Chapter 3
Population Genetics of African Frugivorous Fruit Flies (Diptera, Tephritidae): Current Knowledge and Future Perspectives

Massimiliano Virgilio and Hélène Delatte

Abstract Population genetics studies provide valuable information about the patterns of connectivity and range expansion of African frugivorous fruit flies. Human-mediated movements related to trade of commodities and transport are generally indicated as one of the primary mechanisms by which tephritid pests expand their contemporary and historical ranges. This results in complex colonisation dynamics, as suggested for the widely distributed pests *Bactrocera dorsalis s.s.* and *Zeugodacus cucurbitae*, and for the cosmopolitan pest of African origin *Ceratitis capitata*. Analysis of the population structure of African fruit flies can also reveal cryptic genetic structures and incipient speciation, as observed for the *Ceratitis* FAR complex (*Ceratitis fasciventris*, *Ceratitis anonae*, *Ceratitis rosa*) and the mango fruit fly, *Ceratitis cosyra*. Here we provide a synthesis of the current knowledge about the population structure of the main frugivorous fruit flies that are pests in Africa.

Keywords Microsatellite markers • Genotypic groups • Range expansion • Cryptic speciation • Inductive/deductive approaches

1 Introduction

Population genetics deals with the ecological and evolutionary processes that affect the population structure of species. Inferences from population genetics studies rely on both inductive and deductive approaches (reviewed in Hamilton 2009). Inductive approaches are typically adopted in descriptive studies when measures of genetic variation (parameters) are collected from representative population samples and

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used to infer the evolutionary processes that generated the observed population structure. Conversely, the deductive approach uses general population genetics models that describe evolutionary processes (e.g. bottlenecks and genetic drift, mutation, natural selection) to make predictions about spatial and temporal changes in the genetic patterns of the target species.

Allozyme markers were commonly used to describe the population structure of tephritid flies in early studies (e.g. McPheron et al. 1988; Feder et al. 1997; Abreu et al. 2005). Microsatellite markers (or single sequence repeats, SSR) were then widely adopted for the description of native and introduced African tephritids (see below). Microsatellite markers are co-dominant, polymorphic nuclear loci, that are distributed throughout the genome and generally neutral unless linked to loci under selection. They are short repeated sequences of nuclear DNA (one to six base pairs in length) with allelic states that simply correspond to the number of repeats present at each locus that can be scored after electrophoresis of PCR-amplified DNA fragments (Hamilton 2009). These characteristics make microsatellite markers good candidates for comparing different populations and their colonization dynamics (Tautz 1989; Hamilton 2009). The more recent population genomic approaches that rely on high-throughput sequencing techniques (i.e. Next Generation Sequencing, or NGS) now allow the population structure of species to be described in unprecedented detail (Davey and Blaxter 2010; Elshire et al. 2011; Narum et al. 2013); studies using NGS on tephritid fruit flies are becoming more and more common (Shen et al. 2011; Zheng et al. 2012; Nirmala et al. 2013; Geib et al. 2014). During the past three decades a number of studies have been published on the population genetics of African fruit flies. Below we synthesise current knowledge on the population genetics of the main African fruit fly species in the genera *Ceratitis* (i.e. the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), the mango fruit fly, *Ceratitis cosyra* (Walker), and the *Ceratitis* 'FAR' complex); *Bactrocera* (i.e. the oriental fruit fly, *Bactrocera dorsalis* [Hendel]); and *Zeugodacus* (i.e. the melon fruit fly, *Zeugodacus cucurbitae* Coquillett).

