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## REVIEW

# Why so many polyphagous fruit flies (Diptera: Tephritidae)? A further contribution to the ‘generalism’ debate

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It has been suggested that generalist herbivorous insects are an evolutionary ‘improbability’. However, many species of tephritid fruit flies are generalists utilising larval hosts across two or more plant families. Focusing on the genus *Bactrocera*, it is argued that this high frequency of generalism is due to four evolutionary drivers which both decrease the need for specialism and promote generalism. Decreasing the need for specialism, there is firstly no co-evolutionary arms race between host plant and herbivore as *Bactrocera* do not negatively impact on plant fitness; this removes the need for specialism to counter plant defences. Secondly, the endemic hosts of most *Bactrocera* are plants with vertebrate-dispersed fleshy fruits. Fruit morphology and their display are highly constrained to attract those seed dispersers; *Bactrocera* thus do not need to specialize to increase host location capacity as many hosts produce a common signal. Thirdly, in native rainforest ecosystems *Bactrocera* are rare and so specialization to avoid competition seems unlikely. Promoting generalism are braconid parasitoids, which utilise plant cues to find their hosts. If a fly can use a novel host plant then it moves into enemy-free space, so promoting generalism. From this multi-part hypothesis, a group of testable predictions emerge. If shown to be correct then for the generalism/specialism debate frugivorous tephritids would provide an example where generalism may be a ‘probable’ evolutionary outcome. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2017, 120, 245–257.

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## INTRODUCTION

Some 98% of insect herbivores are specialists, feeding on only one or a small number of related plants (Jaenike, 1990). Because of their frequency, the theory supporting the evolution of specialism is well developed and mature (Strong, Lawton & Southwood, 1984; Bernays, 1988; Futuyama & Moreno, 1988; Funk, 2010), but this is not the case for generalism which has been dismissed as a transitory evolutionary event, e.g. *It appears that generalism is only a passing means to an end* [of specialism], or as simply a human mistake of clustering together unrecognized specialist lineages, e.g. ...*so it is with specialism vs generalism,*

*such that the more molecular markers that are applied, the phenomenon of generalism, certainly in terms of polyphagy, is perhaps seen to be largely illusory* (both quotes from Loxdale & Harvey, 2016). Nevertheless, recent studies have demonstrated that generalism is perhaps not as rare as has been previously considered (Forister *et al.*, 2015), nor are all generalists simply specialists waiting to happen as generalist lineages can arise from other generalists (Hardy & Otto, 2014), and diet breadth can even increase in the daughter species of more specialist ancestral species (Mao, Schuler & Berenbaum, 2007; Day, Hua & Bromham, 2016). Developing a more robust understanding of what drives the evolution of generalism in insect herbivores should therefore be regarded as an equally valid endeavour as

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understanding specialism. Meeting a comment of Loxdale and Harvey for the need of better definition of terms, in this paper I use *generalism* as synonymous and interchangeable with *polyphagy* to refer to a herbivore which feeds across two or more plant families, and *specialism* as synonymous with *monophagy* + *oligophagy* to refer to a herbivore which feeds within one plant family.

Normark & Johnson (2011) made a significant contribution to the herbivory literature when they reviewed what they referred to as extreme polyphagy; the ability of a herbivore to feed across more than 20 plant families. In so doing they identified what I consider to be two critical issues. The first was that while generalism is normally rare in herbivorous insects, there are certain evolutionary lineages [e.g. armoured scale insects (Diaspididae), bagworm moths (Psychidae), tussock moths (Lymantriidae)], where generalism is much more prevalent. For such groups, testable theories can be developed as to why polyphagy has arisen and is common. The second issue they raised was that one answer will not fit all, and that groups with different biological attributes are likely to need different explanations for the evolution of polyphagy within those groups. For example the 'niche explosion model' they developed was applicable to organisms where the juveniles randomly disperse to find feeding sites, but was more difficult or impossible to apply to groups where the choice of juvenile feeding site was made through active host-plant selection by an ovipositing female.

That different explanations for generalism may be needed for different lineages makes sense when it is remembered that generalism is rare. If there was a simple set of evolutionary drivers which promoted generalism then we would expect to see it more frequently, and spread more equally across herbivore groups. But as generalism is rare, but when present disproportionately represented within certain lineages, then it might be logically argued that the drivers for generalism are probably unique sets of biological attributes restricted to those lineages. To some extent the importance of unique attributes in promoting generalism has been recognised since the 2000s. For example for insects feeding on toxic plants the ability to detoxify the plant is considered important (Mao *et al.*, 2007; Niu *et al.*, 2011), while for insects which actively forage across many plants a complex of factors including diet optimization and enemy free space may become important (Singer, 2001; Singer & Stireman, 2001, 2003; Forister *et al.*, 2009; Smilanich *et al.*, 2011).

