Journal of Economic Entomology, 109(6), 2016, 2317–2328
doi: 10.1093/jee/tow196
Advance Access Publication Date: 4 September 2016
Research article

Analysis of Seasonal Risk for Importation of the Mediterranean Fruit Fly, *Ceratitis capitata* (Diptera: Tephritidae), via Air Passenger Traffic Arriving in Florida and California

A. M. Szyniszewska,[1,2] N. C. Leppla,[2,3] Z. Huang,[4] and A. J. Tatem[5,6,7]

[1]Geography Department, University of Florida, Gainesville, FL 32611 (aniasz@gmail.com), [2]Entomology and Nematology Department, University of Florida, Gainesville, FL 32611 (aniasz@gmail.com, ncleppla@ufl.edu), [3]Corresponding author, e-mail: ncleppla@ufl.edu, [4]Chinese Center for Disease Control and Prevention, Division of Infectious Disease, Key Laboratory of Surveillance and Early Warning on Infectious Disease, Beijing, China (seenhzj@gmail.com), [5]Department of Geography and Environment, WorldPop Project, University of Southampton, Highfield, Southampton, United Kingdom (Andy.Tatem@gmail.com), [6]National Institutes of Health, Fogarty International Center, Bethesda, MD 20892, (Andy.Tatem@gmail.com) and [7]Flowminder Foundation, Stockholm, SE (Andy.Tatem@gmail.com).

Received 27 May 2016; Accepted 10 August 2016

Abstract

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), is one of the most economically damaging pests in the world and has repeatedly invaded two major agricultural states in the United States, Florida and California, each time requiring costly eradication. The Mediterranean fruit fly gains entry primarily in infested fruit carried by airline passengers and, since Florida and California each receive about 13 million international passengers annually, the risk of Mediterranean fruit fly entering the United States is potentially very high. The risk of passengers bringing the pest into Florida or California from Mediterranean fruit fly-infested countries was determined with two novel models, one estimated seasonal variation in airline passenger number and the other defined the seasonal and spatial variability in Mediterranean fruit fly abundance. These models elucidated relationships among the risk factors for Mediterranean fruit fly introduction, such as amount of passenger traffic, routes traveled, season of travel, abundance of Mediterranean fruit fly in countries where flights departed, and risk of the pest arriving at destination airports. The risk of Mediterranean fruit fly being introduced into Florida was greatest from Colombia, Brazil, Panama, Venezuela, Argentina, and Ecuador during January–August, whereas primarily the risk to California was from Brazil, Panama, Colombia, and Italy in May–August. About three times more Mediterranean fruit flies were intercepted in passenger baggage at airports in Florida than California, although the data were compromised by a lack of systematic sampling and other limitations. Nevertheless, this study achieved the goal of analyzing available data on seasonal passenger flow and Mediterranean fruit fly population levels to determine when surveillance should be intensified at key airports in Florida and California.

Key words: *Ceratitis capitata*, Mediterranean fruit fly, risk analysis

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), one of the world's most destructive pests, has >250 hosts and is present in most of Africa, the Middle East, the Mediterranean region of Europe, Central and South America, western Australia, and the Pacific region, including Hawaii (Papadopoulos et al. 2001, 2002; Bakri 2013; Liquido et al. 2013; Badii et al. 2015). It has high dispersal capacity, and the most recent molecular studies revealed its likely historical invasion pathway as being initial colonization of Europe from Africa followed by secondary colonization of Australia from Europe (Karsten et al. 2015). Most of the Mediterranean fruit fly invasions outside of Africa have been due to expanding human travel and global trade (Malacrida et al. 2007). The Mediterranean fruit fly invaded Florida first in 1929 and later in 1956, 1962, 1963, 1967, 1981, 1990, 1997, 1998, and 2010 (Thomas et al. 2010), each time followed by eradication and continued surveillance and suppression. Eradication of a single outbreak in the Tampa Bay area in 1997 cost US$25 million (Szyniszewska 2013), but the economic consequences of Mediterranean fruit fly establishment would have been considerably greater. In California, the Mediterranean fruit fly was detected in 1975, 1980, 1984, and about annually in 1986–1994 before continuous suppression tactics were implemented (Dawson et al. 1998), without which the pest would have caused enormous economic losses by damaging crops and disrupting trade (Siebert and Cooper 1995). Elimination of Mediterranean fruit fly outbreaks in California during the past 25 yr cost taxpayers nearly US$500 million (Szyniszewska and Tatem 2014). If the Mediterranean fruit fly were to establish widely in California, long-term control would be expensive and a likely trade embargo by Asian countries on commodities from the state would result in further reductions in revenue, estimated at a total cost of control and lost trade of about US$1.2 billion in gross state product, plus elimination of thousands of jobs (Siebert and Cooper 1995). Relatively inexpensive eradication and suppression measures therefore are warranted, even though the pest may be established in some areas of the state (Carey 2010, Papadopoulos et al. 2013, Carey et al. 2014). Estimates of agricultural industry losses and eradication costs ranged from US$300,000 to US$200 million for individual incursions of the Mediterranean fruit fly into the United States between 1970 and 1990 (APHIS 1992).

Global air transportation greatly facilitates the unintended spread of organisms, including invasive pest species, such as the Mediterranean fruit fly, and the amount of goods and people transported internationally increases every year (Klassen et al. 2002, Drake and Lodge 2004, Tatem et al. 2006a, Westphal et al. 2008, Hulme 2009, Lopes-da-Silva et al. 2014, Papadopoulos 2014). There has been a particularly rapid increase in air travel in recent decades, with ~38 million scheduled flights and 3.3 billion passengers worldwide in 2014, about a 4% increase from the previous year (Tyler 2015). As a consequence, the expanding air traffic network and associated number of passengers have increased the rate of immigration and dispersal of organisms (Ware et al. 2011, Tatem et al. 2012, Tatem 2014). Disease-carrying mosquitos have survived long-haul flights as stowaways in aircraft cabins (Lounibos 2002, Tatem et al. 2006b, Benedict et al. 2007), and many invasive pest species are being encountered in cargo, passenger baggage, and postal shipments (Work et al. 2005, Liebhold et al. 2006, McCullough et al. 2006, Horton et al. 2013). However, to establish a pest population at the destination, an adequate number of colonizing individuals must travel on a route and encounter suitable environmental conditions (Levine and D'Antonio 2003; Drake and Lodge 2004; Lockwood et al. 2005, 2009; Tatem and Hay 2007; Tatem 2009). Based on interception data and recurrent outbreaks, the Mediterranean fruit fly seems to arrive in the United States, including Florida and California, at a sustained rate, mostly via infested fruit in airline passenger baggage (Liebhold et al. 2006).

While the international air travel network is constantly expanding and traffic on it increasing, the resources for passenger and cargo surveillance are limited and there is a proliferation in the number of potentially invasive species being intercepted (Klassen et al. 2002, McCullough et al. 2006). The U.S. Department of Agriculture (USDA), Animal and Plant Inspection Service (APHIS) maintained a record of pest interceptions at the ports of entry, known as the PestID database (formerly Port Information Network, PIN) from 1984 to 2003 before the Department of Homeland Security (DHS) assumed responsibility for inspection activities and the database. Between 1984 and 2000, 725,000 pest interceptions were recorded in the PestID database, 73% occurring at airports. More than half of those interdictions were associated with small parcels and baggage carried by travelers. Miami (MIA), New York (JFK), and Los Angeles (LAX) international airports accounted for 43% of all interceptions and 73.5–84.6% of the pests were insects. In Florida, 69% of the organisms seized were on flights that came from South and Central America and 22% originated in the Caribbean. Roughly 62% of the total was associated with passenger baggage, 30% with cargo, and 7% with plant propagative material. When the entire contents of randomly selected cargo aircraft arriving at MIA between September 1998 and August 1999 were inspected in an attempt to detect every foreign insect, the infestation rate was unacceptably high at 10.4% of all flights and about 23% for flights arriving from Central America (Dobbs and Brodel 2004). In southern California, arrival and detection of the Mediterranean fruit fly has fluctuated annually but continued at a substantial level even after its eradication was repeatedly declared and associated extensive public information campaigns were conducted (Liebhold et al. 2006). The number of Mediterranean fruit fly interceptions was positively correlated with the amount of passenger traffic from a country and negatively associated with its gross national product.

