different host species may be utilised, not all are utilised equally. In laboratory trials, with limited numbers of hosts, host suitability (as assessed by oviposition preference, larval development times and survival rates) varied across hosts from different plant families (20, 59, 124) and within a family (98). From field collections, the yield of flies from fruits is rarely proportional to the presence of different fruit species within samples. For example, *Terminalia catappa* (Pacific almond) reared 2-5 times more *B. dorsalis* and *B. papayae* in samples from Thailand than would have been expected based on the number or weight of *T. catappa* fruit in overall samples (19). In stark contrast, no *B. papayae* were reared from rainforest fruit samples in far North Queensland during the incursion in the mid-1990's, despite plant species recorded as hosts from South-east Asia being present (39), nor were any reared from fruit samples collected in tropical lowland rainforest of Papua New Guinea (87). Such results strongly imply that simple host lists (3) are not sufficient in themselves for identifying biological host range in these polyphagous species.

PEST STATUS AND INVASION BIOLOGY

A common perception among applied entomologists and quarantine biologists is that the *B. dorsalis* complex is a major pest group, arguably one of the most important pest species complexes in world agriculture. Two core assumptions underlie this accepted pest ranking: (i) the extreme polyphagy and hence assumed pest status of species within the complex; and (ii) the known invasiveness of at least some species within the complex. For quarantine and trade, particularly, the perception of risk posed by the complex is very large and the presence or absence of species within a country or region can have dramatic effects. It has been estimated that the mid-1990's incursion of *B. papayae* into north Queensland caused losses of nearly Aus\$100mill, most of this due to lost export markets (24). Because much of the real pest status of the *B. dorsalis* complex actually stems from these indirect trade losses, two areas crucial to understanding this issue are reviewed below. The first of these is the pest status of the complex in its native range, i.e. South-east Asia, as an incomplete understanding of an organism's pest status in its endemic range will confound any understanding of its potential pest status in a newly invaded region. The second area reviewed is the invasion biology of the complex: those factors which may influence invasiveness and current research methodology to understand this issue.

Pest Status in South-east Asia

The South-east Asian region comprises Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, the Philippines, Singapore, Thailand and Vietnam. This region lies at the center of distribution of the *B. dorsalis* complex, with 51 of the 75 species being found there (Table 1). South-east Asia is also a center for tropical fruit production, with approximately 400 edible tropical fruit and nut species being grown (122). Fruits are commonly grown for local consumption and domestic markets, however, several countries supply export markets with a diverse range of fresh tropical and temperate fruits. Given the coincidence of substantial fruit-growing areas with the geographic ranges of numerous frugivorous *B. dorsalis* complex species, it is not surprising that several of these fly species are fruit pests in the region.

Based on FAOSTAT production and export statistics (32), 28 fresh fruit commodities are of major economic importance to South-east Asia. Using South-east Asian literature to expand the FAOSTAT commodity categories, which combine many fruit species, lengthens the list to 42 economic fruit types (Table 2). Of the 51 *B. dorsalis* complex species present in South-east Asia, nine, viz *B. carambolae*, *B. dorsalis*, *B. irvingiae*, *B. occipitalis*, *B. papayae*, *B. philippinensis*, *B. pyriformis*, *B. raiensis* and *B. trivialis*, have been reared from fruits of 27 of these commercial fruits (Table 2).

Table 2: Fruits of economic importance to South-east Asia and the members of the *Bactrocera dorsalis* complex that infest them.