One group identified by Normark & Johnson (2011) as having high levels of polyphagy but not fitting their 'niche explosion' model, were frugivorous tephritids (Diptera: Tephritidae). Normark and Johnson commented that these fruit flies feed in

chemically unprotected fruit, but took the discussion no further. In this paper I develop a fuller argument as to why polyphagy and extreme polyphagy is common in frugivorous tephritids, with a focus on the genus *Bactrocera* Macquart. In so doing it is not my intent to criticise the many well established reasons as to why evolutionary selection pressure most commonly leads to dietary specialism, but I do wish to make the point that generalism should not be considered 'improbable' among insect herbivores (*sensu* Loxdale, Lushai & Harvey, 2011), but given certain situations might even be regarded as inevitable.

### GENERALISM IN *BACTROCERA* FRUIT FLIES

The *Bactrocera* fruit flies are a super-diverse genus of insect herbivores found in the old-world rainforests of Asia, Australia and the Pacific (Drew, 2004; Drew & Romig, 2013). The flies lay their eggs into sound fruit on-plant, where the resultant maggots feed. The maggots are restricted for their full development to the individual fruit piece into which the eggs were laid by the free flying and actively host-searching female (Fletcher, 1987). In this genus specialism or generalism is based on the number of larval hosts that adults have been reared from; a definition matching the recommendation of Loxdale & Harvey (2016) that *generalists and specialists* [be defined] *on the basis of diet that is essential for immature to adult growth*. Importantly for this analysis host-plant usage by *Bactrocera* is well documented and for the ~600 species in the genus there are published host lists for well over 200 (Allwood *et al.*, 1999; Hancock *et al.*, 2000; Leblanc *et al.*, 2012, plus numerous miscellaneous sources for individual flies or hosts).

From these records, it is clear that *Bactrocera* is highly unusual in its level of generalism. Of the 200 + documented species, ~40% have been reared from host plants from two or more plant families (Drew, 2004; plus records above). Further, extreme polyphagy (*sensu* Normark & Johnson, 2011) is also common in *Bactrocera* with 11 species having published host lists of 20 plant families or greater, these being: *B. carambolae* Drew & Hancock, *B. correcta* (Bezzi), *B. curvipennis* (Froggatt), *B. dorsalis* (Hendel), *B. fascialis* (Coquillett), *B. frauenfeldi* (Schiner), *B. kraussi* (Hardy), *B. neohumeralis* (Hardy), *B. passiflorae* (Froggatt), *B. tryoni* (Froggatt) and *B. xanthodes* (Broun). There are also several other species that have recorded host ranges nearly as large, e.g. *B. kirki* (Froggatt) (19 families) and *B. melanotus* (Coquillett) (18 families), and from an evolutionary perspective they probably need to be considered in the same way.

Before proceeding to a discussion of generalism in *Bactrocera*, I need to acknowledge the 60% of the genus which are specialists. True monophagy occurs within *Bactrocera*, but feeding on several closely related hosts is the most common dietary habit within the genus (Drew, 2004; Novotny *et al.*, 2005). In most other frugivorous tephritid genera, such as *Rhagoletis* Loew, specialism is also the norm (Prokopy & Papaj, 2001). For such flies I assume the same evolutionary pressures that have driven specialism in other insect herbivore groups have also acted upon them. Thus *Bactrocera oleae* (Rossi), narrowly oligophagous on commercial olive, *Olea europaea*, and two other *Olea* species (Daane & Johnson, 2010), may have specialized because it attacked fruit when they were still toxic and so had to develop mechanisms to handle that toxicity, or because in its native state the hosts may have been rare and so specialism increased host location capacity. Research on the host use and oviposition behaviour of specialist tephritids is surprisingly scarce (Díaz-Fleischer *et al.*, 2001) and more work on tephritid host specialism is justified. Nevertheless, in this paper I deal only with the disproportionately large, in comparison to most insect herbivore groups, number of generalists.

