

*Annual Review of Entomology*The Global Epidemic of
Bactrocera Pests: Mixed-Species
Invasions and Risk AssessmentZihua Zhao,^{1,2} James R. Carey,³ and Zhihong Li^{1,2,*}¹Department of Plant Biosecurity, College of Plant Protection, China Agricultural University, Beijing, China, email: zhzhao@cau.edu.cn, lizh@cau.edu.cn²MARA Key Laboratory of Surveillance and Management for Plant Quarantine Pests, China Agricultural University, Beijing, China³Department of Entomology and Nematology, University of California, Davis, California, USA, email: jrcarey@ucdavis.eduANNUAL
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**Keywords**

biological invasions, life history, interception, invasion pathways, invasion risk, tephritid fruit flies

Abstract

Throughout the past century, the global spread of *Bactrocera* pests has continued to pose a significant threat to the commercial fruit and vegetable industry, resulting in substantial costs associated with both control measures and quarantine restrictions. The increasing volume of transcontinental trade has contributed to an escalating rate of *Bactrocera* pest introductions to new regions. To address the worldwide threat posed by this group of pests, we first provide an overview of *Bactrocera*. We then describe the global epidemic, including border interceptions, species diagnosis, population genetics, geographical expansion, and invasion tracing of *Bactrocera* pests. We further consider the literature concerning the invasion co-occurrences, life-history flexibility, risk assessment, bridgehead effects, and ongoing implications of invasion recurrences, as well as a case study of *Bactrocera* invasions of California. Finally, we call for global collaboration to effectively monitor, prevent, and control the ongoing spread of *Bactrocera* pests and to share experience and knowledge to combat it.

1. INTRODUCTION

The genus *Bactrocera* Macquart is one of the most pestiferous within the Dipteran family Tephritidae. Members of this genus are of major economic importance because many *Bactrocera* species attack commercial fruits and vegetables in tropical, subtropical, and Mediterranean regions (21, 136). Throughout the past century, *Bactrocera* pests have posed significant threats to agriculture, international trade, and ecosystem functions (17, 41, 86). Evidence-based risk assessment studies have shown that the magnitude of the invasion threat from *Bactrocera* pests is still increasing (105, 127), especially for fruit production (60). Specifically, *Bactrocera* pests cause economic losses by damaging fruits, increasing production costs, decreasing yields, reducing quality due to contaminants, and limiting trade to importing countries (99).

Because of the economic importance of *Bactrocera* pests (61, 103), many countries with tephritid-friendly climates have intensive, ongoing monitoring programs (91). Studies have reported the interception (95), monitoring (33, 136), establishment (91), and management (32) of *Bactrocera* pests. In this article, we review the global epidemic of *Bactrocera* pests to understand the basic principles of invasion biology, as well as to aid in developing both local and regional policy.

2. INVASIVE BACTROCERA PESTS

2.1. General Overview

Tephritidae comprises more than 5,000 species classified into 500 globally distributed genera (4, 39, 141). Among them, *Bactrocera* Macquart was first described in 1835 but subsequently moved to *Dacus* as a subgenus (56, 57). Its current taxonomic status as a genus was established by Drew (37). Currently, *Bactrocera* Macquart is considered to be closely related to two sister genera within the Dacini: *Dacus* and *Zeugodacus* (21, 136). Many *Bactrocera* species have been documented to be invasive aliens, including *Bactrocera dorsalis* (Hendel) (122, 143, 145), *Bactrocera oleae* (Rossi) (106), *Bactrocera zonata* (Saunders) (150), *Bactrocera correcta* (Bezzi) (84), *Bactrocera latifrons* (Hendel) (92, 119), and *Bactrocera carambolae* Drew & Hancock, the last of which has recently become established in South America, having been introduced from Indonesia (87, 89).

2.2. Global Prevalence

Bactrocera constitutes a group of agricultural pests that, although collectively attacking a wide variety of crops, show wide interspecific variation in host range from oligophagous to polyphagous pests (122). A total of 73 *Bactrocera* species have been considered as pests and reported to have become established in new regions outside their areas of origin (136). Throughout the past century, *Bactrocera* species have repeatedly invaded many islands (e.g., Hawaii and Okinawa) (24, 119) and five continents, namely, Africa (86, 112), South America (89), North America (17), Oceania (131, 136), and Europe (95), causing substantial economic losses and trade restrictions in these regions.