Fruit species (common name) ^a	Countries in which crop is economically important ^b	Fly species recorded to infest fruit in SE Asia ^{cd}
<i>Abelmoschus esculentus</i> (okra)	i	-
<i>Actinidia chinensis</i> (kiwi fruit)	i, n	-
<i>Ananas comosus</i> (pineapple)	c, d, g, h, i, m, n, q, r	-
<i>Annona spp.</i> (custard apple)	m, q	car, dor, pap
<i>Artocarpus altilis</i> (breadfruit)	i	car, dor, pap, phi, rai
<i>Artocarpus heterophyllus</i> (jackfruit)	i, m, q, r	car, dor, irv, pap
<i>Averrhoa carambola</i> (carambola)	i	car, dor, pap
<i>Capsicum spp.</i> (chillie)	g, m, n, q	car, dor, pap, tri
<i>Carica papaya</i> (papaya)	g, i, m, n, q, r	dor, pap, phi
<i>Chrysophyllum spp.</i> (star apple)	m, r	car, dor, pap
<i>Citrullus lanatus</i> (watermelon)	g, i, m, n, q, r	-
<i>Citrus spp.</i> (orange, lemon, lime, etc)	c, d, g, h, i, m, n, q, r	car, dor, occ, pap, tri
<i>Cucumis melo</i> (cantaloupe)	g, h, i, m, n, q	dor
<i>Cucumis sativus</i> (cucumber)	g, i, m, n, q	dor, pap
<i>Cucurbita spp.</i> (pumpkin, gourd)	g, i, m, q	-
<i>Dimocarpus longan</i> (longan)	q, r	dor
<i>Durio zibethinus</i> (durian)	g, i, m, q, r	-
<i>Ficus carica</i> (fig)	g	-
<i>Fragaria spp.</i> (strawberry)	g, i, n, q	-
<i>Garcinia mangostana</i> (mangosteen)	g, i, m, q, r □	car, pap
<i>Litchi chinensis</i> (litchi)	q, r	dor
<i>Lycopersicon esculentum</i> (tomato)	g, i, m, n, q	car, pap
<i>Malus domestica</i> (apple)	g, i, m, n, q	dor
<i>Mangifera indica</i> (mango)	g, h, i, m, n, q, r	car, dor, occ, pap, phi
<i>Manilkara zapota</i> (sapodilla)	i, m, q	car, dor, pap
<i>Musa spp.</i> (banana and plantain)	c, d, g, h, i, j, m, n, q, r	dor, pap
<i>Nephelium lappaceum</i> (rambutan)	g, i, m, q, r	dor, pap
<i>Passiflora edulis</i> (passion fruit)	i	pap
<i>Persea americana</i> (avocado)	g, i, m, n, q	car, dor, pap
<i>Phoenix dactylifera</i> (date)	g, i, n	-
<i>Pouteria sapota</i> (sapote)	r	pap
<i>Prunus armeniaca</i> (apricot)	g, n	-
<i>Prunus avium</i> (cherry)	g, i, n	dor
<i>Prunus domestica</i> (plum)	i, n, q	dor
<i>Prunus persica</i> (peaches,	i, n	dor, pap, pyr, tri

nectarine)		
<i>Prunus spp.</i> – species not specified	h	
<i>Psidium guajava</i> (guava)	i, m, q, r	car, dor, occ, pap, pyr, tri
<i>Pyrus communis</i> (pear)	g, i, n, q	-
<i>Rubus idaeus</i> (raspberry)	m	-
<i>Solanum melongena</i> (aubergine)	g, i, m, q	pap
<i>Tamarindus indica</i> (tamarind)	m, r	-
<i>Vitis vinifera</i> (grape)	g, i, m, n, q, r	-

^aPlant nomenclature follows (58).

^bCountry abbreviations as in Table 1.

^c*Bactrocera dorsalis* complex species infesting South-east Asian fruit derived from (60). car – *B. carambolae*; dor – *B. dorsalis*; irv – *B. irvingiae*; occ – *B. occipitalis*; pap – *B. papayae*; phi – *B. philippinensis*; pyr – *B. pyrifoliae*; rai – *B. raiensis*; tri – *B. trivialis*.

^dNote that columns two and three are independent. They are not meant to imply that for a particular fruit, every fly species listed as attacking that fruit does so in every listed country. For example, *B. philippinensis* attacks papaya in the Philippines, but not in other countries because it is absent from those countries (see Table 1 for country records).