#### DO CURRENT EXPLANATIONS ANSWER WHY THERE ARE SO MANY GENERALIST *BACTROCERA*?

The most obvious explainer for why there are so many generalist *Bactrocera* is because they not really generalists, only ‘apparent’ generalists (terminology and emphasis from Loxdale & Harvey, 2016). Loxdale *et al.* (2011) and Loxdale and Harvey offer three major explanations as to why ‘apparent’ specialists are most likely simply unrecognised specialists. Firstly, the apparent generalists are actually specialists and, given a choice, will show specialist feeding behaviour; secondly, that generalism is an ecological ‘time-slice’ problem and if studied at another period in evolutionary time the generalist would have evolved to become a specialist; and thirdly that generalists are actually groups of unrecognised specialists, for which deeper molecular analysis will identify those cryptic groups. Each of these arguments is considered below for the polyphagous *Bactrocera*.

#### GENERALISTS, BUT EXHIBITING SPECIALIST BEHAVIOUR

Generalist *Bactrocera* species do show preferences between available host fruits. For example, in Thailand, *B. dorsalis* (inclusive of its synonym *B. papayae* Drew & Hancock) were reared from

anywhere from 30 to 120 different host fruit species in each of five different sampling districts, but generally fewer than ten hosts provided the greater percentage of specimens reared at any one location (Clarke *et al.* 2001). Additionally, in laboratory studies not all hosts are equally suitable for a species’ offspring development and differences can occur between hosts in offspring survival to the F1 adult (Rattanapun, Amornsak & Clarke, 2010; Balagawi, Drew & Clarke, 2013). Loxdale & Harvey (2016) argue that disproportionate use of a subset of potential hosts is evidence of specialism (e.g. see their fig. 1) and, for *Bactrocera*, if all the preferred hosts came from one plant family then this argument would have significant merit. Indeed, such an argument has been previously made by Clarke *et al.* for the ‘generalist’, but more correctly specialist *B. latifrons* (Hendel), which while having host rearing records encompassing ten plant families (Allwood *et al.*, 1999), was predominantly reared (90–95% of occasions) only from the family Solanaceae, and then nearly always from the genus *Solanum*. However, evidence of ‘specialist generalists’ does not appear to hold for most of the polyphagous *Bactrocera*. Also in Clarke *et al.*, the ‘generally fewer than ten hosts that reared most flies’ were spread across five to seven plant families. If generalism is to be defined as the ability to feed across multiple plant families (as argued in Loxdale & Harvey, 2016), then the generalist *Bactrocera* species definitely still qualify despite showing differences in preference and performance for some hosts over others.

#### GENERALISTS ARE SPECIALISTS WAITING TO HAPPEN

Loxdale *et al.* (2011) and Loxdale & Harvey (2016) discuss the problem of ‘time-slice’ ecology and argue that *...all such examples* [of generalists] *could well be seen to be temporary apparent generalisms en route to full specialization* (Loxdale *et al.*: 11). If this argument holds for *Bactrocera*, then it should be detectable in phylogenetic analyses. Within a phylogeny, if generalists are simply ancestors of specialists, then it should be detectable in one of two evolutionary signals. Firstly, the generalist *Bactrocera* species would most likely be basal within an evolutionary tree, with more terminal lineages being predominantly specialists [e.g. as found in heliothine moths (Pogue, 2013) and scolytid beetles (Kelley & Farrell, 1998)]; or if specialists are terminal then they should be isolated among specialists as polyphagy is considered a transient evolutionary phase whose phylogenetic signature is quickly lost to specialists (Janz & Nylin 2008). While a full analysis of diversification and host range is yet to be done on *Bactrocera* [e.g. of the type done on some butterflies

(Nylin, Slove & Janz, 2013; Hardy & Otto, 2014)], existing phylogenies suggest that neither of the above two predicted signals hold in *Bactrocera*. Generalism has arisen on numerous occasions within *Bactrocera*, in both ancestral and derived clades (Krosch *et al.*, 2012; Virgilio *et al.*, 2015), and even recently evolved clades, such as the *Bactrocera dorsalis* species complex, have large numbers of generalist species (Clarke *et al.*, 2005; Leblanc *et al.*, 2015).

#### GENERALISTS ARE UNRECOGNISED COMPLEXES OF SPECIALISTS

Can generalism in *Bactrocera* be attributed to the generalist species being unrecognised complexes of specialist species? While it cannot be conclusively stated for every generalist *Bactrocera* species that it is not a cluster of unrecognised cryptic, host-specialist lineages, we can say it with some level of confidence for a least some species.