The overall aim of this study was to determine the seasonally changing risk of importing the Mediterranean fruit fly into high-traffic airports in Florida or California via passengers arriving from airports in Mediterranean fruit fly-infested countries. This was accomplished partly by analyzing risk factors for departure and arrival airports with direct flight connections, including distance between airports, flight frequency, passenger number and demography, travel seasons, Mediterranean fruit fly geographic distribution, the life cycle and environmental requirements of the pest, and comparing the risk of importation with Mediterranean fruit fly interceptions at the high-traffic airports in Florida (Miami, MIA; Ft. Lauderdale, FLL; Orlando, MCO) and California (Los Angeles, LAX; San Francisco, SFO). Both states are vulnerable to Mediterranean fruit fly importation and establishment due to their numerous international transportation connections, high number of international passenger arrivals, expanding populations of ethnic minorities with relatives in tropical countries, extensive commodity importation, substantial agricultural industries, and generally mild climates. Arrival rates of the Mediterranean fruit fly and many other invasive organisms into these states show strong seasonal patterns, as does their population dynamics in the countries of origin (Caton et al. 2006, Liebhold et al. 2006, Escudero-Colomar et al. 2008, Dixon et al. 2009). Specific objectives of this study were to: 1) Estimate the number of seasonal passengers traveling from airports in Mediterranean fruit fly-infested countries on flights connecting directly to the major airports in Florida and California, 2) Use an environmental suitability model to categorize seasonal Mediterranean fruit fly population levels surrounding each departure airport, 3) Calculate seasonal and annual risk indicators for passengers departing from all or individual international airports in Mediterranean fruit fly-infested countries and arriving in Florida or California potentially transporting the pest, and 4) Calculate seasonal and annual risk indicators for Mediterranean fruit fly introductions from a subset of high-risk Mediterranean fruit fly-infested departure airports paired with arrival airports in Florida or California. The resulting information can be used to assess relationships among the risk factors for Mediterranean fruit fly importation, justify increased agricultural inspection (preclearance) at departure airports, and strengthen arrival airport surveillance for high-risk pathways.

Materials and Methods

Countries, Flight Routes, and Passenger Numbers

Airport coordinates, city names, and International Air Transport Association (IATA) airport codes were obtained for 3,416 airports from Flightstats (www.flightstats.com). Because the 2010 dataset was the latest available on monthly seat capacity for each international flight, it was purchased from OAG (www.oag.com). These data were used to construct a table that delineated direct international flight connections between departure airports and the high-traffic arrival airports in Florida (MIA, FLL, and MCO) and California (LAX and SFO). However, the dataset tended to overestimate passenger numbers because the flights usually did not operate at full seat capacity. Data existed on actual passenger numbers but was not used in this study due to prohibitive cost, requirements for confidentiality, and legal restrictions. Consequently, a model based on the global passenger flow matrix was used to estimate passenger numbers for the direct flight connections (Huang et al. 2013, Mao et al. 2015). The model included annual and monthly open-access matrices of passenger flow for the global air network serving cities with populations of at least 100,000. Hawaii is Mediterranean fruit fly infested but was excluded from the analysis because it is not an international connection relative to the U.S. mainland and passengers undergo stringent preclearance before departure and their possessions are not inspected on arrival. Currently, passenger preclearance operations officially take place only at 15 foreign airports in six different countries: Canada, the Bahamas, Bermuda, Aruba, Ireland, and the United Arab Emirates (https://www.cbp.gov/border-security/ports-entry/operations/preclearance, accessed 24 August 2016).

The passenger flow model estimated air passenger numbers by considering route and departure airport node (area around an airport) characteristics as dependent variables. Node characteristics included passenger demographic and socio-economic information and Mediterranean fruit fly abundance relative to the climate. To incorporate the economic status of the cities in which airports were situated, G-Econ data (http://gecon.yale.edu/, accessed 24 August 2016) was accessed on local area purchasing power parity per capita. The human populations surrounding airports were obtained from the most recent Gridded Population of the World, Version 4 (GPWv4) released by the Center for International Earth Science Information Network (CIESIN 2014). The number of people residing within 200 km of each departure airport, a maximum travel time of about 2 h, was compared as a covariate of origin and destination airports (Marcucci and Gatta 2011). Although passenger numbers for the routes had to be based on seat capacities in the Official Airline Guide (OAG) dataset, the modeled numbers were validated using data assembled from various transportation organizations in the United States, Canada, and European Union (Huang et al. 2013, Mao et al. 2015).

Seasonal Occurrence of Mediterranean Fruit Fly at Departure Airports

The databases on Mediterranean fruit fly occurrence from 1980 to 2013 contained 2,328 unique geo-located entries on Mediterranean fruit fly detection sites in 43 countries and nearly 500 unique localities (European and Mediterranean Plant Protection Organization [EPPO] 2009, International Atomic Energy Agency [IAEA] 2013a). Using these data, a seasonal environmental suitability model was built for the Mediterranean fruit fly based on the maximum entropy species distribution modeling algorithm (MaxEnt) combined with a set of seasonally changing environmental variables (minimum, mean, and maximum temperature; minimum, maximum, and total rainfall), a normalized difference vegetation index (NDVI), and a digital elevation model (DEM) (Szyniszewska and Tatem 2014). The annual model was divided into three seasons for the months of January–April, May–August, and September–December to have enough data points on Mediterranean fruit fly occurrence and be able to produce suitable pathway maps (Szyniszewska and Tatem 2014). The output of this analysis was used to classify infestation risk within 200 km of each airport in the countries where Mediterranean fruit fly is officially present (EPPO 2009, IAEA 2013b). The same distance to an airport was used in the passenger flow model to define the likely passenger cohort for each airport. Descriptive statistics for Mediterranean fruit fly occurrence (maximum max, mean $\bar{x}$, and standard deviation s) were calculated for the area around each airport (node). These statistics were used to classify the airport nodes as low risk for Mediterranean fruit fly occurrence with a weight of 0.2 if $max = < 0.8$, $\bar{x} = < 0.1$, and $s = < 0.15$. Nodes categorized as medium risk for Mediterranean fruit fly occurrence were assigned a weight 0.6 if the $max = 0.8$–0.9, $\bar{x} = 0.1$–0.3, and s was not considered. In all other instances, an airport node was classified as high risk for Mediterranean fruit fly occurrence and assigned a risk weight of 1.0.

Seasonal Risk Indicators for Passengers Arriving with Mediterranean Fruit Fly

Three risk indicator values were calculated for each individual destination airport, departure airport, and pair of origin–destination airports to assess the risk of passengers transporting the Mediterranean fruit fly into Florida or California during the three seasons. For each arrival airport in Florida or California (i) and passenger departure airport (k), the passenger flow (p_{ik}) was estimated. This (p_{ik}) value was segregated by the three seasons (j) to determine the seasonally adjusted passenger flow (p_{ijk}). The risk indicators (RI) for passengers arriving with Mediterranean fruit fly from all international departure airports, including Mediterranean fruit fly-infested countries, to individual airports in Florida or California (i) in season (j) were defined as (ARI_{ij}). Risk indicator values were derived by multiplying the risk of Mediterranean fruit fly occurring at the departing flight location (low = 0.2, medium = 0.6, and high = 1.0) in each season by the estimated number of passengers on the route and dividing the product by the total estimated number of seasonal passengers on the route. For passengers arriving in Florida or California from an individual origin airport (k) in season (j), the risk indicator was defined as (ORI_{jk}). The risk indicator for arrival at a specific airport (i) in season (j) by passengers from a pair of origin–destination airports (k) was defined as ($AORI_{ijk}$). The notation (o_{jk}) represents the risk of seasonal Mediterranean fruit fly abundance at departure airports. Risk indicators were calculated for the following direct international flight connections to Florida or California: 1) All arriving flights from international airports to a destination airport (ARI_{ij}), 2) Departing flights from an individual origin airport (ORI_{jk}), and 3) Pairs of specific origin–destination airports ($AORI_{ijk}$). Higher risk indicator values indicated greater annual risk of Mediterranean fruit fly arrival relative to the total estimated passenger number. The following equations were used to calculate seasonal Mediterranean fruit fly risk indicators for passengers arriving in Florida or California:

$$ARI_{ij} = \frac{\sum_k p_{ijk} o_{jk}}{\sum_k p_{ijk}} \quad (1)$$

$$ORI_{jk} = \frac{\sum_i p_{ijk} o_{jk}}{\sum_i p_{ijk}} \quad (2)$$

$$AORI_{ijk} = \frac{p_{ijk} o_{jk}}{p_{ijk}} \quad (3)$$

Mediterranean Fruit Fly Interceptions, Countries of Origin, Seasons, and Host Plants

Mediterranean fruit fly interception data from U.S. ports of entry documented in the PestID database for 2003–2014 contained