2 *Ceratitis capitata*

Ceratitis capitata, is one of the most economically important and widely distributed tephritid pests of African origin (White and Elson-Harris 1994). After considering morphological cladistics, host plant abundances and parasitoid distributions, De Meyer et al. (2002) proposed that Eastern and Southern Africa are the most likely geographic origin of this cosmopolitan pest. Historical records provided important clues to develop hypotheses about the worldwide range expansion of *C. capitata*. For example, *C. capitata* was first reported in Costa Rica (1955) and then Guatemala (1976) before reaching Mexico, possibly due to rapid movement through the so-called 'coffee belt' (Malacrida et al. 1998 and references therein). It has also been reported intermittently in Florida since 1929, in California since 1975, and in Texas since 1966 (Gasparich et al. 1997). *Ceratitis capitata* was introduced into Australia

from Europe in around 1897 (Malacrida et al. 1998) where it is currently confined to Western Australia with occasional detections in South Australia and the Northern Territory. Its distribution in Australia has remained unchanged for the last half century and this is likely to be due to the geographical barriers that prevent free movement of this species across Australia and /or to extensive Australian monitoring systems and quarantine restrictions (Dominiak and Daniels 2012).

The first large-scale descriptions of the population structure of *C. capitata* were largely inferred using allozyme markers (e.g. Gasperi et al. 1991). An early reconstruction of the worldwide range expansion of *C. capitata* was attempted when two African populations (from Kenya and La Réunion), two Mediterranean populations (from Procida and Sardinia), and one Central American population (from Guatemala) were genotyped at 27 allozyme loci (Malacrida et al. 1992). Combining these results with historical records, Malacrida et al. (1992) was able to separate *C. capitata* populations in to three groups: ancestral (from sub-Saharan Africa), ancient (Mediterranean) and new (American) and suggested that the colonisation of Central America started from a recent African introduction. Furthermore, they were also able to describe temporal variability in the genotypic patterns of one of the Mediterranean samples, which they attributed to seasonal population fluctuations (see also Gasperi et al. 2002). A more extensive study (Malacrida et al. 1998) used 26 allozyme markers to compare 17 populations from six regions: Africa, Mediterranean, 'extra-Mediterranean islands' (e.g. Gran Canaria and Madeira), Latin America, Pacific and Australia. Levels of genetic variability (as estimated from the number of alleles per locus, percentage of polymorphic loci and mean heterozygosity) suggested that *C. capitata* originated in East Africa (where the highest genetic diversity was observed), and expanded its range to the African–Mediterranean region first (as suggested by a gradual pattern of decreasing genetic variability) and, most recently, to the Latin American–Pacific region. Gene flow estimates, determined from the average frequency of private alleles and the number of migrants, also suggested a route of colonization from South East Africa to northwest Africa and from there to Spain, followed by a West-east Mediterranean range expansion. Additionally, Malacrida et al. (1998) hypothesised that the Latin American and Pacific populations originated from a few, recent and geographically separated colonization events followed by population expansions. In this context, both ancient and recent colonization events involving *C. capitata* were largely attributed to human-mediated transportation and to the history of human trading activities (Malacrida et al. 1998).

Despite the important role that allozyme studies played in the first large scale descriptions of the population structure of *C. capitata*, they could only provide indicative, rather than categorical, information about the chronology of range expansion (Gasparich et al. 1997). It was hoped that new alternative methods and approaches would achieve this and they included: the analysis of intron size polymorphisms (Gomulski et al. 1998); restriction site variation (Haymer et al. 1992; Sheppard et al. 1992; McPheron et al. 1994; Gasparich et al. 1995; Gasparich et al. 1997); Random Amplified Polymorphic DNA (Haymer et al. 1997); and Sanger sequencing (Davies et al. 1999). These approaches did support the African origin of