In this review, we use the invasion framework proposed by Blackburn and colleagues (11) that divides the process into a series of stages, each of which imposes barriers that need to be overcome for a population to transition to the next stage (**Figure 1a**). Due to their high abundance, high reproductive rate, and broad host ranges, pests in *Bactrocera* have extraordinarily high propagule pressure potential (**Figure 1b**). The invasion records involving *Bactrocera* pests date back to the early to mid-1900s and have increased in recent decades. For example, *B. dorsalis* was first detected in Hawaii in 1945 (24) and quickly became a prominent pest. This species invaded the island of Tahiti in 1996, most likely having been introduced from Hawaii (135). Two other *Bactrocera* species had previously invaded Tahiti: *Bactrocera kirki* (in 1928) and *Bactrocera tryoni* (in 1970). *Bactrocera dorsalis* was first detected in California in 1960 (99) and in Mauritius in 1996 (116). *Bactrocera*

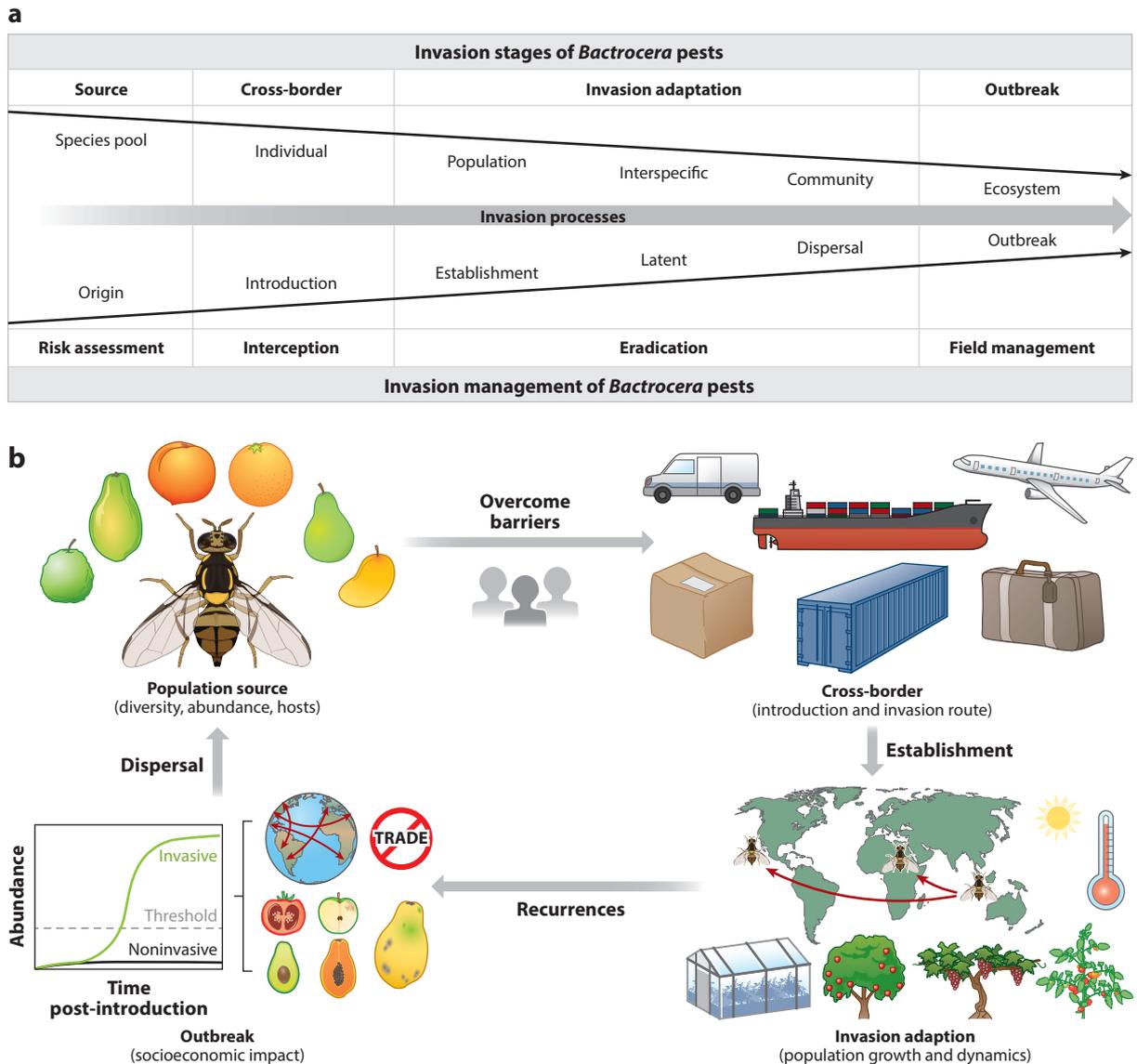


Figure 1

Diagram of general invasion patterns for *Bactrocera* pests. (a) Invasion processes. The invasion stages and management issues are listed in the upper and lower parts of the panel, respectively. (b) The detailed invasion stages (nodes) of *Bactrocera* pests. The invaded regions would be converted into new invasion sources, which indicates that the invasion stages result in cyclic dispersal globally.

zonata previously invaded Mauritius in 1987 and, in turn, displaced *Ceratitis* species to become the most economically important fruit pest (41). In North Queensland, invasion by *Bactrocera papayae* (synonym of *B. dorsalis*) was reported in 1998 (53). Both the speed and scale of *Bactrocera* invasions are historically unprecedented (143). Prior to 2016, *B. dorsalis* had never been detected in Europe. However, that year, it began appearing periodically in Switzerland, France, and Italy (95). Invasion events by *Bactrocera* pests are continuously increasing with globalization and are likely harbingers for the invasion of other tephritids and for the invasion of other insect groups in general.