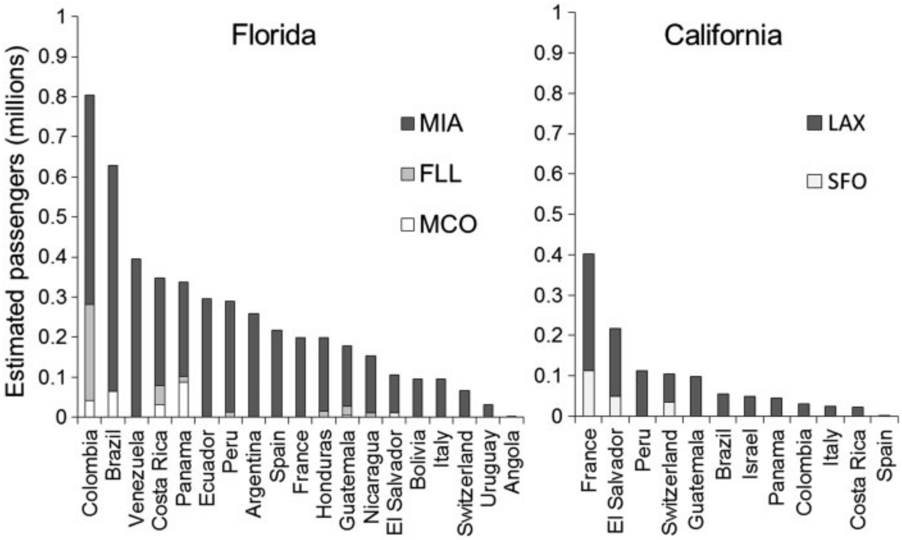

Fig. 1. Estimated number of passengers arriving at international airports in Florida and California from Mediterranean fruit fly-infested countries during 2010. Airport codes: MIA (Miami), FLL (Fort Lauderdale), MCO (Orlando), LAX (Los Angeles), and SFO (San Francisco).

records on pest interceptions from agricultural commodities in cargo, airline passenger baggage, and other conveyances, such as mail. It provided detailed information on pest interceptions, including the port of entry, date, origin of the pest, commodity, part of the plant harboring the pest, species of the pest, and other pertinent information. However, information in the PestID database could not be used to quantify entry rates of nonindigenous species into the United States because it was not based on systematic sampling, was subject to varying detection priorities resulting from changing commodities and pests of concern, and lacked records on inspections without pest interceptions (Work et al. 2005). Consequently, for specific countries and seasons, Pearson correlation coefficients were calculated to measure the strength of association between the estimated and risk-adjusted number of passengers and the number of Mediterranean fruit flies intercepted from a departure airport.

Results

Countries, Flight Routes, and Passenger Numbers

The number of international passengers arriving at Florida in 2010 was about 13.3 million, whereas California received 12.9 million. They traveled from 130 and 81 locations, including countries with multiple connections in the Caribbean region, Central and South America, and Western Europe. Based on the passenger flow model, 9.05 million passengers traveled to Florida and arrived at MIA, and there were 106 direct connections. The number of direct connections and passengers for FLL was 48 and 1.85 million and for MCO 45 and 1.96 million, respectively. Fewer than 450,000 passengers arrived at the remaining airports, e.g., Jacksonville, Tampa, and Palm Beach. California had 78 direct airline connections for LAX and 30 for SFO on which 8.1 and 4.3 million passengers were transported, respectively. About 516,000 international passengers traveling to California arrived at airports other than LAX and SFO, and most of them were from countries where Mediterranean fruit fly did not occur officially.

For direct flights from Mediterranean fruit fly-infested countries, MIA, FLL, and MCO received 4.1, 0.36, and 0.24 million passengers (43, 15, and 9 direct connections) and LAX and SFO received 0.96 and 0.2 million (14 and 3 direct connections), respectively. Thus, during 2010, about 4.7 million passengers were potentially carriers of Mediterranean fruit fly on direct flights into Florida and 1.2 million into California. The number of passengers on direct flights to Florida from Mediterranean fruit fly-infested countries was highest from Colombia (805,000), Brazil (684,000), and Venezuela (395,000) (Fig. 1). Passenger numbers on flights into California from Mediterranean fruit fly-infested countries were highest for France (402,000), El Salvador (217,000), and Peru (112,141). MIA was the primary destination airport for most passengers arriving in Florida but some of them from Colombia, Costa Rica, Panama, Peru, Honduras, Guatemala, and Nicaragua ended their trips at FLL and from Brazil, Costa Rica, Panama, and El Salvador at MCO. For California, LAX received passengers from all of the Mediterranean fruit fly-infested countries, whereas passengers arrived at SFO only from France, El Salvador, and Switzerland.

Seasonal Occurrence of Mediterranean Fruit Fly at Departure Airports

Mediterranean fruit fly population levels varied seasonally at the airline flight origins, mainly in Europe, but also in Australia, and some locations in South and Central America (Figs. 2 and 3). The very low seasonal risk of Mediterranean fruit fly arriving in Florida from most of Europe in January–April was followed by an increase in May–August that persisted into September–December. The risk of Mediterranean fruit fly-infested fruit being transported from Mediterranean countries was elevated during the summer and fall months due to high Mediterranean fruit fly populations and passenger numbers. The Mediterranean fruit fly is seasonally abundant in Sub-Saharan Africa (Manrakhan and Addison 2014) from which relatively few passengers travel to Florida, and in regions of South America with continuous arrivals in Florida and California. Eradication of the Mediterranean fruit fly from Mexico and Belize has eliminated the risk of introductions directly into the United States from those locations. The pattern of international passenger travel into California is very different than into Florida, with most flights arriving in California from countries that are not Mediterranean fruit fly infested. Exceptions are flights from Mediterranean countries (France, Italy, Israel, and Spain) and South and Central America.

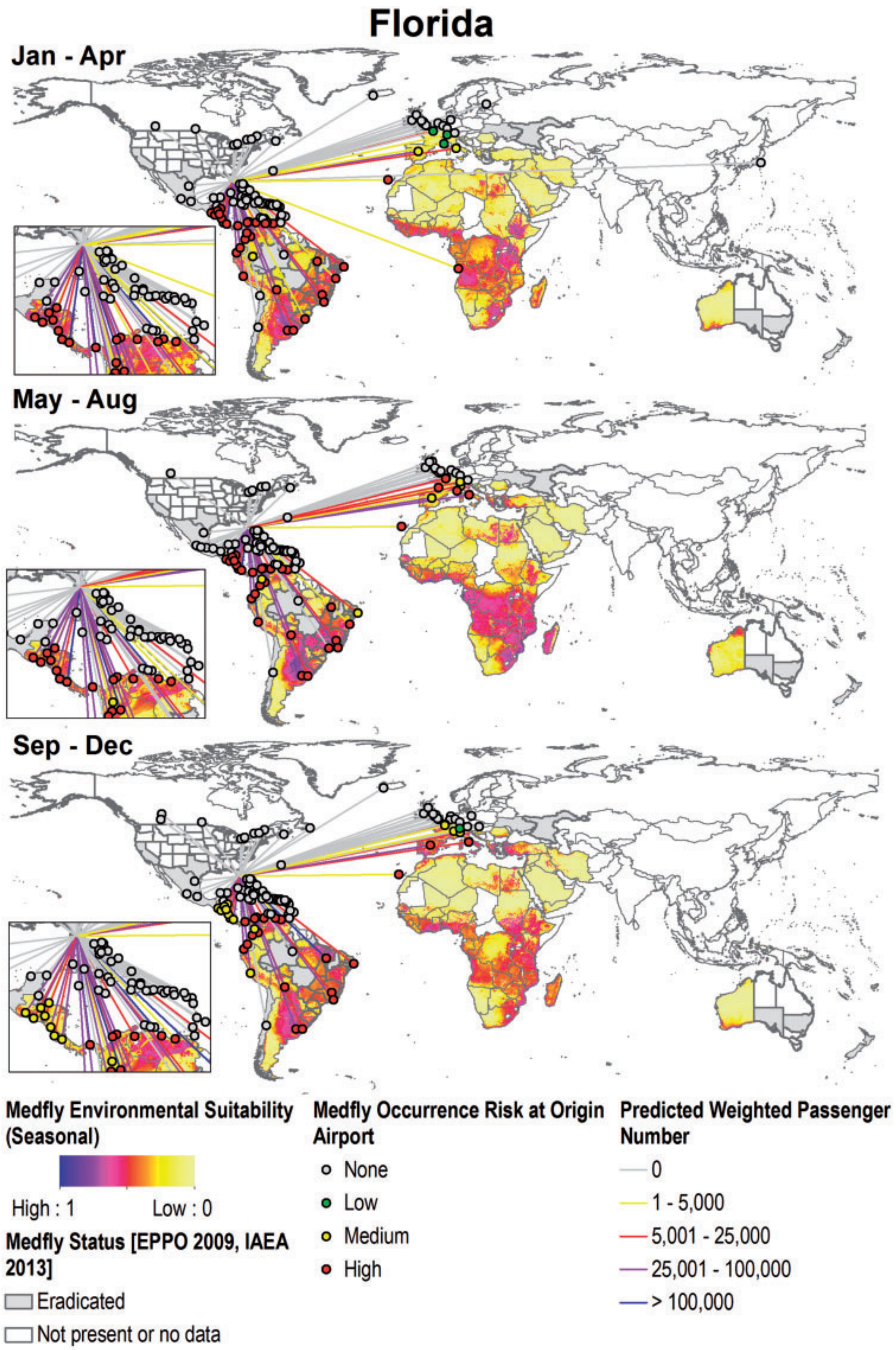

Fig. 2. Three panel pathway map illustrating seasonal Mediterranean fruit fly environmental suitability, Mediterranean fruit fly occurrence risk at origin airports, and predicted passenger flow to Florida during 2010. The passenger number was obtained from vbd-air.com (Mao et al. 2015) and adjusted (weighted) for risk of Mediterranean fruit fly occurrence. Mediterranean fruit fly presence or absence was designated according to the European and Mediterranean Plant Protection Organization and International Atomic Energy Agency (EPPO 2009, IAEA 2013b). Mediterranean fruit fly seasonal suitability maps were derived from Szyniszewska and Tatem (2014).