*Bactrocera tryoni* is Australia's major horticultural insect pest and has been extensively researched using multiple genetic approaches, starting with allozymes (McKechnie, 1974) and most recently whole genome assemblage (Gilchrist *et al.*, 2014): to date there is no evidence that cryptic lineages occur within the species (Clarke *et al.*, 2011). For example the work of Yu *et al.* (2001, using six microsatellite markers), Gilchrist *et al.* (2006, 26–29 microsatellites), Cameron, Sved & Gilchrist (2010, 10–12 microsatellites), and Gilchrist & Meats (2010, 26–29 microsatellites) deal collectively with ~5000 *B. tryoni* from over 80 sites across the species' entire Australian distribution. While population structuring is evident at geographic range edges, within *B. tryoni*'s primary endemic region of Queensland and far-northern NSW it is simply one large panmictic population. Similarly the very widely distributed and highly pestiferous *B. dorsalis* has been studied as part of a major international coordinated project using molecular (microsatellites, COI haplotype, multiple neutral mitochondrial and nuclear genes), pheromonal and behavioural tools including mating tests (Schutze *et al.*, 2012; Boykin *et al.*, 2014; Hendrichs *et al.*, 2015). Not only is there no evidence of cryptic lineages within this species, but previously separated taxonomic species have been synonymized back into it (Schutze *et al.*, 2015). *Zeugodacus cucurbitae* (Coquillett), until recently placed in the genus *Bactrocera*, is a predominantly cucurbit specialist fruit fly, but it is also frequently reared from hosts in other families, especially the Fabaceae (Allwood *et al.*, 1999). An integrative study using COI haplotype diversity, microsatellite analysis and geometric morphometric wing-shape analysis specifically looked

for cryptic diversity within this taxon at the within and across plant family level, but failed to find any (Boontop, 2016). The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), is yet another example of a closely related tephritid species which exhibits extreme polyphagy and which has been globally studied genetically and shows no sign of being a cryptic complex (Bonizzoni *et al.*, 2001; Malacrida *et al.*, 2007).

Species complexes are a major field of study for *Bactrocera* and other tephritid workers (De Meyer *et al.*, 2015) and we are very aware of the problems they cause theoretically and operationally (Clarke & Schutze, 2014; Schutze *et al.*, 2017). While a small number of generalist *Bactrocera* species may consist of unrecognised complexes of more specialist species, I do not consider it a likely explanation for the potentially hundreds of generalist *Bactrocera* species.

#### WHY THEN GENERALISM IN BACTROCERA – OR MORE IMPORTANTLY WHY NOT SPECIALISM?

A long standing paradox of insect herbivore diet breadth is why generalism is so rare (Fox & Morrow, 1981; Bernays & Minkenberg, 1997). It seems intuitively logical that being able to feed on as many host plants as possible should be an evolutionary advantage, as food would be less limiting. Yet clearly for most herbivores any advantages gained are outweighed by selective disadvantages, because the evolutionary evidence before our eyes is the dominance of specialists. Therefore in trying to understand the prevalence of generalism in *Bactrocera* I have first turned the question around and have asked not why there are so many generalists, but why are there (relatively) so few specialists? The answer to this question then helps inform why generalism is prevalent (see following section).

The benefits of specialism for herbivorous insects (as summarized from Bernays, 1988; Jaenike, 1990; Berenbaum & Feeny, 2008; Diamond & Kingsolver, 2010; Loxdale *et al.*, 2011; Loxdale & Harvey, 2016) are as follows:

1. *Overcome plant defences.* Many plants have physical and chemical traits which act defensively against herbivores. In a co-evolutionary 'arms race' argument, specialization is thought to assist in the evolution of physiological or behavioural adaptations to overcome such defences.
2. *Decreased competition.* Specialization is thought to decrease interspecific competition with generalist species, or conversely increase the ability of



a specialist to compete against generalists for a particular plant.

3. *Enhanced host location.* Increased specialization leads to better physiological and behavioural mechanisms to find the host in a temporally and spatially patchy environment.
4. *Enemy free space.* Specialization on particular hosts may be a mechanism to avoid the searching of *generalist* natural enemies (paradoxically, this argument involving *specialist* natural enemies can also be used for increasing host range, see further below).

In asking why the proportion of specialists in *Bactrocera* is so much lower than in most other herbivore groups, I ask why the above evolutionary drivers may be less critical in this genus.