C. capitata but did not allow any better resolution of its expansion history beyond Africa.

Subsequently microsatellite markers were developed for *C. capitata* (Bonizzoni et al. 2000; Stratikopoulos et al. 2008) and, due to their high levels of polymorphism, provided much better resolution compared to earlier molecular techniques; they were used successfully to investigate the population structure of *C. capitata* (Karsten et al. 2013) and the origin of *C. capitata* infestations in North America (Bonizzoni et al. 2001) and Australia (Bonizzoni et al. 2004). Microsatellites suggested that flies captured in California originated from independent introduction events, including introductions from Central America (Bonizzoni et al. 2001), but also that incomplete eradication might have resulted in endemic Californian populations. The origin of periodic *C. capitata* infestations in California is highly controversial and there remains disagreement as to whether the flies captured over the years represent independent introductions from external sources, or resident populations with sizes fluctuating from non-detectable to detectable levels (Carey 1991; Papadopoulos et al. 2013; Carey et al. 2014; Gutierrez et al. 2014). Conversely, colonization of Australia was more convincingly attributed to secondary colonization from the Mediterranean basin, and the Perth area was indicated as the source for secondary invasion into both Western and South Australia (Bonizzoni et al. 2004). The possible invasion routes of *C. capitata* were reviewed and summarised by Malacrida et al. (2007) who further stressed the importance of human-mediated transportation in the worldwide range expansion of *C. capitata*. Human-mediated movements related to trade of commodities and transport by air, sea and land are generally accepted as the primary mechanism by which *C. capitata*, and other economically important tephritid species, have spread (White and Elson-Harris 1994; see also Karsten et al. 2015 and references therein).

To date, only one study has adopted a deductive approach to investigating the range expansion dynamics of *C. capitata* (Karsten et al. 2015). This approach proved useful, particularly since recent improvements to model-based analyses became available, such as Approximate Bayesian Computation (ABC; Estoup and Guillemaud 2010). ABC modeling allows the complex evolutionary scenarios that are expected in range expansions of cosmopolitan pests to be taken into consideration, and inferences to be made on parameters such as: date of founding of different populations (in numbers of generations); current effective population size (as numbers of diploid individuals); number of founders in the introduced populations; and duration of the initial bottleneck. Results of the Karsten et al. (2015) study suggested that the most likely route of *C. capitata* from Africa closely matched the patterns indicated from historical records, though with much earlier introductions. An initial colonization of Europe, a secondary colonization of Australia from Europe, an introduction from Greece to Central America and, eventually, a back introduction into South Africa from Europe were also implied. This reconstruction did, however, differ from those previously proposed (Malacrida et al. 2007) as it supported secondary colonisation of Central America from admixed European populations (hence, not from Africa) and secondary reintroduction in Africa from Europe.

3 *Ceratitis cosyra*

The mango fruit fly, *C. cosyra*, is possibly the most important pest of mango throughout sub-Saharan Africa (Lux et al. 2003a; Vayssières et al. 2009). Out of the mango season, *C. cosyra* shifts to alternative host plants including wild fruits such as marula, *Sclerocarya birrea* (A. Rich.) Hochst. (Copeland et al. 2006) and soursop, *Annona muricata* L. (Mwatawala et al. 2009). Barr et al. (2006) were the first to suggest that *C. cosyra* was comprised of highly divergent mitochondrial haplotypes; DNA barcodes from two specimens sampled along the coast of southern Kenya (Shimba Hills) were clearly separated from the main haplotype group, thus suggesting cryptic speciation (Barr et al. 2006). In order to further investigate this hypothesis, a set of microsatellite markers was developed (Delatte et al. 2014) and used to describe the population structure of *C. cosyra* across its distribution (Virgilio et al. 2015a). Analysis of 348 specimens from 13 African populations showed that *C. cosyra* was indeed represented by two separate genotypic groups (Fig. 3.1); one included the vast majority of specimens sampled in Burundi and Tanzania as well as a number of outliers from other African countries, while the other included all other specimens sampled. The two genotypic groups were also found, in sympatry, in populations from Kenya, Senegal, Sudan and Tanzania (Virgilio et al. 2015a). Sequential Bayesian assignment of microsatellite genotypes (as described by Coulon et al. 2008) also revealed that, within the second genotypic group, specimens could be further subdivided between a West African cluster (including individuals from Burkina Faso, Ivory Coast, Mali and Nigeria) and an East / South African cluster (including specimens from Ethiopia, Tanzania, Malawi, Mozambique and South Africa) (Virgilio et al. 2015a). This more subtle genetic differentiation was less clear-cut as, for example, specimens from Sudan were genetically closer to the West African samples, and populations from Kenya and Senegal included individuals from both clusters.