Seasonal Risk Indicators for Passengers Arriving With Mediterranean Fruit Fly

Seasonal Risk Indicators for Passengers Arriving in Florida and California From All International Departure Airports (ARI_{ij})

Depending on season, destination airports in both Florida (MIA, FLL, and MCO) and California (LAX and SFO) were subject to considerable risk of passengers arriving with Mediterranean fruit fly (Table 1). Higher ARI_{ij} values indicated increased risk due to more passengers arriving from countries with high or medium Mediterranean fruit fly population levels. Considering all international arrivals, including locations where Mediterranean fruit fly is not established or has been eradicated, MIA had the greatest risk for

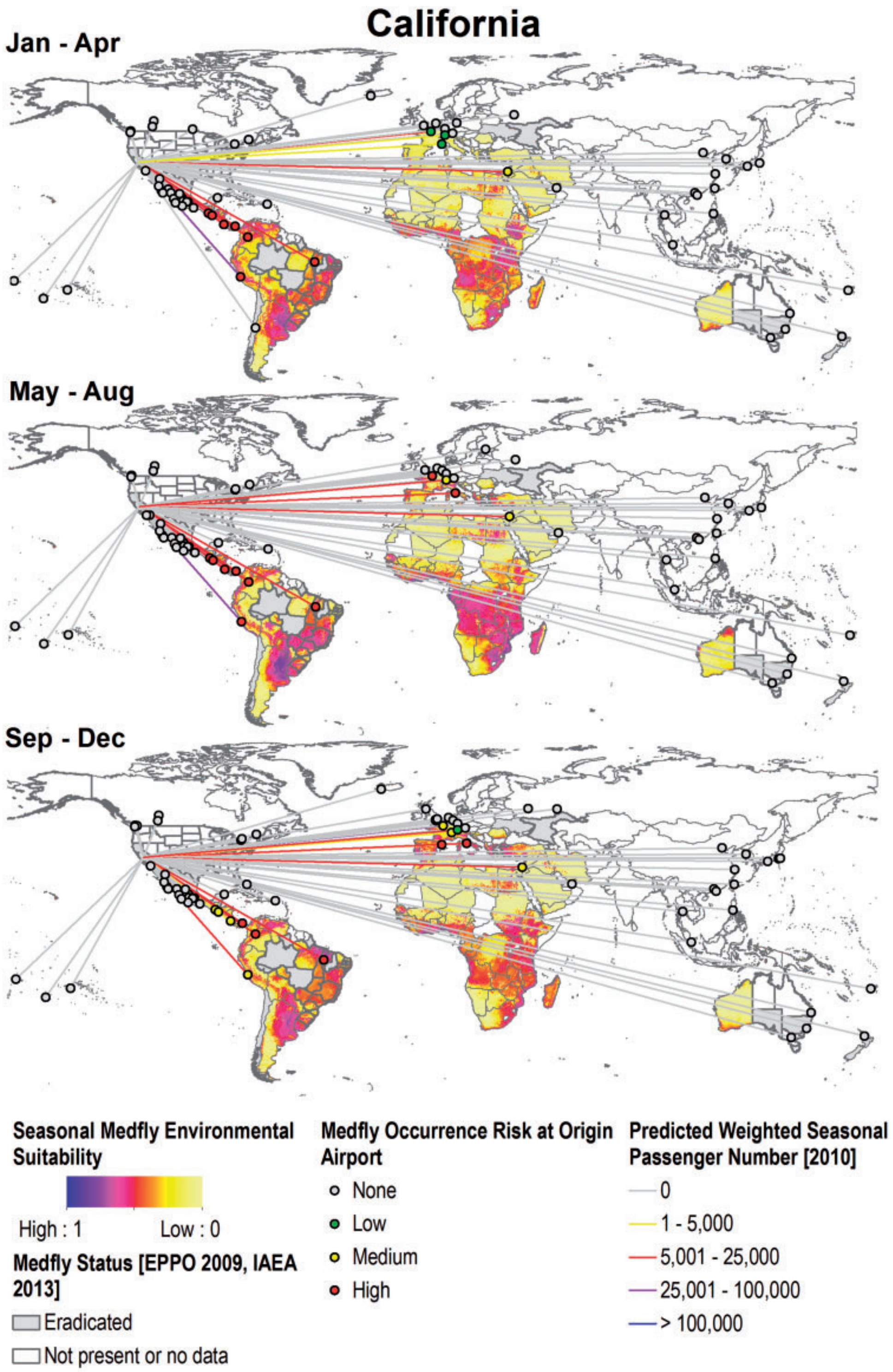

Fig. 3. Three panel pathway map illustrating seasonal Mediterranean fruit fly environmental suitability, Mediterranean fruit fly occurrence risk at origin airports, and predicted passenger flow to California during 2010. The passenger number was obtained from vbd-air.com (Mao et al. 2015) and adjusted (weighted) for risk of Mediterranean fruit fly occurrence. Mediterranean fruit fly presence or absence was designated according to the European and Mediterranean Plant Protection Organization and International Atomic Energy Agency (EPPO 2009, IAEA 2013b). Mediterranean fruit fly seasonal suitability maps were derived from Szyniszewska and Tatem (2014).

Mediterranean fruit fly introduction into Florida, arrival risk indicators (ARI_{ij}) of 0.38–0.44 for the three seasons. Indicators ranged from 0.84 to 0.95 for passengers who arrived at MIA from Mediterranean fruit fly-infested countries. Also, Miami had a much greater adjusted total number of passengers from these countries, about 3.7 million. FFL and MCO had considerably lower ARI_{ij} values with 344,382 and 235,449 adjusted total passenger numbers, respectively, arriving from locations where Mediterranean fruit fly was present. The greatest risk for Mediterranean fruit fly introduction into Florida from Mediterranean fruit fly-infested countries

Table 1. Risk indicators (ARI_{ij}) for international passengers arriving from all and Mediterranean fruit fly-infested countries to destination airports in Florida and California during 2010

IATA destination airport code[a]	All countries			Mediterranean fruit fly-infested countries			Adjusted total passenger no.[b]	Arrival risk ratio[c]
	Jan.–April	May–Aug.	Sept.–Dec.	Jan.–April	May–Aug.	Sept.–Dec.		
Florida								
MIA: ARI_{ij}[d]	0.41	0.44	0.38	0.93	0.95	0.84	–	0.45
Passengers[e]	2,983,863	3,119,406	2,947,184	1,312,486	1,447,002	1,336,231	3,716,075	–
FLL: ARI_{ij}	0.17	0.21	0.19	1.00	0.96	0.88	–	0.20
Passengers	678,740	684,353	484,219	113,851	146,010	102,611	344,382	–
MCO: ARI_{ij}	0.11	0.11	0.14	1.00	1.00	0.92	–	0.12
Passengers	707,617	703,899	543,759	79,538	80,975	81,892	235,449	–
California								
LAX: ARI_{ij}	0.08	0.12	0.08	0.70	0.95	0.64	–	0.12
Passengers	2,481,421	2,962,131	2,702,507	270,308	364,436	329,395	746,892	–
SFO: ARI_{ij}	0.02	0.05	0.02	0.47	0.92	0.49	–	0.05
Passengers	1,220,005	1,635,193	1,420,457	42,643	84,541	69,265	131,752	–

[a] International Air Transport Association (IATA) airport codes: MIA (Miami), FLL (Fort Lauderdale), MCO (Orlando), LAX (Los Angeles), and SFO (San Francisco).

[b] The adjusted total passenger number was derived by summing the products of the estimated number of passengers arriving from Mediterranean fruit fly-infested countries multiplied by the seasonal risk (ARI_{ij}) of Mediterranean fruit fly occurrence at a departing flight location.

[c] An arrival risk ratio was derived for each destination airport by summing the risk-adjusted number of passengers arriving each season from Mediterranean fruit fly-infested locations and dividing the sum by the total of all passengers that arrived on international flights.

[d] Risk indicators (ARI_{ij}) were derived by multiplying the risk of Mediterranean fruit fly occurring at the departing flight location in each season by the estimated number of passengers on the route and dividing the product by the estimated total number of seasonal passengers on the route. Higher ARI_{ij} scores indicate greater annual risk of Mediterranean fruit fly arrival relative to the total estimated passenger number.

[e] The estimated number of passengers arriving at Florida and California on direct flights from all and Mediterranean fruit fly-infested countries was derived from the open-access passenger flow model for 2010, Vbd-air.com (Mao et al. 2015).

occurred in January–August. In California, LAX and SFO had the highest ARI_{ij} values for arrivals from Mediterranean fruit fly-infested countries in May–August, 0.95 and 0.92, respectively. LAX had an ARI_{ij} score of 0.70 in January–April and 0.64 in September–December, whereas scores for the respective seasons at SFO were 0.47 and 0.49. The arrival risk ratio for LAX was 0.12 and for SFO 0.05.