Mixed-species

introduction: several species of the same genus are introduced simultaneously

Species complex:

a group of closely related species with similar morphological traits

2.3. Current Geographical Distribution and Economic Impact

Tropical and subtropical Asia are the major distribution centers of *Bactrocera* species (21). With the intensification of international trade, the species pools of *Bactrocera* pests have greatly enlarged via geographical expansion of the species. Indeed, invasion events involving *B. dorsalis* have been accelerating since the 1990s (143). *Bactrocera dorsalis* and *B. oleae* appear to be the most invasive and have been reported to have invaded more than 70 (143) and 34 (131) countries, respectively. Furthermore, *B. dorsalis* is expanding in its native region as a neonative (46) and in its invaded range in part due to global warming (55, 86). Consequently, the prevalence of *Bactrocera* pests is the outcome of both new introductions and geographical expansions in regions where they are currently established.

Pest *Bactrocera* spp. are of considerable economic importance due to losses in both the quantity and quality of fruits and other commodities (see 98). The cost of the tephritid invasion threat alone has been estimated at over US\$25 billion in California (17). The presence of *Bactrocera* pests in Asia continues to threaten the fruit industry (22, 104). For example, *B. dorsalis* caused yield loss due to a high fruit dropping rate (>50%) in Zhejiang, China (148), and *B. dorsalis* and *B. correcta* are estimated to have the potential to cause losses in the citrus industry of approximately US\$40 billion and US\$14 billion, respectively, in China (79). The implementation of consistent management actions and policy agreements designed to reduce the burden of *Bactrocera* pests is needed (91, 98).

2.4. International Trade and Interception

Because *Bactrocera* interceptions are commonly reported at ports during cross-border exchange (8, 80, 132), most countries with climates suitable for fruit flies either have imposed quarantine restrictions on fruit imports or require a phytosanitary treatment for all imported fruits (83). The Compendium of Fruit Fly Host Information of the USDA's Animal and Plant Health Inspection Service has documented 7,900 interceptions of 10 *Bactrocera* species and 20,560 records of 14 other tephritid species (81). The number of interceptions of *Bactrocera* species indicates a continuous propagule pressure of multiple species. *Bactrocera* species have been intercepted at ports of entry in many countries around the world, including the United States (140), China (65), France (95), Australia (22), South Africa (94), Korea (70), and New Zealand (74, 75). Interceptions of *Bactrocera* pests at Chinese ports increased by 180% in the 10-year period from 2010 to 2019 relative to interceptions done in the prior decade with the same sampling methods (68). Several *Bactrocera* species were intercepted as mixed-species introductions in a single container of imported fruits or vegetables (68). The development of intense transport networks has increased the number of routes for *Bactrocera* invasions (62, 97) (**Figure 1b**). The interception records reveal a high coin-troduction probability of multiple *Bactrocera* species, with coinvasions occurring in California and Hawaii (17, 136, 146).

3. THE POPULATION GENETICS OF *BACTROCERA* PESTS

3.1. Species Diagnosis

The taxonomy of *Bactrocera* is complicated, with more than 750 species placed in different subgenera within which there are species complexes (35, 37, 39). Four species complexes in a monophyletic species group have been described, including the *B. dorsalis* complex (38), the *Bactrocera musae* complex (40), the *B. tryoni* complex (23), and the *Bactrocera frauenfeldi* complex (36). Of these, the *B. dorsalis* complex is the most pestiferous, polyphagous, and widespread, with more than 70 described species (22). This complex is arguably the most taxonomically challenging (36). Unfortunately, a lacuna in the larval taxonomy of *Bactrocera* pests impedes accurate species

diagnosis if only immature larvae or residual corpses are present (114). Species diagnoses are needed at ports of entry in which morphological diagnoses are often impractical due to lack of whole adult specimens (7).

The Barcode of Life Data (BOLD) system (107) provides identification for candidate species and returns a species-level identification (59). A search using BOLD for “*Bactrocera*” revealed 18,508 records of 341 species (accessed on January 17, 2023). Several new tools have been developed to identify *Bactrocera* species, including real-time quantitative polymerase chain reaction (65, 134), sandwich hybridization assay, loop-mediated isothermal amplification, rolling circle amplification, and recombinase polymerase amplification (3); many of these technologies have been used to identify *Bactrocera* species based on an already established library (12, 72).