4 The ‘FAR’ Complex

The so call *Ceratitis* ‘FAR’ complex is a group of African frugivorous flies including the Natal fruit fly, *C. rosa,* and the morphologically similar but less economically important pests, *Ceratitis fasciventris* (Bezzi) and *Ceratitis anonae* Graham. The three species all show clear sexual dimorphism, with the males having distinct leg ornamentation patterns, while in females these are almost indistinguishable (De Meyer 2001). All members of the ‘FAR’ complex are highly polyphagous with partially overlapping ranges of host plants and geographic distributions (Copeland et al. 2006). Two of these species, *C. rosa* and *C. fasciventris*, have weak reproductive barriers as, when crossed under laboratory conditions, they can produce fertile offspring (Erbout et al. 2008). Phylogenetic analyses of morphological characters (De Meyer 2005) and of mitochondrial and nuclear gene fragments could not fully

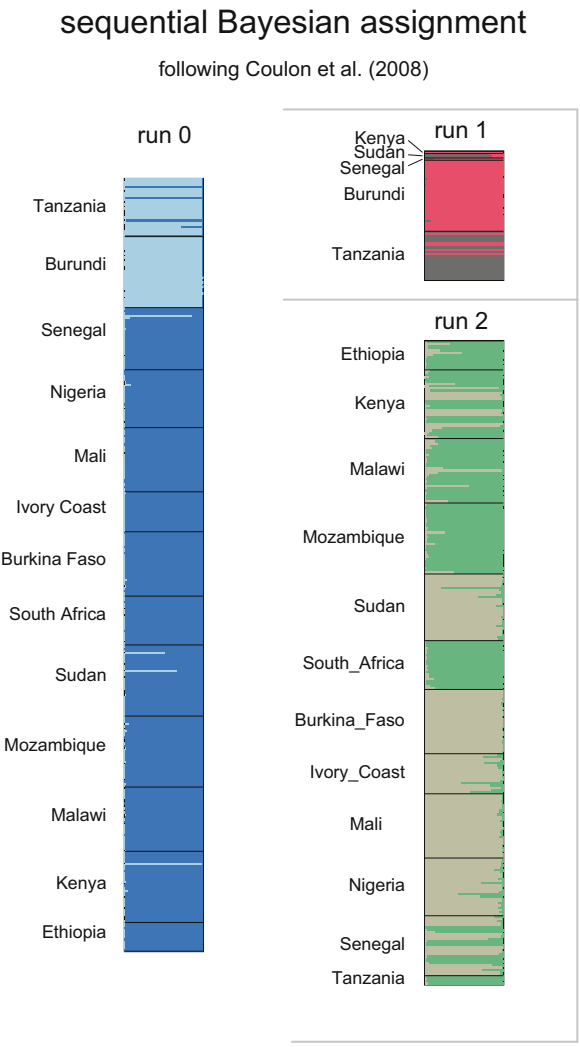

Fig. 3.1 Population structure of *C. cosyra* as inferred from individual Bayesian assignment of multilocus microsatellite genotypes (From Virgilio et al. 2015a)

resolve these three species as distinct monophyletic entities (Virgilio et al. 2008; Barr and Wiegmann 2009). Despite this, genetic differentiation has been reported between samples of *C. fasciventris* from West and East Africa (Virgilio et al. 2008) and between samples of *C. rosa* from Kenya and South Africa (Douglas and Haymer 2001). An earlier study using microsatellites also revealed differences between populations of *C. rosa* from the African mainland and populations of *C. rosa* from the Indian Ocean islands, as well as between populations of *C. fasciventris* from Kenya and populations of *C. fasciventris* from Uganda (Baliraine et al. 2004).