Seasonal Risk Indicators for Passengers Arriving in Florida and California From Individual Departure Airports (ORI_{jk})

Risk indicators for passengers departing from individual Mediterranean fruit fly-infested airports were based on the estimated number of passengers and the Mediterranean fruit fly seasonal environmental suitability model (Table 2). The estimated number of passengers in the table was less than in Fig. 1 because the table included only origin airports with the highest number of passengers. In 2010, the highest total estimated number of passengers came into Florida from airports in Colombia (BOG 413,039 and MDE 154,013), Brazil (GRU 406,040 and GIG 136,945), Panama (PTY 336,481), and Venezuela (CCS 332,507). Airports in Colombia, Brazil, Panama, Venezuela, Argentina, and Ecuador were at high risk of Mediterranean fruit fly being carried by passengers year-round (ORI_{jk} = 1.0). Higher annual risk indicators for the origin airports indicated a greater risk of Mediterranean fruit fly arriving at the destination. The risk decreased from high to medium (0.6–0.87) in France (CDG), Colombia (MDE), Spain (MAD), Honduras (SAP), Costa Rica (SJO), Peru (LIM), Guatemala (GUA), and Nicaragua (MGA) primarily due to Mediterranean fruit fly population declines in these departing countries during the last four months of the year. It was estimated that only four countries had >100,000 passengers traveling to California: France (401,918), El Salvador (217,318), Peru (112,141), and Switzerland (103,667). California had a greater estimated number of passengers than Florida arriving from France and unilaterally had direct flights from Switzerland and Italy. The two states received a similar number of passengers from Spain. California had incoming flights from additional Mediterranean fruit fly-infested countries, including Guatemala, Brazil, Panama, Colombia, Israel, and Costa Rica. The ORI_{jk} values ranged from 0.35 for flights from Switzerland to 1.0 for Brazil, Panama, Colombia, Italy, and Spain.

Seasonal Risk Indicators for Passengers Arriving in Florida and California on Routes With Paired Origin and Destination Airports ($AORI_{ijk}$)

Risk indicators were calculated for high-risk departure airports paired with individual arrival airports in Florida and California. Passengers traveled to Florida (MIA) from Mediterranean fruit fly-infested departure airports in Brazil (GRU), Venezuela (CCS), Peru (LIM), Argentina (EZE), and Colombia (BOG). Other passengers from Colombia (BOG, MDE) and those originating in Costa Rica (SJO) arrived at FLL. Passengers departing Panama (PTY) and some from Brazil (GRU) and Colombia (BOG) traveled to MCO (Table 3). The number of passengers destined for Florida decreased significantly in September–December for LIM–MIA, EZE–MIA, SJO–FLL, and MDE–FLL. The $AORI_{ijk}$ values were high (0.86–1.0) for all pairs of airports, except Medellin, Colombia (MDE)–FLL (0.74). France (CDG)–LAX, at nearly 290,000 passengers per year, had the highest number into California. Totals above 100,000 passengers also were estimated for El Salvador (SAL)–LAX, Peru (LIM)–LAX, and France (CDG)–SFO. El Salvador (SAL)–SFO and Switzerland (ZRH)–SFO had <50,000 passengers per year. The $AORI_{ijk}$ values for pairs of airports in California were highest (0.86–0.88) for LIM–LAX, SAL–LAX, and SAL–SFO and lowest (0.38–0.67) for ZRH–SFO, CDG–LAX, and CDG–SFO.

Table 2. Risk indicators for passengers with Mediterranean fruit fly departing from airport locations infested with Mediterranean fruit fly and arriving in Florida and California in 2010

Country of origin	IATA origin airport code[a]	Seasonal risk of Mediterranean fruit fly at a departing flight location[b]			Estimated seasonal passenger number[c]			Total estimated passenger no.[c]	Total adjusted passenger no.[d]	Annual origin risk indicator (ORI_{jk})[e]
		Jan.–April	May–Aug.	Sept.–Dec.	Jan.–April	May–Aug.	Sept.–Dec.			
Florida										
Colombia	BOG	1	1	1	135,103	141,682	136,254	413,039	413,039	1.00
Brazil	GRU	1	1	1	132,339	137,668	136,033	406,040	406,040	1.00
Panama	PTY	1	1	1	118,902	113,359	104,220	336,481	336,481	1.00
Venezuela	CCS	1	1	1	110,849	111,948	109,710	332,507	332,507	1.00
Costa Rica	SJO	1	1	0.6	103,337	100,666	97,479	301,482	262,490	0.87
Argentina	EZE	1	1	1	88,575	99,461	71,352	259,388	259,388	1.00
Peru	LIM	1	1	0.6	87,055	108,009	94,831	289,895	251,963	0.87
Spain	MAD	0.6	0.6	1	52,293	81,948	76,027	210,268	156,572	0.74
Guatemala	GUA	1	1	0.6	58,544	60,157	58,841	177,542	154,006	0.87
Nicaragua	MGA	1	1	0.6	47,017	52,429	40,618	140,064	140,064	0.87
Colombia	MDE	1	0.6	0.6	49,077	54,839	50,097	154,013	133,974	0.73
Honduras	SAP	1	1	0.6	37,565	47,322	45,171	130,058	130,058	0.86
Brazil	GIG	1	1	1	38,806	49,356	48,783	136,945	117,432	1.00
Ecuador	UIO	1	1	1	51,429	53,318	50,107	154,854	113,484	1.00
France	CDG	0.2	1	0.6	59,999	62,212	64,218	186,429	112,743	0.60
California										
France	CDG	0.2	1	0.6	102,599	163,616	135,703	401,918	265,558	0.66
El Salvador	SAL	1	1	0.6	64,645	83,610	69,063	217,318	189,693	0.87
Peru	LIM	1	1	0.6	35,331	38,023	38,787	112,141	96,626	0.86
Guatemala	GUA	1	1	0.6	29,928	35,913	32,279	98,120	85,208	0.87
Brazil	GRU	1	1	1	15,729	19,806	18,914	54,449	54,449	1.00
Panama	PTY	1	1	1	15,067	16,498	14,669	46,234	46,234	1.00
Switzerland	ZRH	0.2	0.6	0.2	20,247	39,821	43,599	103,667	36,662	0.35
Colombia	BOG	1	1	1	9,934	10,310	9,839	30,083	30,083	1.00
Israel	TLV	0.6	0.6	0.6	12,331	18,574	18,340	49,245	29,547	0.60
Italy	FCO	0.6	1	1	–	15,153	10,235	25,388	25,388	1.00
Costa Rica	SJO	1	1	0.6	7,134	7,653	7,049	21,836	19,016	0.87
Spain	BCN	0.6	1	1	–	–	173	173	173	1.00
Switzerland	GVA	0.2	0.6	0.6	–	–	10	10	6	0.60
France	NCE	0.2	1	0.6	6	–	–	6	1	0.20

[a] International Air Transport Association (IATA) airport codes for departure airports in Mediterranean fruit fly-infested countries with the highest estimated number of passengers arriving at Florida and California in 2010.

[b] The seasonal risk of Mediterranean fruit fly abundance at departing flight locations was derived from the Mediterranean fruit fly environmental suitability model (Szyniszewska and Tatem 2014) and classified as high (1.0), medium (0.6), or low (0.2).

[c] The estimated seasonal number of passengers departing on direct flights from international airports in Mediterranean fruit fly-infested countries and arriving in Florida and California was derived from the open-access passenger flow model for 2010, Vbd-air.com (Mao et al. 2015).

[d] The adjusted total passenger number was derived by multiplying the total estimated passenger number by the annual origin risk indicator (ORI_{jk}) for each country of origin.

[e] The annual origin risk indicators (ORI_{jk}) were derived by multiplying the risk of Mediterranean fruit fly occurring at the departing flight location (low = 0.2, medium = 0.6, and high = 1.0) in each season by the estimated number of passengers on the route and dividing the product by the total number of seasonal passengers on the route. Higher ORI_{jk} scores indicate greater annual risk of Mediterranean fruit fly arrival relative to the total estimated number of passengers.

Mediterranean Fruit Fly Interceptions, Countries of Origin, Seasons, and Host Plants

According to the PestID database for 2003–2014, Mediterranean fruit flies were intercepted in passenger baggage from Mediterranean fruit fly-infested countries 462 times in Florida and 178 times in California (Table 4). Peru (95) was the most common origin of Mediterranean fruit flies intercepted in Florida, followed by Spain (76), Bolivia (50), and Ecuador (45). Romania (31), Nicaragua (26), Nigeria (26), and Portugal (23) were the other significant sources, 80% for the eight countries. The primary sources of Mediterranean fruit flies intercepted in California were Australia (50), Nigeria (42), Israel (29), and Spain (25), 82% for the four countries. Considerably fewer Mediterranean fruit flies were intercepted from each of the other 13 countries. Florida had a range of 8–91 interceptions per year, while a more variable 0–52 Mediterranean fruit flies were encountered in California. Florida had 73 and 35 interceptions, respectively, during 2013 and 2014. In 2007, 2008, 2010, and 2013, no Mediterranean fruit flies were found in passenger baggage in California, and only two were encountered in 2014. The peak year was 2011 for both states during the period. Based on the number of Mediterranean fruit flies intercepted and source countries, the pest pressure appeared to be greater for Florida than California.