3.2. Population Genetics

Eight *Bactrocera* genomes are available to interested researchers through the database of the National Center for Biotechnology Information, including those of *Bactrocera neobumeralis*, *B. latifrons*, *B. correcta*, *B. tryoni*, *B. dorsalis*, *B. oleae*, *Bactrocera minax*, and *B. cucurbitae* (moved to *Zeugodacus* in 2018) (35). The chromosome-level genome of *B. dorsalis* revealed expansion of the DDE transposase superfamily related to environmental adaptation and enrichment of the unique gene families in defense response pathways (66). The high diversity of heat shock proteins in *B. dorsalis* may explain an intrinsic mechanism underlying its adaptation to varied environments, while the mitogen-activated protein kinase pathway facilitates adaptation to thermal stress (49). Inasmuch as the *CYP6a9* gene is thought to facilitate the thermal adaptation of *B. dorsalis*, it follows that understanding the role of this gene may provide important insights into the evolutionary adaptability that underlies its high invasion potential (51, 145). This trait may help explain its ability to spread and grow so rapidly (138) in an area with a climate different to the one from which it came. Based on a chromosome-level reference genome, 27 genes of *B. dorsalis* were shown to be associated with bioclimatic variables and thus to represent genetic properties that may enhance the thermal adaptation and ultimately the invasion potential of this species (145).

3.3. Invasion Tracing

The cross-border exchange of commercial fruits increases the possibility of *Bactrocera* dispersal, and population tracing is needed to monitor the invasion routes of introduced individuals (67, 148). The enzyme polymorphism of the *Adb2* gene was used to explore the origin of *Bactrocera* pests (48). Additionally, microsatellite markers revealed a western-oriented migration route of *B. dorsalis* within Asia, findings that imply genetic isolation in the complex geographical conditions of Bangladesh, Myanmar, and Hawaii (2).

The origins of *B. dorsalis* have been analyzed to deepen understanding of the underlying invasion processes involved in the spread of this species across Asian countries (70). Two invasion routes were reconstructed to reveal genetic bottlenecks of *B. dorsalis* in Pakistan and Hawaii (137). Genetic and geometric morphometric traits suggest that *B. dorsalis* dispersal to Africa and Hawaii was the result of separate, single introductions from South Asia, and South Asia was also the likely source of other Asian populations of *B. dorsalis* (103). The northward invasion of *B. dorsalis* into central China was the result of repeated introductions caused by the increasing domestic movement of infested fruits. The recent evidence based on a high-quality chromosome-level genome showed that *B. dorsalis* originated from southern India, with three independent invasion routes worldwide (145).

Invasion complexities generate complicated genetic structures that are confounded and thus cannot be interpreted straightforwardly. This is because successful invasions are seldom the result

Mixed-species invasion:

co-occurrence of several species of the same genus in a non-native region

Sibling species:

several related species that are morphologically nearly identical but are incapable of producing fertile hybrids

of a single beachhead event but rather of a hierarchy of events involving sequential or overlapping invasions, the results of which are referred to as metainvasions (111). Multiple introductions are often correlated with the success of *Bactrocera* establishment (113). The haplotypes of intercepted flies indicated that there are several pathways by which *B. dorsalis* invaded the United States. Indeed, this result is consistent with genetics-based studies of *B. dorsalis* that found no evidence of a single source in California (9).

4. MIXED-SPECIES INVASIONS OF *BACTROCERA* PESTS

4.1. Life-History Flexibility

Generally, *Bactrocera* species are invasive due not only to their wide distribution and rapid adaptability, but also to their demographic flexibility (64). Virtually all introduced populations need to adapt to the new environment (e.g., host and temperature) through a lagged process of naturalization (25, 26). Indeed, most successful invaders have high life-history flexibility that enables adaptation to varied environments (101) by modifying lifespans, fecundity, and host ranges (15, 19, 47). *Bactrocera dorsalis* has more than 250 fruit hosts (149), ranging from low-sugar tomato to high-sugar lychee. Life-history flexibility leads acclimation-induced responses to varied hosts (142), a response that is crucial for adaptation-driven resilience during invasion (108).

Not only can females of *B. tryoni* resorb their eggs to sustain survival during the winter (21), but the decrease in extreme cold events is likely to lead to improved fly survival in temperate Australia. The longevity of *B. tryoni* showed strong seasonality in a captive cohort, indicating a short-lived population in autumn and a longer-lived population in winter (128). Heat stress has the potential to increase fitness in the adult stage of *B. dorsalis*, the consequences of which would increase their economic impact (133). The hatch rate of eggs of young female partners paired with aging males increased with the age of the males, a pattern that supports the hypothesis that, under some circumstances, male fertility may increase rather than decrease with age (129, 130). Recently, the life-history flexibility of *Bactrocera* pests has been shown to be associated with the microbiome (54, 76, 110) and to enhance nutrition intake (109), fecundity (77, 144), resistance to pesticides (108), and lifespan (1).

4.2. Co-Occurrence

Trombik and colleagues (131) listed a total of 44 tephritid species as invasive aliens introduced from regions where they are endemic, including eight *Bactrocera* species (*B. carambolae*, *B. dorsalis*, *B. frauenfeldi*, *B. latifrons*, *Bactrocera ocbrosiae*, *B. oleae*, *B. tryoni*, and *B. zonata*). In this list of invasive *Bactrocera* pests, all species were associated with at least one serious invasion event. Interestingly, the *Bactrocera* invasions not only involve a single species, but also include co-occurrence of mixed-species invasions (99). We define mixed-species invasions as co-occurrences of several *Bactrocera* species in a non-native region. Ten tephritids (99), including four *Bactrocera* species (123), were reported to be cointroduced into both California and Florida. Furthermore, the co-occurrence of several *Bactrocera* species in a single infested fruit would lead to cointroduction and coinvasion of multiple species with similar life histories (82). The *Bactrocera* invasions in Africa were mixtures of multiple species of *B. dorsalis*, *B. zonata*, and *B. oleae* in Kenya (112). The invasions of *Bactrocera* pests tended to consist of multiple species in California (99), Florida (5), and Hawaii (136) in the United States; the Campania region of Southern Italy (95); the southern and central part of China (78); and Kenya (112).