#### OVERCOMING PLANT DEFENCES

A fundamental aspect of insect-herbivore/plant interactions theory is the concept of a co-evolutionary arms race between the herbivores and the plants they feed upon (Stamp, 2003; McCall & Fordyce, 2010; Loxdale & Harvey, 2016). This theory assumes that there is a fitness cost to plants in being eaten and they should evolve counter mechanisms (generally physical and/or chemical) to avoid being eaten. Insect herbivores become increasingly specialized as they, in turn, evolve physiological and/or behavioural capacity to overcome these defences. But what if no arms race exists?

*Bactrocera* larvae consume fruit when that fruit is mature (Fletcher, 1987) and the seeds fully developed. Experimentation has shown that *Bactrocera* larval feeding impacts negatively on neither seed number nor germination (Webber & Woodrow, 2004; Wilson *et al.*, 2012): this has also been demonstrated in another frugivorous tephritid genus, *Rhagoletis* (Bauer, 1986, 1988). Further to not having a negative impact, *Bactrocera* larval feeding has even been argued to be beneficial to the host plant (Drew, 1987, 1988). Fruit fly maggots help the fruit flesh break down faster (Drew, 1987), so promoting the amount and rate of seed germination (Wilson *et al.*, 2012). *Bactrocera* infested fruit has also been shown to be preferentially consumed by seed dispersing vertebrate frugivores (Drew, 1987, 1988; Fletcher, 1987; Frith, 1992; Webber & Woodrow, 2004; Wilson *et al.*, 2012), which has indirect benefits to the plant by increasing seed dispersal. While the concept of beneficial herbivory is controversial and is not an argument being developed here, the literature can be summarised as there being no data to date to suggest that *Bactrocera* maggots negatively impact plant fitness.

Even if *Bactrocera* do cause minor plant fitness costs, a need to specialize to overcome plant defences appears largely unnecessary. *Bactrocera* are endemic to old-world rainforests (Drew & Romig, 2013), and 70–80% of the fruit in those forests are evolved for frugivorous vertebrate consumption and subsequent seed dispersal (Dew, 2005). Vertebrate-dispersed fruits are often non-toxic, or of low toxicity at maturity (even if toxic before maturity) and have evolutionary constraints against becoming toxic (McKey, 1975, 1979). They are typified by high pulp content (69%), high water content of the pulp (78%), moderate fibre content (14%), high carbohydrate (53%) and low nitrogen (0.46%) and lipid (2%) levels [values the median of 153 vertebrate-dispersed fruit species from Hong Kong (Corlett, 1996)]. While larval development for generalist *Bactrocera* may be slightly modified by the host, larval survival remains high across divergent host fruit (Fitt, 1986; Rattanapun, Amornsak & Clarke, 2009; Balagawi *et al.*, 2013), and there appears little evolutionary need for host specialization by the flies. The evolutionary constraints of vertebrate-dispersed fruit are discussed further below under *Bactrocera* specialization for host location.

#### DECREASED COMPETITION

There is no evidence that specialization decreases competition in *Bactrocera* – indeed the reverse is considered true in most fruit fly literature. In invasive situations, as have occurred in Hawaii, La Réunion and sub-Saharan Africa, the highly polyphagous *B. dorsalis* and *B. tryoni* are considered to have very significant competitive advantages over more specialized species (in both *Bactrocera* and other frugivorous tephritid genera) due to greater intrinsic rates of increase, increased larval competitive ability within fruit, and pre-emptive use of fruit (Duyck, David & Quilici, 2004; Ekesi *et al.*, 2009; Rwomushana *et al.*, 2009; Geurts, Mwatawala & De Meyer, 2014). However, invasions are biologically unusual situations, as in evolutionary terms are agroecosystems where most *Bactrocera* infestation rate studies are carried out. What about the likelihood of intraspecific competition in native endemic areas? Studies of fruit infestation rates of non-invasive *Bactrocera* in endemic rainforest are unfortunately very rare, but in the one study to have focused on this most potentially susceptible fruit was not infested. Novotny *et al.* (2005), working in lowland tropical rainforests of Papua New Guinea, found only a median of one (range 0–12) fly per kilogram of fruit, and a median of one (range 0–17) fly per 100 fruit pieces. While only one study, these figures do not suggest that competition for fruit is likely to be an evolutionary significant aspect of *Bactrocera* life-history, a

conclusion also reached by Fitt (1984) based on analysis of other life-history characteristics of the genus.