Table 3. Risk indicators for passengers with Mediterranean fruit fly departing from airport locations infested with Mediterranean fruit fly and arriving at specific airports in Florida and California in 2010

IATA airport code[a]		Seasonal risk of Mediterranean fruit fly at a departing flight location[b]			Estimated passenger no.[c]				Annual risk indicator $AORI_{ijk}$[d]
Origin	Destination	Jan.–April	May–Aug.	Sept.–Dec.	Jan.–April	May–Aug.	Sept.–Dec.	Total	
Florida									
GRU	MIA	1.0	1.0	1.0	111,695	114,978	114,051	340,724	1.00
CCS	MIA	1.0	1.0	1.0	110,849	111,948	109,710	332,507	1.00
LIM	MIA	1.0	1.0	0.6	84,997	97,832	56,062	276,265	0.86
EZE	MIA	1.0	1.0	1.0	88,575	99,461	71,352	259,388	1.00
BOG	MIA	1.0	1.0	1.0	82,020	84,996	85,961	252,977	1.00
BOG	FLL	1.0	1.0	1.0	39,061	41,823	37,168	118,052	1.00
SJO	FLL	1.0	1.0	0.6	18,393	19,572	5,849	47,714	0.92
MDE	FLL	1.0	0.6	0.6	12,376	7,808	5,570	34,672	0.74
PTY	MCO	1.0	1.0	1.0	28,171	28,922	29,402	86,495	1.00
GRU	MCO	1.0	1.0	1.0	20,483	22,690	21,982	65,155	1.00
BOG	MCO	1.0	1.0	1.0	14,022	14,863	13,125	42,010	1.00
California									
CDG	LAX	0.2	1.0	0.6	14,845	114,555	60,519	289,648	0.66
SAL	LAX	1.0	1.0	0.6	50,374	64,136	32,617	168,872	0.87
LIM	LAX	1.0	1.0	0.6	35,331	38,023	23,272	112,141	0.86
CDG	SFO	0.2	1.0	0.6	5,674	49,061	20,902	112,270	0.67
SAL	SFO	1.0	1.0	0.6	14,271	19,474	8,820	48,446	0.88
ZRH	SFO	0.2	0.6	0.2	0	9,603	3,945	35,733	0.38

[a] International Air Transport Association (IATA) airport codes: GRU (Brazil), CCS (Venezuela), LIM (Peru), EZE (Argentina), BOG (Colombia), SJO (Costa Rica), MDE (Colombia), PTY (Panama), CDG (France), SAL (El Salvador), ZRH (Switzerland), MIA (Miami), FLL (Fort Lauderdale), MCO (Orlando), LAX (Los Angeles), and SFO (San Francisco). Origin–destination airports were selected based on the highest number of passengers arriving to Florida and California.

[b] The seasonal risk of Mediterranean fruit fly abundance at departing flight locations was derived from the Mediterranean fruit fly environmental suitability model (Szyniszewska and Tatem 2014) and classified as high (1.0), medium (0.6), or low (0.2).

[c] The estimated seasonal number of passengers departing on direct flights from international airports in Mediterranean fruit fly-infested countries and arriving in Florida and California was derived from the open-access passenger flow model for 2010, Vbd-air.com (Mao et al. 2015).

[d] The annual risk indicators for paired origin–destination airports (*AORIijk*) were derived by multiplying the risk of Mediterranean fruit fly occurring at the departing flight location (low = 0.2, medium = 0.6, and high = 1.0) in each season by the estimated number of passengers on the route and dividing the product by the total number of seasonal passengers on the route. Higher *AORIijk* scores indicate greater annual risk of Mediterranean fruit fly arrival relative to the total estimated number of passengers.

Regardless of countries of origin, Mediterranean fruit flies were intercepted at Florida international airports every month during 2003–2014 and in California during all months except April and September (Fig. 4). For Florida, Mediterranean fruit flies were detected most often in September (70) but also were encountered at relatively high levels in July (66), November (60), December (46), and February (48). A somewhat lower level of cumultive interceptions was reported for January (38), April (43), May (44), June (34), August (42), and October (39). The lowest level was in March (18). California interceptions peaked in June (62) and July (58), with a possible second surge in October (27) and to a lesser extent November (14). There were <10 interceptions during the remaining months.

The major kinds of infested fruit intercepted in passenger baggage at airports in Florida and California were different except for peach, guava, peppers, citrus, apple, and pomegranate (Table 5). Overwhelmingly, the most common fruit containing Mediterranean fruit fly larvae intercepted from flights arriving at Florida airports was peach (133), followed by mango (46), quince (36), guava (35), plums/cherries (33), orange (31), and mandarin orange (23). Fewer than 20 Mediterranean fruit flies were found in the other nine kinds of fruit. Most Mediterranean fruit flies intercepted in California were from guava (50) and peppers (49). Additionally, only peach (15), orange (17), apple (24), rough lemon (11), and pomegranate (10) exceeded 9 interceptions.

Pearson correlation coefficient values (r) were calculated to determine the strength of linear association between the number of intercepted Mediterranean fruit flies in the PestID database and the estimated number of passengers on the routes of interest. Positive associations indicated that there were more Mediterranean fruit fly interceptions at the ports of entry with increasing numbers of passengers or elevated risk indicator values. Negative associations denoted the opposite. A strong linear association occurred if values were above 0.7 but the association was weak at 0.3. There was a weak negative relationship between the cumulative number of Mediterranean fruit flies from individual departure countries intercepted at airports during 2003-2014 and the adjusted number of passengers arriving in Florida from these locations ($r = -0.21$). California had a strong negative association ($r = -0.97$), although because interception data in the PestID database was limited, only four origin–destination pairs could be compared: Venezuela (CCS)–MIA, Peru (LIM)–MIA, El Salvador (SAL)–LAX, and France (CDG)–LAX (Table 3). In 2010, however, there was a positive correlation between the total number of intercepted Mediterranean fruit flies and the estimated number of passengers arriving at the five main airports in Florida and California (MIA, FLL, MCO, LAX,

Table 4. Cumulative number of Mediterranean fruit flies intercepted at airports in Florida and California from Mediterranean fruit fly-infested and all other countries in 2003–2014 (PestID database)

Country	Florida	California	Total
Spain	76	25	101
Peru	95	–	95
Nigeria	26	42	68
Australia	–	50	50
Bolivia	50	–	50
Ecuador	45	–	45
Israel	16	29	45
Romania	31	–	31
Nicaragua	26	–	26
Portugal	23	–	23
Lebanon	16	5	21
El Salvador	11	8	19
France	13	3	16
Venezuela	15	–	15
Egypt	13	–	13
Algeria	2	10	12
Cameroon	4	6	10
Total from Mediterranean fruit fly-infested countries	462	178	640
Total from all countries	548	194	742

Table 5. Cumulative number of Mediterranean fruit flies intercepted at airports in Florida and California from specific host plants that originated from all countries with connecting flights during 2003–2014 (PestID database)

Host	Florida	California	Total
Prunus persica	133	15	148
Psidium guajava	35	50	85
Capsicum sp.	10	41	51
Citrus sinensis	31	16	47
Mangifera indica	46	0	46
Cydonia oblonga	36	0	36
Prunus sp.	33	0	33
Citrus reticulata	23	0	23
Capsicum annuum	14	8	22
Citrus sp.	19	1	20
Annona muricata	19	0	19
Malus sp.	2	16	18
Punica granatum	8	10	18
Garcinia sp.	15	0	15
Malus domestica	5	8	13
Manilkara zapota	13	0	13
Ficus carica	12	0	12
Citrus jambhiri	0	11	11
Dennettia tripetala	10	0	10
Total	176	464	640

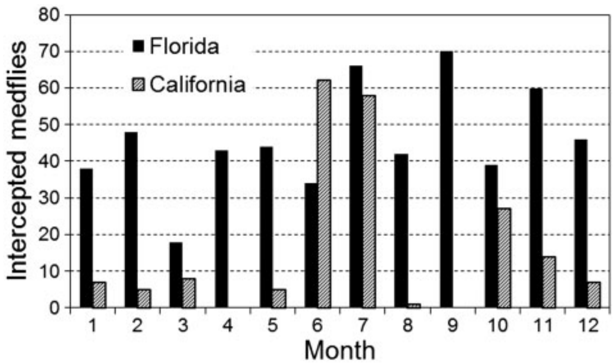

Fig. 4. Cumulative number of living and dead Mediterranean fruit flies intercepted in passenger baggage at Florida and California airports each month in 2003–2014 (PestID database).

and SFO; $r = 0.78$), and an even stronger correlation when comparing the interception counts with the risk adjusted number of passengers ($r = 0.98$) or annual ARI values ($r = 0.81$). A strong association also occurred between the seasonal number of intercepted Mediterranean fruit flies and the estimated seasonal number of passengers ($r = 0.75$) and adjusted number of passengers ($r = 0.93$) arriving at the five main airports. When examined by state, the relationship between the adjusted seasonal passenger number versus the seasonal number of intercepted Mediterranean fruit flies was stronger in Florida than California, $r = 0.97$ and 0.52, respectively.