Co-occurrences of several *Bactrocera* species are also very common in their originating regions of India (69), China (63), and Australia (96, 102). Especially for the *B. dorsalis* complex, several sibling species could be trapped in a single orchard due to overlapping host and geographic ranges

(22). Border interceptions of multiple *Bactrocera* species in the entry port indicate a high propagule pressure of mixed-species invasions (75, 81). Additionally, the increased transboundary movement of infested fruits has resulted in a high possibility of introduction events involving a mixture of several species of *Bactrocera* (7). Such mixed-species invasions of *Bactrocera* will impact border quarantine, pest management, and general biological research (31).

4.3. Invasion Succession

Species-specific traits have led to environment-dependent dominance in mixed-species invasions. Several *Bactrocera* pests have replaced species that were previously introduced. For example, *B. carambolae* replaced *Anastrepha* pests in French Guiana (43), and *B. dorsalis* replaced *Ceratitis capitata* in Hawaii (30). The species replacement of tephritids has been summarized (41), including evidence that the competitiveness of *Bactrocera* pests exceeds that of *Anastrepha* and *Ceratitis* pests. Many currently established *Bactrocera* pests will likely continue to expand their geographical ranges into new areas, the results of which will probably facilitate interspecific competition with already-established species (146). During coinvasion of multiple *Bactrocera* pests, the profound differences in mixed-species invasions could be determined by the partitioning model (146). For example, *B. dorsalis* are the most important tephritid pests in California, while other species (*B. zonata*, *B. tryoni*, and *B. correcta*) are rare invasive tephritid species.

4.4. Niche Shifts

After the *B. dorsalis* invasion, a shift in the host range and spatial distribution of previously established tephritids was observed for *B. zonata* and *C. capitata* in La Réunion (90), a change that could explain the competitive displacements of previous invaders. This interspecific competition will result in a decrease in abundance, and niche shifts of previous invaders of a polyphagous tephritid have been observed in areas already occupied by other tephritids (41, 42). *Bactrocera dorsalis* replaced *C. capitata* as the dominant pest on mango and citrus in Comoros, thus ultimately leading to coexistence through a niche shift, where higher-altitude regions with few host fruits constitute a refugial niche (58). Additionally, the host range of *B. dorsalis* has the potential to expand inasmuch as the species may not yet have encountered all potential hosts. Such host shifts may be occurring in China and South Africa (55, 86). The coexistence of several *Bactrocera* species caused by niche shifts provides a potential mechanism for mixed-species invasions (90); understanding niche shift is essential for the coinvasion and for modeling invasion risk.

5. INVASION RISK

5.1. Potential Geographical Distributions

Potential geographical distributions (PGDs) (44) normally rely on realized niches (98), together with occurrence records and climate data, and are capable of projecting the joint effects of environmental filtering and biotic interactions (71, 100). Data and information on more than 10 *Bactrocera* species have been analyzed to estimate the PGDs. For example, the PGDs of *B. dorsalis* have been estimated more than five times (28, 29, 34, 105, 121, 125); each analysis revealed that *B. dorsalis* had the potential to spread globally. In particular, these models indicate that many South American countries are highly vulnerable to *B. dorsalis* invasions (105).

PGD analysis indicated that, as would be expected from the endemic origins of *Bactrocera* spp., regions with tropical and subtropical climates were highly suitable for *Bactrocera* species. The Mediterranean climate could benefit the colonization of invasive *Bactrocera* pests in Europe, California, and Chile due to the relatively mild winter in these locations (150). Future climate

warming will likely enhance the global expansions of *Bactrocera* pests, including *B. dorsalis* (105), *B. correcta* (78), *B. tryoni* (120), and *B. oleae* (52).

5.2. Bridgehead Effects

Newly invaded regions could serve as sources of secondary introduction for alien organisms, a self-accelerating process known in invasion ecology as the bridgehead effect (10). The high frequency of secondary introductions will facilitate introduction of *Bactrocera* pests in the bridgehead regions. A large number of *Bactrocera* pests have been intercepted in passenger and cargo inspections at many ports in China (50) and the United States (80) from various source countries, indicating that secondary introductions are common in the current transport network. The global prevalence of *Bactrocera* pests results from the increased volume of trade, high propagule pressure, and the bridgehead effect, all of which act as drivers of global invasion rates. The probability of introduction of an alien organism was positively related to the frequency of interceptions, and most *Bactrocera* pests that are commonly intercepted at ports of entry are already established (13).