The extent to which each *B. dorsalis* complex species affects fruit production and agricultural economics in the South-east Asian region is vital information for setting research priorities for these species. Several South-east Asian species within the *B. dorsalis* complex have been accorded status as pests ranging from “significant” (*B. occipitalis*), through “serious” (*B. pyrifoliae*) and “major” (*B. carambolae*, *B. dorsalis*), to the “most destructive of all *dorsalis* complex species” (*B. papayae*) (29). Similar terms have been used by others to describe the pest importance of *B. dorsalis* complex species (132). The justification for using these descriptors is seldom explicitly stated in the literature. Nevertheless, three ecological criteria, i.e., the range of host fruit species, especially that of economically important hosts, geographic distribution, and fruit infestation rates, seem important in the literature for defining a fly species importance as a pest. A fourth criterion for establishing pest status, their economic effects, is rarely addressed in the literature. Each of these criteria will be discussed here in relation to the nine pest species in the *B. dorsalis* complex that infest South-east Asian commercial fruit.

The known distributions of the nine *B. dorsalis* complex pest species vary tremendously, both in terms of the commercial fruits they infest (Table 2) and of the countries in which they are found (Table 1). *Bactrocera dorsalis* and *B. papayae* have the greatest host ranges, with each having been found infesting, respectively, fruits of 21 and 22 of the 41 commercially-important crops in South-east Asia. *Bactrocera carambolae* also infests fruits from many plant species, having been recorded from 13 commercial fruits. The remaining six potentially pestiferous *B. dorsalis* complex species, *B. irvingiae*, *B. occipitalis*, *B. philippinensis*, *B. pyrifoliae*, *B. raiensis* and *B. trivialis*, have each been recorded from fruits of fewer than five economically-important crops. *Bactrocera occipitalis*, *B. philippinensis*, *B. pyrifoliae* and *B. trivialis* are all considered to need more extensive fruit surveys to establish their pest status (29). The addition of commercial fruits to the host fruit ranges of *B. irvingiae* (jackfruit and santol) and *B. raiensis* (breadfruit) (60), since these flies were described (26) highlights the need for further host fruit surveys.

Bactrocera carambolae, *B. dorsalis* and *B. papayae*, the three members of the *B. dorsalis* complex with the greatest commercial host fruit ranges, also have the widest distributions,

with each having been recorded in four or more of the 10 South-east Asian countries. Each of the other six *B. dorsalis* complex pest species occurs in three or fewer countries. *Bactrocera carambolae* has been found in Vietnam and *B. occipitalis* in Brunei (60) since their first descriptions (26). The distributions of the nine *B. dorsalis* complex pest species will undoubtedly increase as more surveys are done throughout the region.

Fruit infestation rates are of vital importance for determining the pest status of fruit flies. Generally, just one larva in a fruit is enough for rejection by a consumer (or by quarantine in an export destination country). The level of infestation determines the quantity of produce that can be sold and, therefore, the economic returns to farmers. Despite the importance of knowing infestation rates, virtually no literature is available concerning *B. dorsalis* complex species in South-east Asian fruit crops. Literature concerned with infestation from areas outside the region, where *B. dorsalis* complex species have been introduced (*B. carambolae* in Surinam and *B. dorsalis* s.s. in Hawaii), is therefore presented (Table 3).

Infestation rates for both *B. carambolae* and *B. dorsalis* show a similar pattern, i.e., that infestation rates are markedly higher in some fruit species than in others. Thus, more than 40% of carambola fruit samples in Surinam were found infested with *B. carambolae*, whereas only 1.2% of sweet orange samples were infested by this fly, with a wide range of infestation rates in between (Table 3). Similar infestation patterns were found for *B. dorsalis* in Hawaii where a maximum 55% of papaya fruits were infested, compared with 0.026% for rambutan. Although infestation rates are of major importance for determining pest status, they may fluctuate considerably within the same fruit species with season and geographical location (7). Methods which take such fluctuations into account need to be developed so as to enable comparisons of infestation rates among fruit species.

The final criterion for determining pest status of *B. dorsalis* complex species is their economic effects, e.g., losses or control costs associated with infestation. Some basic economic analyses have been conducted (123). However, these were concerned with tephritid fruit flies in general rather than individual fly species and do not ascertain the economic impact of one fly species relative to others. There is a clear need for species-specific economic analyses.

Although some *B. dorsalis* complex species have been accorded status as “serious“ or “major” pests in South-east Asia, very little evidence has been published that supports these descriptors being placed on them. The efficient development of research effort towards the management of pest species of the *B. dorsalis* complex can only be done when such information becomes available.