In order to finally resolve the molecular taxonomy and population structure of the 'FAR' complex, a set of 16 microsatellite markers was developed (Delatte et al. 2013) and used to genotype 27 African populations of the three morphospecies (Virgilio et al. 2013). This revealed the presence of five genotypic clusters: two contained *C.*

rosa specimens (R1, R2; allopatric and sympatric populations), two contained *C. fasciventris* specimens (F1, F2; allopatric and parapatric populations) and one contained *C. anonae* specimens (A). Surprisingly, intra- and interspecific genetic diversity was not hierarchically structured; differences in diversity between clusters from the same morphospecies (e.g. between F1 and F2, or between R1 and R2) was greater or comparable with differences between clusters from different morphospecies (e.g. between F1 and A, or between R2 and A). The two *C. fasciventris* genotypic clusters roughly corresponded to West and East African samples, respectively, with the exception of a single population from Tanzania that was more closely related to the West African samples than the East African samples. Relationships amongst the 'FAR' morphospecies and the genotypic clusters were further investigated using an integrative taxonomic approach that included spatial ecology, wing morphometrics, larval morphology, analysis of cuticular hydrocarbons, developmental physiology and pre- and postzygotic mating compatibility. The results of these studies (reviewed in De Meyer et al. 2015a) indicated that the *Ceratitis* 'FAR' complex includes between three and five different taxonomic entities. Males from the two *C. rosa* clusters were morphologically different and were provisionally acknowledged as either 'R1' or 'R2' (De Meyer et al. 2015a) but also, in relation to their different distributional/altitudinal ranges (Mwatawala et al. 2015), as 'lowland' or 'hot' *C. rosa*, and 'highland' or 'cold' *C. rosa*. The integrative approach implemented on the *Ceratitis* FAR complex provided sufficient evidence to consider R1 and R2 as two different biological species, with the type material of *C. rosa* belonging to the R1 type and the R2 type considered as a new species, *Ceratitis quilicii* (De Meyer et al. submitted).

5 *Zeugodacus cucurbitae*

Zeugodacus cucurbitae (Coquillett) stat. rev. (formerly classified as *Bactrocera* (*Zeugodacus*) *cucurbitae* (Coquillett)) was originally described from material collected in Honolulu, Hawaii, USA (Coquillett 1899). Its systematic position was recently revised due to reconstruction of its phylogenetic history. The former subgenus *Zeugodacus* is now considered as a separate genus that is independent from both *Bactrocera* and *Dacus*, and more closely related to the genus *Dacus* than to the genus *Bactrocera* (Krosch et al. 2012; Virgilio et al. 2015b; De Meyer et al. 2015b).

The genus *Zeugodacus* includes approximately 115 species (Norrbom et al. 1999; Drew and Romig 2013) of which the majority are restricted to the Oriental and Australian regions with a few species in the eastern Palearctic regions of China and Japan. The exception is *Z. cucurbitae* which is considered as an invasive pest in Africa and the islands of the Indian Ocean. Jacquard et al. (2013) analysed two mitochondrial gene fragments (COI-ND6 genes, 1297 bp) from 100 specimens of *Z. cucurbitae* sampled from across its distribution (Asia, Hawaii, African mainland and islands of the Indian Ocean). They found remarkably limited intraspecific variability amongst specimens with only 22 haplotypes, 21 polymorphic sites and an average p-distance of 0.003 %. Despite this, a Minimum Spanning Network revealed the occurrence of two clearly distinct haplotype groups corresponding to

specimens from (a) Asia and Hawaii, and (b) the African mainland and La Réunion. A finer resolution of the geographic structuring of *Z. cucurbitae* was obtained using microsatellite genotyping of 25 populations sampled from across its entire distribution range (Virgilio et al. 2010). This macrogeographic study of its population genetics revealed the existence of five population groups corresponding to populations from (i) the African continent, (ii) Reunion Island, (iii) Central Asia, (iv) East-Asia and (v) Hawaii. The proportions of inter-regional Bayesian assignments and the high values for genetic diversity in populations from Pakistan, India and Bangladesh suggested that *Z. cucurbitae* originated in Central Asia and expanded its range in one direction to East Asia and Hawaii and in the other direction to Africa and the islands of the Indian Ocean. However, there were a number of outliers with high levels of admixing ($Q>0.70$) amongst populations from different regions which suggested there were more complex patterns of inter-regional gene flow ongoing, possibly as a result of human-mediated transport (Virgilio et al. 2010).