Discussion

This investigation was conducted to determine the seasonal risk of importing the Mediterranean fruit fly into Florida or California via direct airline connections with Mediterranean fruit fly-infested countries. The approach was to estimate the number of passengers traveling seasonally between these states and major connecting international airports, determine seasonal risk for Mediterranean fruit fly occurrence at the origin airports, identify high-risk departure airports and flight routes, and use this information to calculate annual and seasonal risk indicators for passengers arriving from these airports with Mediterranean fruit fly. This was accomplished by developing a passenger flow model that incorporated passenger and airport characteristics, such as passenger affluence and distance to the departure airports. The indicators of seasonal risk then were compared with seasonal Mediterranean fruit fly interceptions at airports in Florida and California that included data on the countries of origin and host plants. The risk of Mediterranean fruit fly being introduced was not constant throughout the year. The probability of introducing Mediterranean fruit fly into Florida airports from Mediterranean fruit fly-infested countries was higher during the first two annual seasons, January–April and May–August, than in September–December. Risk peaked in California during May–August.

The analysis defined the relative risk that passengers will transport Mediterranean fruit fly on direct flights from airports in Mediterranean fruit fly-infested countries to high traffic airports in Florida and California. The risk of Mediterranean fruit fly entry was potentially very high for both states since ∼13 million international passengers arrived in both Florida and California during 2010. MIA and LAX are particularly at risk because these two airports received most of the passengers from Mediterranean fruit fly-infested countries. However, passengers on high-risk flights also entered Florida through FLL and MCO, and California via SFO. Specific Central and South American countries were implicated as likely sources of Mediterranean fruit fly arriving in Florida: Colombia, Brazil, Panama, Venezuela, Argentina, and Ecuador. Brazil, Panama, Colombia, and Italy were the high-risk sources of Mediterranean fruit fly for California. The analysis was refined further by pairing departure and arrival airports, so that high-risk sources of Mediterranean fruit fly could be linked to the exact pathways. The risk for Florida was greatest from Brazil (GRU), Venezuela (CCS), Argentina (EZE), and Colombia (BOG) to Miami (MIA), from Colombia (BOG) to Ft. Lauderdale (FLL), and from Panama (PTY) to Orlando (MCO). The risk of Mediterranean fruit fly entering California was relatively low but was greatest for flights originating in El Salvador (SAL) and Peru (LIM) and terminating in Los Angeles (LAX). Risk of Mediterranean fruit fly introduction at San Francisco (SFO) was mostly from El Salvador (SAL).

The number of intercepted Mediterranean fruit flies did not correlate consistently with the estimated number of passengers traveling between origin and destination airports. However, there was a strong relationship between the risk-adjusted number of arriving passengers and number of Mediterranean fruit fly interceptions at both Florida and California. Also, there was a strong positive association if the level of risk was high. Adjusting the number of passengers by risk indicator values tended to improve the Pearson correlation coefficients in every instance, suggesting that the indicators accounted for some of the risk of Mediterranean fruit fly importation on specific routes. The relationship between passenger numbers and Mediterranean fruit fly interceptions could be strengthened further by obtaining more information on Mediterranean fruit fly carry rates (frequency and amount) for the passengers on incoming flights. Moreover, there is a need for more systematic sampling of incoming passenger baggage, an increase in the amount of sampling, and inclusion of records on negative outcomes. Mediterranean fruit flies were intercepted in a range of fruit typically carried by passengers but the difficulty in detecting larvae in different kinds of fruit and the unknown frequency of fruit interception also limited the usefulness of the data.

Historically, Florida had fewer Mediterranean fruit fly outbreaks compared to California, about 5 versus 11 (Thomas et al. 2010), but Florida received considerably more direct flights than California from Mediterranean fruit fly-infested countries and had much higher risk indicators. The climate in the area of past Mediterranean fruit fly outbreaks in South Florida is subtropical, whereas California is characterized as Mediterranean and both states have an abundant variety of host plants year-round. The Caribbean fruit fly is well-established in Florida and may compete with the Mediterranean fruit fly, as does the oriental fruit fly, *Bactrocera dorsalis* (Hendel), in Hawaii (Duyck et al. 2004). It also is possible that the Mediterranean fruit fly was not eliminated completely in California, as it apparently was in Florida, given the number of successive years it was detected in California during the past 25 yr. Modeling risk factors, as in this study, in concert with molecular genetic analyses (Kirk et al. 2013, Karsten et al. 2015), could provide a means of determining the probable sources, frequencies, and pathways of Mediterranean fruit fly invasions.

This study assessed how a set of primary factors contributed to seasonally changing risk of Mediterranean fruit fly importation into specific airports in Florida and California. However, the passenger flow model was subject to a range of uncertainties and limitations. Mediterranean fruit fly interception information from many locations was incomplete, sampling methodology was inconsistent, and there were many undefined factors, such as the distribution of hosts and competitor species that influenced estimates of Mediterranean fruit fly occurrence and seasonal abundance. The passenger flow model also did not account for longer, more complex itineraries which are common for passengers traveling internationally. For example, passengers from Africa arriving on connecting flights through European hubs that are not Mediterranean fruit fly infested. Regardless of the limitations, however, this modeling approach can generate risk indicators for a wide range of pests for use in targeting intervention efforts, safeguarding trade, defining data acquisition requirements at ports of entry, and strengthening risk assessments for commodity importation. By assigning seasonal risk of Mediterranean fruit fly introduction to high-risk flights arriving from Mediterranean fruit fly-infested countries, airport surveillance personnel should be able to concentrate their effort where it is most needed.

Acknowledgments

We thank Daniel Borchert (USDA, APHIS) for accessing the pest interception records. Kevin Bigsby (North Carolina State University, Center for Integrated Pest Management), Barney Caton (USDA, APHIS), and Denys Yemshanov (Natural Resources Canada) provided helpful reviews of the manuscript. This research was made possible, in part, by Cooperative Agreements No. 12-8130-0158-CA and 14-8130-0158-CA from the USDA, APHIS. It may not necessarily express the views of APHIS. Funding support for A.J.T. was provided by the RAPIDD program of the Science and Technology Directorate, Department of Homeland Security, and the Fogarty International Center, National Institutes of Health. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References Cited

APHIS. 1992. Risk assessment, Mediterranean fruit fly. Planning and Risk Analysis Systems. Policy and Program Development. USDA, Animal and Plant Health Inspection Service, Washington, DC.

Badii, K. B., M. K. Billah, K. Afreh Nuamah, D. Obeng Ofori, and G. Nyarko. 2015. Review of the pest status, economic impact and management of fruit-infesting flies (Diptera: Tephritidae) in Africa. Afr. J. Agric. Res. 10: 1488–1498.

Bakri, A. 2013. Geographical distribution map of the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann). Designed by FAO/IAEA. (https://nucleus.iaea.org/sites/naipc/twd/Picture%20Gallery/Forms/DispForm.aspx?ID=131) (accessed 24 August 2016).

Benedict, M. Q., R. S. Levine, W. A. Hawley, and L. P. Lounibos. 2007. Spread of the tiger: Global risk of invasion by the mosquito *Aedes albopictus*. Vector-Borne Zoonotic Dis. 7: 76–85.

Carey, J. R. 2010. The Mediterranean Fruit Fly. Am. Entomol. 56: 159–163.

Carey, J. R., R. E. Plant, N. T. Papadopoulos. 2014. Response to commentary by Gutierrez et al. Proc. R. Soc. Lond. B Biol. Sci. 281: 20132989.

Caton, B. P., T. T. Dobbs, and C. F. Brodel. 2006. Arrivals of hitchhiking insect pests on international cargo aircraft at Miami International Airport. Biol. Invasions 8: 765–785.

CIESIN. 2014. Gridded Population of the World, Version 4 (GPWv4), Preliminary Release 2, Socioeconomic Data and Applications Center (SEDAC), Columbia University, New York.

Dawson, A., S. Hassenpflug, and J. Sloan. 1998. California Agricultural Trade: Combating the Medfly Menace. Institute for Trade & Commercial Diplomacy. (http://www.commercialdiplomacy.org/pdf/case_studies/medfly/medfly.pdf) (accessed 24 August 2016).

Dixon, A.F.G., A. Honěk, P. Keil, M.A.A. Kotela, A. L. Šizling, and V. Jarošík. 2009. Relationship between the minimum and maximum temperature thresholds for development in insects. Funct. Ecol. 23: 257–264.