Invasion Biology

Species within the *B. dorsalis* complex vary widely in the extent of their geographical range (26). Most species are very restricted (e.g., 50 of 75 species are recorded from only 1 country, Table 1), with relatively few species more widely distributed (e.g., only 5 of 75 are found in 5 or more countries). Only a few species, including *B. dorsalis*, *B. carambolae*, *B. philippinensis* and *B. papayae*, are actively expanding their range (15, 67, 109) and are by definition, invasive: these species are also characterized by a relatively broad host range and all are economically important. Explaining the ability of such species to invade new regions, and the consequences of these invasions, represent active areas of research and many of the scientific tools used to study biological invasions have

Table 3: Maximum infestation rates for *B. carambolae* and *B. dorsalis* in fruits of economic importance to the South-east Asian region. Data were not available from South-east Asia and so infestation rates from other regions of the world, where the flies have been introduced, were used.

Bactrocera carambola– Surinam, South America (118)		Bactrocera dorsalis – Hawaii, USA (63, 69, 102)		Bactrocera dorsalis – Hawaii, USA (45, 46)	
Fruit	% infested fruit samples	Fruit	% infested fruit (reference)	Fruit	No. flies emerging / kg fruit (reference)
Carambola	41.6	Papaya	54.87	Tangerine	42.8
Star apple	17.2	Rambutan	0.12	Guava	30.8
Mango	16.3	Pineapple	0 0	Litchi	8.2
Guava	11.4			Mango	5.8
Sapodilla	8.7			Guava	23.8
Grapefruit	8.0			Mango	10.7
Mandarin	5.7			Tangerine	6.1
Sweet orange	1.2				
Lime	0				
Banana	0				
Custard apple	0				
Papaya	0				
Passion fruit	0				
Pineapple	0				
Tamarind	0				

originated through case studies of tephritid flies, including *Bactrocera* species. The impetus for this research stems largely from active programs to develop molecular genetic methods for diagnostics, particularly in Australia (125, 135), New Zealand (9), the US (71), and elsewhere (67, 75).

Compared to our understanding of the invasion biology of *Ceratitidis capitata*, the Mediterranean fruit fly (71) and *B. tryoni*, the Queensland fruit fly (112, 135), relatively little is known about species in the *B. dorsalis* complex. However, as with these other invasive tephritids, global and regional transport of fruit and vegetable products results in constant propagule pressure by species such as *B. dorsalis* (92). Fly interceptions at airports and other points of entry bear this out, but also demonstrate that actual colonization and establishment is less frequent than immigration (16). This conclusion is complicated, however, by the fact that recently established populations may persist below detection levels for some time. An important question for pest management, critical for assessing whether populations can be completely eradicated or merely controlled, is whether fruit fly populations represent transient outbreaks or have become established. To address this question, research on the historical demography of invasive fruit fly populations has prompted the development of novel approaches to determine population origins and structure, including statistical assignment tests (22) and resampling statistics based on heterozygosity and shared alleles (112). Using these approaches, studies of *C.*

capitata, *B. tryoni* and other *Bactrocera* species, show that population histories are typically not simple, with established populations comprising both ancestral and invading lineages (76). For estimation of other population parameters, such as invading population size and current gene flow, new Monte-Carlo approaches show much promise (14, 31).

The impacts of invasions of *Bactrocera* species on other arthropods have been little studied with the noted exception of the interaction between *B. dorsalis* and previously established *C. capitata* in the Hawaiian Islands. Because of the disappearance of medfly in low elevation areas following introduction of *B. dorsalis*, it had been assumed that *B. dorsalis* would displace *C. capitata* elsewhere in the Hawaiian Islands and eradication strategies were developed based on this reasoning (121). However, more recent experimental work has shown that in higher elevation coffee plantations, *C. capitata* prevails as a result of a very different life history: *C. capitata* is more of an “r-selected” species, being smaller and capable of rapid colonization of newly planted coffee, while *B. dorsalis* is more of a “K-selected” species, being larger with a later onset of reproduction (120). However, the situation can be more complicated: for example, under certain conditions both species may lose in competition to another fly, *B. latifrons* (64). There is also evidence that parasitoids introduced for biological control may influence the competitive outcome between pest fly species and may also impact indigenous fly species (30, 49). The direct impacts of *Bactrocera* species on indigenous arthropod species have not been well studied (39, 87).