Zeugodacus cucurbitae has also been reported from a series of unrelated host plant families in addition to the main host range represented by *Cucurbitaceae* (see De Meyer et al. 2015b and references therein) and geographic differences in host preferences have also been reported between East and West African populations (Vayssières et al. 2007; Mwatawala et al. 2010; Jacquard et al. 2013). Despite these observations cucurbit hosts are generally preferred and are attacked with higher infestation rates and incidences compared to non-cucurbit hosts. Host records also suggest that feeding preferences differ between populations of *Z. cucurbitae* from the native distribution and populations from the adventive distribution, possibly resulting in locally adapted populations or host races. The fine-scale analysis made on data from 2258 specimens collected from 11 locations in La Réunion elucidated relationships between the genetic structure of *Z. cucurbitae* and environmental factors such as altitude (range 0–400 m, 400–600 m and 600–1200 m), host plant (cultivated and wild cucurbits) and season (subtropical winter and summer) (Jacquard et al. 2013). The presence of three main genetic clusters (with limited inter-cluster genetic structuring) were revealed that could be differentiated from African and Asian populations (although they were of possible African origin) and were distinctly distributed on the eastern and western parts of the island. Abundances of specimens from the three clusters were correlated with the average amount of rainfall while no significant differences were detected in their distribution on wild or cultivated host plants, across altitudinal ranges or across different seasons (Jacquard et al. 2013). Other studies, done in Asia, the South-East Pacific and Hawaii (Clark and Boontop, unpublished data), and in Tanzania (De Meyer et al. 2015b), also showed a lack of consistent genetic differentiation across samples of *Z. cucurbitae* with different feeding preferences.

The results of Jacquard et al. (2013) suggested a common ancestry for the African *Z. cucurbitae* but left a number of questions about the potential colonization pathway open. Two alternative hypotheses for this colonization had been proposed previously by Virgilio et al. (2010) who suggested either a relatively recent invasion of the African continent, roughly corresponding to the first historical records for this species in Africa (*viz.* 1936 in East Africa and 1999 in West Africa), or an older range expansion possibly dating back to the first documented trade contact between Africa and Asia

(100 AD, Gilbert 2004). In order to determine whether either of these hypotheses was correct, Delatte et al. (unpublished data) evaluated a large number of populations (17) from East, West and Central Africa using a larger set of markers than the previous study of Virgilio et al. (2010). This allowed better resolution of the population structure of *Z. cucurbitae* in Africa and, using STRUCTURE analysis as described by Pritchard et al. (2000), showed that the populations from Uganda had diverged from Tanzanian populations and that populations from Burundi and Kenya had traces of admixture with West African samples. The ABC analysis in the DIYABC software (Cornuet et al. 2010, 2014) also suggested that *Z. cucurbitae* had expanded its range in to East and West Africa. Recent studies of the routes of worldwide introductions of alien organisms suggest that many widespread invasions may not have originated from the native range, but from a particularly successful invasive population; these invasive populations could serve as the source of colonists for remote new territories and has subsequently been termed the 'invasive bridgehead effect' (Lombaert et al. 2010). In the case of *Z. cucurbitae*, Central Asia was the most likely native source population, and East Africa the source population that adapted and was the start point of the invasive bridgehead effect for all the colonization events that subsequently occurred in Africa. The parameter estimates from DIYABC suggested that these events occurred soon before the first historical records of *Z. cucurbitae* in the African continent and allow us to exclude alternative hypotheses considering older introductions of *Z. cucurbitae* in to Africa or multiple invasion events (Virgilio et al. 2010).