Dobbs, T. T., and C. F. Brodel. 2004. Cargo Aircraft as a Pathway for the Entry of Nonindigenous Pests into South Florida. Fla. Entomol. 87: 65–78.

Drake, J. M., and D. M. Lodge. 2004. Global hot spots of biological invasions: Evaluating options for ballast–water management. Proc. R. Soc. Lond. B Biol. Sci. 271: 575.

Duyck, P. F., P. David, and S. Quilici. 2004. A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). Ecol. Entomol. 29: 511–520.

(EPPO) European and Mediterranean Plant Protection Organization. 2009. Data Sheets on Quarantine Pests: *Ceratitis capitata*. (https://www.eppo.int/QUARANTINE/data_sheets/insects/CERTCA_ds.pdf) (accessed 24 August 2016).

Escudero-Colomar, L. A., M. Vilajeliu, and L. Batllori. 2008. Seasonality in the occurrence of the Mediterranean fruit fly [*Ceratitis capitata* (Wied.)] in the north-east of Spain. J. Appl. Entomol. 132: 714–721.

Horton, D. R., T. M. Lewis, and T. T. Dobbs. 2013. Interceptions of Anthocoridae, Lasiochilidae, and Lyctocoridae at the Miami plant inspection station (Hemiptera: Heteroptera). Fla. Entomol. 96: 482–497.

Huang, Z., X. Wu, A. J. Garcia, T. J. Fik, and A. J. Tatem. 2013. An open-access modeled passenger flow matrix for the global air network in 2010. PLoS ONE 8: e64317.

Hulme, P. E. 2009. Trade, transport and trouble: Managing invasive species pathways in an era of globalization. J. Appl. Ecol. 46: 10–18.

(IAEA) International Atomic Energy Agency. 2013a. Tephritid Workers Database. (http://nucleus.iaea.org/sites/naipc/twd/Pages/default.aspx) (accessed 24 August 2016).

(IAEA) International Atomic Energy Agency. 2013b. Updated Mediterranean Fruit Fly Global Distribution Map. (http://www-naweb.iaea.org/nafa/news/2013-medfly-global-map.html) (accessed 24 August 2016).

Karsten, M., B. Jansen van Vuuren, P. Addison, and J. S. Terblanche. 2015. Deconstructing intercontinental invasion pathway hypotheses of the Mediterranean fruit fly (*Ceratitis capitata*) using a Bayesian inference approach: Are port interceptions and quarantine protocols successfully preventing new invasions? Divers. Distrib. 21: 813–825.

Kirk, H., S. Dorn, and D. Mazzi. 2013. Molecular genetics and genomics generate new insights into invertebrate pest invasions. Evol. Appl. 6: 842–856.

Klassen, W., C. F. Brodel, and D. A. Fieselmann. 2002. Exotic pests of plants: Current and future threats to horticultural production and trade in Florida and the Caribbean Basin. Micronesica-Agana 35: 5–27.

Levine, J. M., and C. M. D'Antonio. 2003. Forecasting Biological Invasions with Increasing International Trade. Conserv. Biol. 17: 322–326.

Liebhold, A. M., T. T. Work, D. G. McCullough, and J. F. Cavey. 2006. Airline baggage as a pathway for alien insect species invading the United States. Am. Entomol. 52: 48–54.

Liquido, N. J., G. T. McQuate, and K. A. Suiter. 2013. MEDHOST: An encyclopedic bibliography of the host plants of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), Version 1.1. USDA, Center for Plant Health Science and Technology, Raleigh, NC. (http://medhost.cphst.org/) (accessed 24 August 2016).

Lockwood, J. L., P. Cassey, and T. M. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends Ecol. Evol. 20: 223–228.

Lopes-da-Silva, M., M. M. Sanches, A. R. Stancioli, G. Alves, and R. Sugayama. 2014. The role of natural and human-mediated pathways for invasive agricultural pests: A historical analysis of cases from Brazil. Agric. Sci. 5.

Lounibos, L. P. 2002. Invasions by insect vectors of human disease. Annu. Rev. Entomol. 47: 233–266.

Malacrida, A. R., L. M. Gomulski, M. Bonizzoni, S. Bertin, G. Gasperi, and C. R. Guglielmino. 2007. Globalization and fruitfly invasion and expansion: The medfly paradigm. Genetica 131: 1–9.

Manrakhan, A., and P. Addison. 2014. Assessment of fruit fly (Diptera: Tephritidae) management practices in deciduous fruit growing areas in South Africa. Pest Manag. Sci. 70: 651–660.

Mao, L., X. Wu, Z. Huang, and A. Tatem. 2015. Modeling monthly flows of global air travel passengers: An open-access data resource. J. Transp. Geogr. 48: 52–60.

Marcucci, E., and V. Gatta. 2011. Regional airport choice: Consumer behaviour and policy implications. J. Transp. Geogr. 19: 70–84.

McCullough, D. G., T. T. Work, J. F. Cavey, A. M. Liebhold, and D. Marshall. 2006. Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biol. Invasions 8: 611–630.

Papadopoulos, N. T. 2014. Fruit fly invasion: Historical, biological, economic aspects and management, pp. 219–252. *In* T. Shelly, N. Epsky, E. B. Jang, J. Reyes-Flores and R. Vargas (eds.), Trapp. Detect. Control Regul. Tephritid Fruit Flies. Springer Netherlands.

Papadopoulos, N. T., B. I. Katsoyannos, and J. R. Carey. 2002. Demographic parameters of the Mediterranean fruit fly (Diptera: Tephritidae) reared in apples. Ann. Entomol. Soc. Am. 95: 564–569.

Papadopoulos, N. T., B. I. Katsoyannos, J. R. Carey, and N. A. Kouloussis. 2001. Seasonal and annual occurrence of the Mediterranean fruit fly (Diptera: Tephritidae) in Northern Greece. Ann. Entomol. Soc. Am. 94: 41–50.

Papadopoulos, N. T., B. I. Katsoyannos, N. A. Kouloussis, J. Hendrichs, J. R. Carey, and R. R. Heath. 2001. Early detection and population monitoring of *Ceratitis capitata* (Diptera: Tephritidae) in a mixed-fruit orchard in Northern Greece. J. Econ. Entomol. 94: 971–978.

Papadopoulos, N. T., R. E. Plant, and J. R. Carey. 2013. From trickle to flood: The large-scale, cryptic invasion of California by tropical fruit flies. Proc. R. Soc. Lond. B Biol. Sci. 280: 20131466.

Siebert, J. B., and T. Cooper. 1995. If medfly infestation triggered a trade ban: Embargo on California produce would cause revenue, job loss. Calif. Agric. 49: 7–12.

Szyniszewska, A. M., and A. J. Tatem. 2014. Global assessment of seasonal potential distribution of Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae). PLoS ONE 9: e111582.

Szyniszewska, A. M. 2013. Analyzing seasonal risk indicators of Mediterranean fruit fly *Ceratitis capitata* (Medfly) importation into Florida via commodity imports and passenger traffic. Dissertation, University of Florida.

Tatem, A. J. 2009. The worldwide airline network and the dispersal of exotic species: 2007–2010. Ecography 32: 94–102.

Tatem, A. J. 2014. Mapping population and pathogen movements. Int. Health 6: 5–11.

Tatem, A. J., and S. I. Hay. 2007. Climatic similarity and biological exchange in the worldwide airline transportation network. Proc. R. Soc. B Biol. Sci. 274: 1489–1496.

Tatem, A. J., Z. Huang, A. Das, Q. Qi, J. Roth, and Y. Qiu. 2012. Air travel and vector-borne disease movement. Parasitology 139: 1816–1830.

Tatem, A. J., D. J. Rogers, and S. I. Hay. 2006a. Global transport networks and infectious disease spread. Adv. Parasitol. 62: 293–343.

Tatem, A. J., D. J. Rogers, and S. I. Hay. 2006b. Estimating the malaria risk of African mosquito movement by air travel. Malar. J. 5: 57.

Thomas, M. C., J. B. Heppner, R. E. Woodruff, H. V. Weems, G. J. Steck, and T. R. Fasulo. 2010. Mediterranean Fruit Fly, *Ceratitis capitata* (Wiedemann) (Insecta: Diptera: Tephritidae). University of Florida, IFAS EDIS EENY-214. (https://edis.ifas.ufl.edu/in371) (accessed 24 August 2016).

Tyler, T. 2015. IATA Annual Review 2015. (http://www.iata.org/about/Documents/iata-annual-review-2015.pdf) (accessed 24 August 2016).

Ware, C., D. M. Bergstrom, E. Müller, and I. G. Alsos. 2011. Humans introduce viable seeds to the Arctic on footwear. Biol. Invasions 14: 567–577.

Westphal, M. I., M. Browne, K. MacKinnon, and I. Noble. 2008. The link between international trade and the global distribution of invasive alien species. Biol. Invasions 10: 391–398.

Work, T. T., D. G. McCullough, J. F. Cavey, and R. Komsa. 2005. Arrival rate of nonindigenous insect species into the United States through foreign trade. Biol. Invasions 7: 323–332.