A number of factors suggest that much will be learned about the invasion biology of the *B. dorsalis* group in the near future. In particular, a wealth of genetic tools is now available, active quarantine programs exist world-wide, and the infrastructure to share data concerning invasive species is rapidly growing. It is also likely that new molecular tools based on genetic modification will permit tracking of genetically marked individuals and provide alternative, albeit controversial, methods of control (43, 100).

CONCLUSIONS

Systematics and evolutionary history

A common question which has circulated in the fruit fly community since 1994 has been: “*did Dick Drew and Dave Hancock get it right when they split B. dorsalis into so many new species?*” Accumulated evidence now suggests that in most cases they did.

Combining cytological, allozyme and nucleotide data, there is generally support for separation of even the most closely related species within the group. However, some species, such as *B. carambolae* and *B. papayae* require molecular tools of extremely high precision for accurate diagnosis. How these slight differences relate to species concepts has not been addressed. For example, is the level of interspecific genetic difference detected between *B. carambolae* and *B. papayae* greater or lesser than intraspecific differences between populations of other species within the complex.

Evidence to date suggests that the *B. dorsalis* complex represents an extremely rapidly evolving species complex and that much of the species diversity we currently see has been generated in very recent evolutionary time (last 1-2 million years). As such the complex represents a good example of a phytophagous insect evolutionary radiation. Contrary to a number of other phytophagous arthropod radiations, we do not in this example have

evidence of a tightly coevolving arthropod/host-plant system. Rather, the radiation has probably been driven by a complicated mixture of host shifting and host range expansion, all happening within the context of an extremely diverse rainforest plant community and a fast evolving South-east Asian geological mosaic of islands and accreted terranes (74). Because of their diversity and likely evolutionary histories, these flies offer a remarkably tractable system for testing the validity of different species concepts and speciation mechanisms.

For the *B. dorsalis* complex to become useful as a model system for wider evolutionary-ecology questions, development of a phylogeny for the group is critical. Phylogenetic work for the complex is in its infancy, currently relying on few morphological characters, short pieces of mitochondrial DNA and small taxon samples. That current taxonomic treatments are geographically limited (e.g. Australia/PNG, Asia, Sri Lanka) has also hindered an overall systematic understanding of the group. A complete phylogeny is urgently needed, developed from a combination of molecular and morphological data, in order to help resolve species limits and their relationship to each other.

Hybridization, which has been reported or suspected between species within the complex (81, 128), needs to be studied further to determine if it is a rare event, with little impact on the integrity of species' gene pools, or if it is common in which case species limits would need to be redefined. The unresolved issue of hybridization is a reflection that little or no effort has yet been made to establish the extent to which morphologically defined species within the complex reflect biological species. Studies of mating systems within the complex, which may help to resolve this issue, are still limited and, with respect to phytochemicals, give conflicting results. Studies of the mate recognition systems (89) of *B. dorsalis* complex flies are needed to help understand the functional cues by which individuals recognise potential mates and so set the limits to gene pools in the complex.

Pest status

The real pest status of flies within the *B. dorsalis* complex remains ambiguous. There is no doubt that in particular localities, and on selected crops, that complex species such as *B. dorsalis*, *B. papayae* and others cause major loss. There is also no ambiguity about the fact that the presence of even one of the pest species from the complex in a country or region can dramatically impact on freedom of market access. What is less well documented, in an economic sense, is exactly how pestiferous are even the best known and widespread of the *B. dorsalis* complex species. Exactly how economically damaging are species such as *B. philippinensis* and *B. occipitalis*, both in comparison to other flies within the complex, other dacine fruit flies, and other pests within the cropping system, has not been determined. If such information does exist, as we suspect it does for at least some localities, then it needs to be much more widely distributed in the standard literature, as such information is vital for directing research efforts for tackling the fruit fly problem.

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