6 *Bactrocera dorsalis s.s.*

In Africa, *B. dorsalis s.s*, has been reported infesting 72 plant species spread across 28 families (Goergen et al. 2011) and, in mango orchards, causes yield losses of up to 80 % (Ekesi et al. 2006). Due to its major impact on horticultural products, *B. dorsalis s.s.* is one of the most devastating fruit fly pests in Africa (De Meyer et al. 2010). *Bactrocera dorsalis s.s.* is part of the notorious *B. dorsalis* complex that includes almost 100 species (Drew and Hancock 1994; Drew and Romig 2013), is of Asian origin (Clarke et al. 2005) and difficult to identify using morphological or molecular techniques (Khamis et al. 2012; Leblanc et al. in press). Recently, the taxonomy of three important pests within this complex (*Bactrocera papayae* (Drew and Hancock), *Bactrocera philippinensis* (Drew and Hancock) and *Bactrocera invadens* (Drew, Tsuruta and White)) was revised and they were synonymized as *B. dorsalis s.s.* (Schutze et al. 2015). *Bactrocera invadens* was initially described as a novel species native to Asia and introduced into East Africa (Drew et al. 2005). In fact, *B. dorsalis s.s.* was recorded for the first time on the African mainland in 2003 (Lux et al. 2003b) where it had already become a pest species of major concern to fruit growers (see De Meyer et al. 2010 and references therein). The African expansion of *B. dorsalis s.s.* was extremely rapid. After the first record in Kenya, it was subsequently recorded in Tanzania and Nigeria, then it rapidly spread to the west and to the south and it is now distributed throughout sub-Saharan Africa (Table 3.1).

Table 3.1 Range expansion of *B. dorsalis s.s.* in Africa

Country	Year of arrival	Reference
Kenya	2003	Lux et al. (2003a)
Tanzania	2003	Mwatawala et al. (2004)
Nigeria	2003	Umeh et al. (2008)
Uganda	2004	Drew et al. (2005)
Benin	2004	Drew et al. (2005); Vayssières et al. (2005)
Ghana	2005	Drew et al. (2005)
Comoros Archipelago	2005	De Meyer et al. (2012)
Cameroon	2005	Ndzana Abanda et al. (2008)
Guinea	2006	Ekesi et al. (2006)
Senegal	2006	Ekesi et al. (2006)
Sudan	2006	Ekesi et al. (2006)
Togo	2006	Ekesi et al. (2006)
Ivory Coast	2007	Goergen et al. (2011)
Ethiopia	2007	EPPO/CABI (2014)
Mayotte	2007	De Meyer et al. (2012)
Burkina Faso	2007	Goergen et al. (2011)
Mali	2007	Goergen et al. (2011)
Namibia	2007	APHIS (2009)
Mozambique	2008	Correia et al. (2008)
Chad	2008	Goergen et al. (2011)
Angola	2008	Goergen et al. (2011)
Congo	2008	Goergen et al. (2011)
Democratic Republic of Congo	2008	Goergen et al. (2011)
Equatorial Guinea	2008	Goergen et al. (2011)
Gabon	2008	Goergen et al. (2011)
Gambia	2008	EPPO/CABI (2014)
Guinea-Bissau	2008	Goergen et al. (2011)
Liberia	2008	EPPO/CABI (2014)
Mauritania	2008	Goergen et al. (2011)
Niger	2008	Goergen et al. (2011)
Sierra Leone	2008	Goergen et al. (2011)
Central African Republic	2008	Goergen et al. (2011)
Zambia	2009	EPPO/CABI (2014)
Burundi	2009	Liu et al. (2011)
Madagascar	2010	Raoelijaona et al. (2012)
Zimbabwe	2010	Cassidy (2010)
Botswana	2011	EPPO/CABI (2014)
South Africa	2007, 2013	Manrakhan et al. (2015)
Swaziland	2014	EPPO/CABI (2014)

Bactrocera dorsalis s.s. has also reached the islands of the Indian Ocean, beginning with the Comoros archipelago in 2006 and Madagascar in 2010. Other invasive populations of *B. dorsalis s.s.* have been reported in Hawaii, French Polynesia, Japan, Nauru, Guam and the Northern Mariana Islands (Stephens et al. 2007).