#### ENHANCED HOST LOCATION

Host location is a major issue for any insect herbivore and the need to specialize to better locate hosts in the complex rainforest environment is possibly the main reason why the majority of *Bactrocera* have specialized (Drew, 2004). Nevertheless, specialization to improve host location may not be as critical for *Bactrocera* as in many other herbivore systems. *Bactrocera* species, especially the generalists, preferentially infest soft, fleshy, vertebrate-dispersed fruit (Hancock *et al.*, 2000). The appearance of vertebrate-dispersed fleshy fruit, especially fruit dispersed by birds, is constrained in both its shape and colour because of the need to match the sensory capabilities, and mechanical feeding attributes, of those frugivores (Burns *et al.*, 2009; Valido, Schaefer & Jordano, 2011; Renoult *et al.*, 2014). For example in a study of 255 vertebrate-dispersed fruit species in Hong Kong, nearly 70% of fruit were black or red in colour, most were spherical in shape and 86% had a mean diameter of < 13 mm (Corlett, 1996). Plants with fruit dispersed by birds also commonly hang the fruit on the outside of the canopy, often in clusters, to ensure the visual signal is maximised and the fruit accessible (Kitamura *et al.*, 2004; Du *et al.*, 2009). Finally rainforest trees regularly ‘mast’ fruit, with super-abundant fruiting 1 year, and then little or no fruit for a year or two following while the tree rebuilds reserves (Visser *et al.*, 2011; Oshima, Tokumoto & Nakagawa, 2015). Given these interplaying factors, it may be that to a generalist *Bactrocera* a fruiting rainforest tree becomes a very large and obvious visual signal, with relatively minor signal variation between plant species.

There is another feature shared by fruit which may allow generalist *Bactrocera* to orientate to even highly divergent fruit types. Most *Bactrocera* preferentially attack mature, ripening fruit (Fletcher, 1987). The physiology of the ripening process in fleshy fruit, while complex, is conserved across fruit and involves biochemical and biophysical changes that lead to sugar accumulation and changes in tissue texture (Singh, Rastogi & Dwivedi, 2010). Commonly associated with ripening are the production of aromatic esters, the classical ‘smells’ of ripening fruit. Cunningham *et al.* (2016) have shown that a blend of three esters (ethyl acetate, ethyl propionate, ethyl butyrate) was as, or more, attractive to the generalist *B. tryoni* than were complex whole-fruit odour blends, and when the ester blend was injected into poorly preferred cucurbit hosts it made those

fruits as attractive to ovipositing females as highly preferred peaches. These authors argue that sensory adaptation to a small suite of volatiles, common across many potential hosts, allows the fly to rapidly locate multiple host species.

In an evolutionary sense, and as discussed by Cunningham *et al.* (2016), an olfactory mechanism of using a small number of volatile cues common across fruits overcomes the problem posed by the neural limitations hypothesis (Bernays, 2001). This hypothesis argues that the evolution of herbivore generalism may be limited by the neurological capacity of generalists to process the diverse range of signal information received from multiple host plants. Usage of common olfactory signals, and infesting fruit which have highly constrained visual cues, offers a mechanistic basis of how generalist *Bactrocera* can locate so many potential hosts.

#### ENEMY FREE SPACE

One reason for specialization in insect herbivores has been attributed to the ability of a herbivore to escape *generalist* natural enemies by moving into ‘enemy free space’, i.e. part of the environment where natural enemies will not search (Bernays, 1988, 2001; Moon & Stiling, 2006). However, it is also recognised that high mortality by *specialist* natural enemies may lead to increases in herbivore host range (Gratton & Welter, 1999; Rodrigues *et al.*, 2010; Pöykkö, 2011). I argue here that such escape into ‘enemy free space’ may also be an important reason for generalism in *Bactrocera*.

As cryptic herbivores (i.e. hidden within host fruit) *Bactrocera* larvae do not suffer from generalist invertebrate predators while in the fruit. However, they do suffer significant mortality from a group of specialist parasitoids, the opiine braconids (Hymenoptera: Braconidae: Opiinae), which are egg/larval/pupal parasitoids of *Bactrocera* and many other frugivorous tephritids (Chinajariyawong *et al.*, 2000; Carmichael, Wharton & Clarke, 2005). Opiine braconids rely heavily on plant derived odours to locate their cryptic hosts (Eitam *et al.*, 2003; Rousse *et al.*, 2007). Ero & Clarke (2012) have shown that when physiologically unsuitable larval hosts (i.e. larvae where the wasp eggs are encapsulated) are experimentally moved into a regularly used host plant of a physiologically suitable larvae, the wasp will still orientate to the fruit and attempt to parasitize the unsuitable larval host. But importantly the reverse also happens. When a physiologically suitable larvae is moved to a host plant the wasp normally does not orientate to, the larvae escapes parasitism. The novel host plant thus becomes enemy free space if the parental female fly lays her eggs into that fruit.