6. IMPLICATIONS FOR ONGOING INVASIONS OF *BACTROCERA* PESTS

6.1. Cyclic Recurrences

Many countries have employed phytosanitary strategies to monitor, trap, and eradicate invasive populations (33, 126). An area-wide eradication program has been applied to remove *Bactrocera* from the infestation area in the United States, Australia, and Senegal (14, 20, 91, 117). However, cyclic recurrence has been an important issue in *Bactrocera* invasions. There are three explanations for cyclic recurrence. First, seasonal introduction commonly leads to cyclic recurrences of *Bactrocera* pests due to the movement of infested fruits via frequent domestic trade (**Supplemental Figure 1a**). Second, the increasing area of greenhouses (**Supplemental Figure 1b**) provides a more stable environment with less fluctuation in climate and thus facilitates the colonization of alien organisms (139). Third, the global trade network facilitates the introduction of *Bactrocera* pests from multiple sources, which would further cause mixed-species invasions (**Supplemental Figure 1c**).

The cyclic recurrences caused by the resurgence from a subdetection level and the reintroduction would complicate the interpretation of data related to *Bactrocera* invasions. Reappearance patterns in invaded regions have been shown to describe the population dynamics of invasive tephritids, suggesting that populations persisting at subdetectable levels were more likely than those resulting from reintroductions (**Figure 2a**). *Bactrocera dorsalis* invasions always remained at low abundance in initial stages and then entered a period of rapid expansion in invaded regions (143). Eradication programs (**Supplemental Boxes 1–4**) are feasible only if alien individuals are detected early along their invasion continuum, and management resources are allocated rapidly (147).

6.2. Poleward Range Expansion

Poleward range expansion of *B. dorsalis* into temperate regions has been observed in Oceania, Asia, and Africa. In Australia, *B. tryoni* can survive temperate winters only in the adult stage (21). In China, *B. dorsalis* has spread to temperate regions, and some pupae were observed to survive winter and emerge successfully in the following year in central China (55). *Bactrocera dorsalis* was detected for the first time on the African continent in Kenya in 2003 (85); thereafter, it rapidly expanded to Zambia and northern Mozambique in 2008 (91), as well as to the Limpopo Province of South Africa in 2013 (86). In 2019, *B. dorsalis* was discovered in the California city of Redding,