After developing a set of 11 polymorphic microsatellite markers, Khamis et al. (2008) published the only study currently available on the African population structure of *B. dorsalis s.s* (Khamis et al. 2009). This study, based on a microsatellite analysis of 13 African populations (from nine countries) and including a population outgroup from Sri Lanka, showed the presence of three main population groups co-occurring across the African distribution of *B. dorsalis s.s.*. One of the three groups included a single population from Nigeria that also shared (limited) co-ancestry with the Asian outgroup. Khamis et al. (2009) hypothesized that the Nigerian population of *B. dorsalis s.s.* could have arisen either from an independent introduction from an unsampled source and/or could represent the outcome of a bottleneck. As a whole these genetic data suggest that the African range expansion of *B. dorsalis s.s.* (resulting from one or more introduction events) was followed by rapid population expansion (Fig. 3.2).

Other studies have investigated the genetic structure of *B. dorsalis s.s.* in Asia (Liu et al. 2007; Shi et al. 2010; Wan et al. 2011), and revealed high levels of genetic diversity between and within samples which supported a South-east Asian origin for *B. dorsalis s.s.* Microsatellite markers also showed relatively high levels of genetic diversity within populations from South-East Asia and high gene flow between

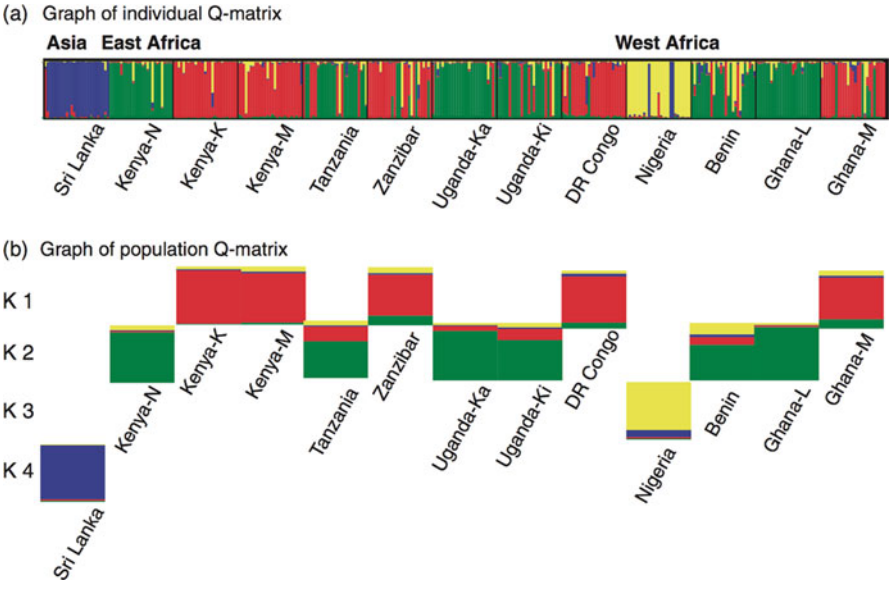

Fig. 3.2 Population structure of *B. dorsalis s.s.* in Africa as inferred from individual Bayesian assignment of multilocus microsatellite genotypes (Modified from Khamis et al. 2009)

population groups but were unable to resolve straightforward geographic patterns (Aketarawong et al. 2007, 2014). Similar results were observed for populations from the Thai/Malay peninsula which were a predominantly panmictic population (Krosch et al. 2013). In adventive Hawaiian populations mitochondrial (Barr et al. 2014) and nuclear markers (Aketarawong et al. 2007) also only detected limited genetic structuring, supporting a recent introduction in to Hawaii followed by genetic differentiation in an environment of isolation.

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