It is possible that parasitoids will identify and adapt to locate a new host plant over time (Roßbach, Löhr & Vidal, 2006), although this will depend on how genetically fixed is their host-searching behaviour (Steidle, Stepphun & Ruther, 2003). However, even if the wasp does follow the host shift, by that time the fly's host range will have expanded. Field data shows that opiine parasitism of *Bactrocera* on native hosts is higher than on evolutionary novel, agricultural hosts (Ero *et al.* 2011), a result also found in the much larger opiine parasitism data sets from the South American fruit fly genus *Anastrepha* (Aguiar-Menezes & Menezes, 1997; Ovruski, Schliserman & Aluja, 2004; Dutra *et al.*, 2013). These natural experiments are indirect support for the enemy free space hypothesis, but formal experiments (*sensu* Berdegue, Trumble & Hare, 1996) are still required. That the fruit fly attacking opiines are also not species specific, but will attack multiple fruit fly species within and across genera (Wharton & Gilstrap, 1983; Waterhouse, 1993; Carmichael *et al.*, 2005), may also slow their evolutionary adaptation to novel host plant use by an individual fruit fly species.

#### REASONS FOR HOST RANGE EXPANSION

Where herbivore generalism occurs, it is commonly only across a few plant families. Extreme polyphagy, the ability to feed across 10s of families is extraordinarily rare, restricted to perhaps as few as 200 herbivore species world-wide (Normark & Johnson, 2011), yet a dozen of these are found within *Bactrocera*. This suggests that additional to the 'removal' of traits driving specialism, and the possibility of enemy free space, there may be other factors promoting host range expansion. What these factors are is speculative, but it is possible that it is a relatively simple interaction between the complex biogeography of the south-east Asian/Australian regions and the fact that the host fruit are largely non-toxic and highly conserved in their generic attributes, making host switching/expansion possible with little or no fitness cost to the fly.

Contrary to the expectations of herbivory specialism theory, there are generally positive genetic correlations between growth and survival traits for herbivores feeding across two or more host plants (Futuyma, 2008; Agosta & Klemens, 2009). This is thought to be because selection acts on populations to be able to use multiple host genotypes, or even multiple host species (Ueno *et al.*, 2003), due to the benefits accrued by having multiple food sources (Bernays & Minkenberg, 1997). This means that many herbivorous insects have the capacity to utilise novel hosts if they become available.

*Bactrocera* underwent its major radiations in the biogeographically complex and floristically diverse rainforests of the south-east Asian, Papuan and Australian regions (Drew & Hancock, 2001; Krosch *et al.*, 2012). Drew (2004) has argued that speciation in the genus was largely driven through cospeciation between flies and host plants during periods of geographical isolation associated initially with landmass rafting and then, in later evolutionary periods, with refugia caused by glacial minima (island refugia) or maxima (moist environment refugia). Rafting has strongly influenced the Papuan fauna (Hedges, 2001; Clarke *et al.*, 2004), while glacial associated sea-level changes and wet/dry periods have strongly influenced the south-east Asian and Australian faunas (Woodruff, 2010; Bryant & Krosch, 2016). The floras of the regions also show strong evidence of localised speciation and restricted endemism (Whitmore, 1986), similarly driven by island separation and sea-level changes (Guo *et al.*, 2015; Holzmeyer *et al.*, 2015).

While isolation and refugial contraction may have led to increased local speciation, subsequent range expansion following landmass docking, or during interglacial periods, would have meant that *Bactrocera* species would have been potentially subject to novel, competitive interactions with other *Bactrocera* species using similar host resources, as well as being exposed to possibly large numbers of novel host plants. Theoretical models have demonstrated that under such situations, if there is a significant cost to host switching to the novel hosts, then scramble competition will lead to increased specialization on the original hosts; but in contrast if the cost of host switching is minimal then the evolutionary likely outcome is host range expansion with the new resources shared (Ackermann & Doebeli, 2004; Rodrigues *et al.*, 2016). This situation has been recorded in the field, where repeated invasion of polyphagous tephritids to the island of La Réunion has resulted in the existing resources simply being shared by successive invasive species, with no evidence of host-associated resource partitioning (Duyck *et al.*, 2008). Even without possible competitive interactions, single species optimality models also predict selection for polyphagy if available hosts are relatively standard in quality and selective pressures to specialize are weak or absent (Michaud, 1990, 1992). As I argue that there is minimal cost in utilising novel hosts by polyphagous *Bactrocera* (in terms of having to overcome plant defences, or in lost host location capacity), then extreme host niche expansion by polyphagous members in the genus may simply be the result of repeated exposure to large numbers of novel hosts.