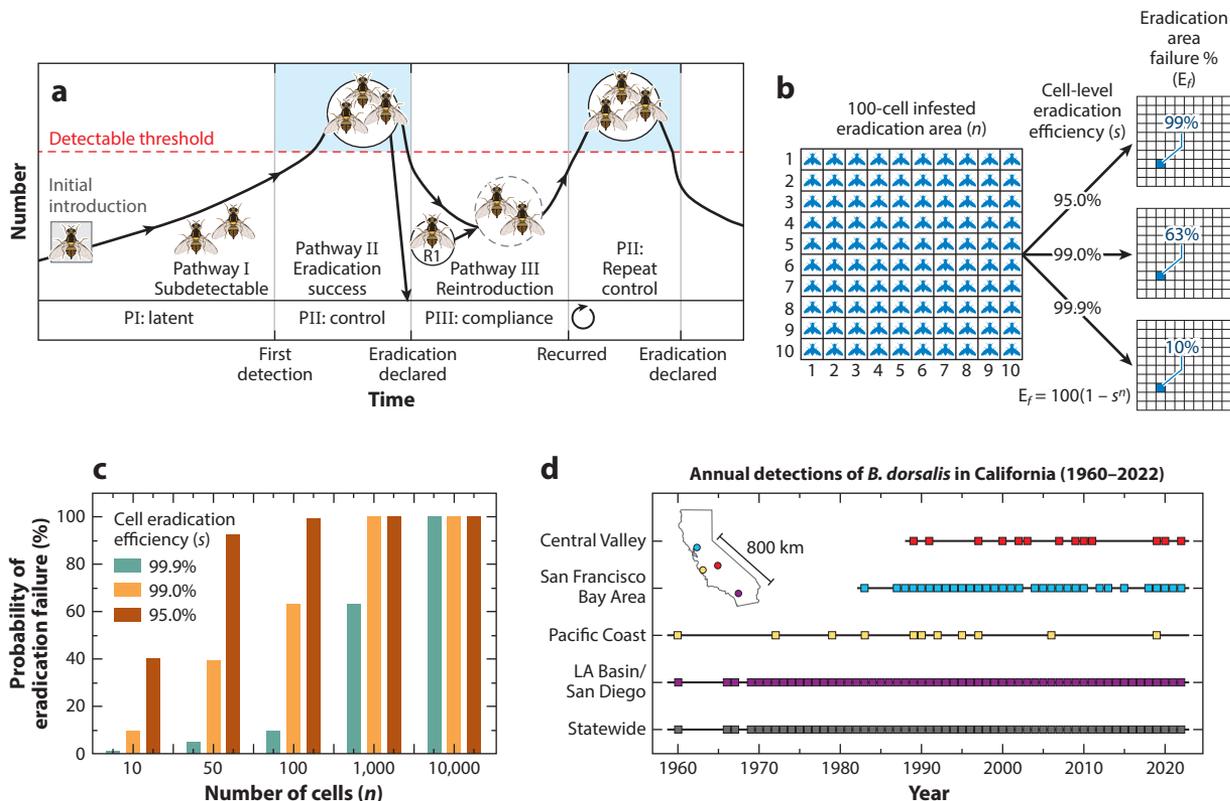


Figure 2

The statistical and practical challenges of eradication projects. (a) Schematic depicting population recurrence. Phase I is the latent phase. This phase is below a detectable threshold but characterized by growing levels. Phase II is the control phase. This phase begins shortly after the first detection, during which time the region is placed under the eradication procedures implemented. Phase III is the compliance phase. This phase begins when phase II ends, i.e., when no additional flies are captured. (b) Visualization of eradication model application to and output for the 100-cell eradication areas. (c) Relationship of grid number and three levels of single-cell eradication probabilities relative to overall likelihood of failure in a 100-cell system (see **Supplemental Boxes 1–3**). (d) Frequency of *Bactrocera dorsalis* detection in California.

a metropolis located in the northernmost region of the Central Valley. In addition, a warming climate would further facilitate range expansion of *Bactrocera* pests (52, 150).

Despite the many tools (6, 27, 117) available for management, *Bactrocera* pests often maintain a high prevalence and thus a high threat of further spread. It is thus not surprising that the numbers of first records of these pests in new regions are increasing. It follows that past plant quarantine measures designed to prevent invasions require updating with increases in globalization (115).

6.3. California as a Harbinger of Global *Bactrocera* Invasions

Nowhere in the world are *Bactrocera* invasions as frequent, recurrent, persistent, continuous, contiguous, widespread, and taxonomically diverse as those that have occurred in California (e.g., see the link to a YouTube animation of *B. dorsalis* invasion in **Supplemental Box 5**). The tephritid detections in this state stand apart in virtually every respect from those in all other fruit fly–friendly US states—17 species in 4 genera have been trapped in over 350 cities, and appearances of one or more species have been recorded for each of the past 60 years (16, 17, 99).

Supplemental Material >

In light of the history, scale, scope, persistence, and costs of the tephritid invasions in general (99) and of *B. dorsalis* in particular (18, 73), we believe that there is much to be learned from a more detailed look at the history of *B. dorsalis* in California, with a particular focus on the nearly 40-year debate on the nature of the problem underlying fly resurgences (17, 18). These reoccurrences underlie one of the most historically challenging, politically sensitive, professionally controversial, legally vexing, and economically consequential dilemmas faced by agricultural administrators: determining whether repeat detections of *B. dorsalis* result from reintroductions in which new incipient populations grow to detectable levels and are 100% eradicated every year or from long-established populations, which are at subdetection levels for long periods following intervention (**Supplemental Boxes 2–3**). The investigation of the long-term history of *B. dorsalis* in California is important because many other regions of the world are experiencing similar challenges, not only with the same species, but also with related ones.

Several factors drive, confound, and even impede deliberations on the nature of the underlying problem of *B. dorsalis* reappearances. One is the total absence of scientific guidelines or criteria upon which a declaration of tephritid establishment can be made (e.g., capture frequency, genetic markers, and/or spatial measures). Another factor is the conflation of eradication as defined operationally as a scientific absolute of 100% extirpation (93, 124) and eradication as defined by a single regulatory criterion of an absence of captures in a predefined period (88). Although declaring a species eradicated each year solves the short-term problem of avoiding quarantine, it may not solve the longer-term problem of population reoccurrences. The challenges involved in achieving eradication across infested regions are profound when these regions are considered as consisting of subregions. These statistical challenges can be illustrated with a simple statistical failure model (**Figure 2b,c**). These results reveal that, even with near-perfect eradication efficiency (e.g., 99.0%), a region with 100 grids yields an eradication failure probability of approximately two-thirds (**Supplemental Boxes 2–4**). Even with a near-perfect grid-level eradication efficiency of 99.9%, the probability of eradication failure in a 1,000-cell region is as high as 6 out of 10. Given these statistical results, as well as the fact that there are not hundreds or even thousands but rather many millions of backyards (each a cell) in the *B. dorsalis* outbreak regions of California, all eradication program managers should consider the long-term problem of population reoccurrences.

Considering the historical detections of *B. dorsalis* in California, we summarize the arguments for invasion status in the state that are presented in the literature (18, 73, 99, 118, 147). We list below four patterns that we believe collectively support the hypothesis that detections are due primarily to established populations rather than to reintroductions.

The first pattern consists of repeat detections after abrupt first appearances. Most first detections can be considered abrupt virtually by definition. However, a combination of one or more first detections that are followed by subsequent detections suggest population establishment. The first detections of *B. dorsalis* were reported in the southern California city of Anaheim in 1960. After several years, more flies were captured in and around Anaheim, and captures have continued.