## THE EVOLUTIONARY ‘PROBABILITY’ OF GENERALISM

Loxdale *et al.* (2011) referred to the evolutionary ‘improbability’ of generalism in nature, and the same position is taken in Loxdale & Harvey (2016). *Apparent* generalists are largely dismissed in both papers as ecological time-slice problems which would disappear if studied at some other period in evolutionary time, as unrecognised clusters of specialist lineages, or as specialists whose speciality has not yet been recognised. Unfortunately the first and third statements are essentially untestable, and while the second is testable and demonstrably true for some polyphagous organisms, it is also demonstrably untrue for others (including several tephritid species). And then finally, if we are still left with apparent specialists, Loxdale and Harvey further argue that they should be considered specialists anyway,

because the attributes allowing generalism (e.g. the ability to detoxify multiple plants) is so rare it is a form of specialism. This last argument, entirely circular as it is, may be valid in lineages where generalism is rare, but for lineages where generalism is common (tephritids, diaspids, lymantrids, etc.) it is not a helpful answer to explain the evolution of their diet breadth.

In the search for understanding the ecological and evolutionary basis of generalist herbivores, rather than simply deny their existence a more fruitful activity is to propose explicit, testable hypotheses as to why observed generalists may be *real*, and not *apparent* (as for example done by Normark & Johnson, 2011). This is particularly important as many of the *apparent* generalists are globally important pests which attack diverse ranges of crop and forestry plants. Simply wishing them away as inconvenient

**Table 1.** To specialize or not: the theoretical drivers of specialism with particular respect to herbivorous insects are on the left; possible counter-arguments for *Bactrocera* in the middle; testable predictions on the right

Theory	Countering observation(s)	Testable predictions (if driver for specialization is absent)
Decreased competition Specialization is thought to decrease interspecific competition with generalist species, or conversely increase the ability of a specialist to compete against generalists for a particular plant	In natural systems, <i>Bactrocera</i> are rare and competition between generalist and specialist species is unlikely	In natural or semi-natural conditions, competition for host use does not occur between generalist species
Overcome plant defences Plants have traits which act defensively against herbivores. In a co-evolutionary ‘arms race’, specialization is thought to assist in the evolution of adaptations to overcome such defences	<i>Bactrocera</i> preferentially attack nearly ripe fruit, which is generally non-toxic; <i>Bactrocera</i> do not impact on host fitness, reducing the need for a co-evolutionary arms race	There is no difference in developmental fitness between eggs and larvae developing in common or novel hosts
Enhanced host location Increased specialization leads to better physiological and behavioural mechanisms to find the host in a temporally and spatially patchy environment	Fruit are phenologically and physiologically conserved, while rainforest trees commonly mast fruit and so make a ‘super’ target. There may be little need to specialize in host location	A generalist fruit fly can find hosts as efficiently as a specialist fruit fly
Enemy free space Specialization on particular hosts may be a mechanism to avoid the searching of generalist natural enemies (paradoxically, this argument can also be used for increasing host range, see opposite)	<i>Bactrocera</i> suffer little from generalist natural enemies, but do have specialist parasitoids. These parasitoids use host-plant cues for searching. Use of novel host plants may be a mechanism to move into enemy free space	Egg/larval parasitism rates on evolutionary novel hosts are lower than on ancestral hosts.

Supporting references for statements within the table are provided within the body of the text.



non-conformers to the theory of specialism is not helping us understand why they are such pests and have such large host ranges. To this end Table 1 provides a summary of the case I have made to explain polyphagy in frugivorous tephritids and the testable hypotheses which arise from it. If after appropriate testing the hypotheses are not disproved then I argue that the release from the drivers for specialization, supported by the benefits of moving into enemy free space and simply having more food resources available, makes generalism a highly probable evolutionary outcome for many frugivorous tephritids.

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