The second pattern consists of long-term annual detections. Inasmuch as an established population is a population that persists over a long period, it follows that annual evidence of the presence of a species over many decades supports the hypothesis of population establishment. Invasion theory also supports the establishment hypothesis inasmuch as each annual invasion of *B. dorsalis* as a tropical species would require a suspension of a multiyear naturalization for each of the 60 years in which it has appeared.

The third pattern consists of repeat local detections. A spatial complement of detection patterns occurring annually over many decades is that many of the repeat detections occur in the same regions and neighborhoods. Approximately half of the cities in which this species has been

discovered experienced recurrence over this 48-year period, including one city that experienced the presence of *B. dorsalis* in each of 23 years.

The fourth pattern consists of contiguous geographic spread. Most areas with new detections were adjacent to and thus contiguous with areas in which this species was previously detected. This pattern of infestation expansion was especially striking in the areas in the Los Angeles Basin, the greater Los Angeles cosmopolitan region, and the San Francisco Bay Area (**Figure 2d**; see **Supplemental Box 5**).

Although all of the patterns listed above are suggestive of and consistent with population establishment (73, 99), no single pattern alone provides sufficient evidence to conclude that the population is likely established. In addition, all detection patterns need to be considered in appropriate spatial and temporal contexts. As noted by Carey et al. (18), data analysis of a single-fly capture database is key to understanding the underlying properties and nature of the invasion.

6.4. Tephritid Invasion Science

Developing an operational framework for conducting a systematic, objective, and comprehensive examination of detections is a requisite step in addressing the question of whether recurrences are due to established populations or to reintroductions. This step is important for at least two major reasons. The first reason is that, if it is determined that reintroductions are the source of the problem, then this immediately points to a failure somewhere in the biosecurity system designed to prevent introductions. For the California case, the question arises as to why prevention for *B. dorsalis* has been effective in the vast majority of at-risk US states despite intense propagule pressure at airports but has failed multiple times every year for over half a century in California. The second reason is because establishment implies that (a) the eradication strategies may effectively be controlling the invasive populations but not truly eradicating them, (b) the effectiveness of the monitoring systems is being overestimated, and/or (c) the criteria for declaring eradication are insufficient and thus in need of revision.

Tephritid invasions and policy must develop channels for effective engagement to ensure that fruit fly research and the detection data in particular are contextualized to deal with the complex ecological, social, and economic challenges posed by these species (45). Indeed, strategies need to be contingent, interactive, and iterative, as well as integrative and collective with respect to analysis of long-term detection data, fruit fly genetics, mathematical modeling, and informed and objective judgment (126).

7. CONCLUSIONS AND FUTURE PERSPECTIVES

The continued movement of infested host fruits among and within countries mediating *Bactrocera* invasions will challenge the plant quarantine system and biosecurity governance. In controlling these pests, the threat of mixed-species invasions underpins the need to build an effective collaborative network among agricultural stakeholders, researchers, and policy makers to identify and halt the spread of these pests.

SUMMARY POINTS

1. Considering that *Bactrocera* is tropical in origin, it is remarkable that these species are invading a variety of ecosystems with climates different from those that they are used to, ranging from semiarid climate to cold temperature.

2. A series of strategies could be applied based on invasion status, including strengthening surveillance, improving the species diagnosis and regulatory capacity of ports, and perfecting pest management methods.
3. Historical evidence of *Bactrocera* pests revealed that several species, including *Bactrocera dorsalis* and *Bactrocera tryoni*, can withstand the abiotic stressors of warm winter in temperate climates.
4. Recurrences of *Bactrocera* pests due to the reintroduction of a new population are indistinguishable from detections generated by established populations at subdetectable levels after eradication programs end.
5. The invasion of California by *B. dorsalis* is likely a harbinger of the future for many regions of the world experiencing repeat invasions and/or persistent and often subdetectable populations of this species.
6. The threat of mixed-species invasions underpins the need to build an effective collaborative network for identifying and halting the spread of tephritids.

FUTURE ISSUES

1. Studies are needed to determine the effects of climate change on *Bactrocera* adaptability for invading New World regions and on their genetics, as they relate to origins and shed light on aspects of population establishment of *Bactrocera* pests.
2. Guidelines are needed for the standardization of databases for detection of individual flies, including both adults and preadults. Analyses of these data need to be based on spatial ecology and ongoing, objective, hypothesis-driven science and be policy oriented. More transparent data on new invaders are essential for global management of tephritids to stop penalizing reporting countries with market access closures.
3. Criteria for launching intervention programs have not changed in decades and are largely ad hoc and universally applied across all species regardless of their differences in behavior, physiology, and ecology. Thus, there is an urgent need to develop new evidence-based protocols for aiding decision makers in deciding whether and when to launch a new intervention program.
4. Like current intervention protocols, the criteria used for declaring a tephritid population eradicated are in need of revisiting in light of the virtual impossibility of determining whether eradication is 100% certain based on trapping data over a single season and the wide detectability ranges between species. Staging concepts could be integrated into declarations, the first level of which would indicate a high likelihood of eradication, with subsequent levels indicating even higher probabilities as zero-detection years accumulate.

DISCLOSURE STATEMENT

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