Pathway Analysis: Likelihood of Coffee Berry Borer (*Hypothenemus hampei* Ferrari) Introduction into the Hawaiian Islands by Air Passenger Travel

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Abstract. The coffee berry borer (CBB) (*Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae, Scolytinae)) is considered the most damaging insect pest of coffee worldwide, causing significant reductions in both the yield and quality of coffee products. CBB was first detected in the Kona coffee-growing district of Hawaii island in 2010. Since then, CBB has spread to all other major coffee-growing regions across the state. In this study, we conducted a quantitative risk assessment to determine the likelihood and frequency of air passengers bringing CBB-infested materials into Hawaii and to estimate human-mediated dispersal pathways between islands. There were over 3.3 million visitors traveling from CBB-occurring countries to Hawaii from 2010 to 2019; we estimated that only 238, 237 of these passengers underwent agricultural inspection at the port of entry. Although the detection rate of CBB on air passengers was very low, the model suggested that there could be at least one passenger bringing CBB-infested materials to Hawaii every year. In addition, we found that Oahu is the most likely source of new pest entries to neighboring islands given the large number of passengers that depart from the Honolulu International Airport. We suggest implementing risk-based inspections of foreign arrivals and inter-island passengers as well as establishing annual inspection routines to intercept infested materials coming into the state. These types of programs will provide the data needed to fine tune statistical models that can be used to predict future introductions. Ultimately these models will serve as critically important tools for crop and commodity protection in Hawaii by improving biosecurity standards and informing the development of emergency response plans for new invasive pests and diseases.

Key words: air passengers, biosecurity, Hawaii, integrated pest management, island invasions, quantitative pathway model

The genus *Coffea* (Rubiaceae) comprises 124 species, most of which are native to tropical and southern Africa (Davis et al. 2006, Davis et al. 2011). Among these species, only two are cultivated widely and used in coffee production: *Coffea arabica* L. and *Coffea canephora* Perre ex A. Froehner. Although these two species originated in Africa, they were introduced to many tropical and subtropical countries and became their most important cash crops. Coffee is currently produced in about 80 tropical and subtropical countries; the top three coffee producing countries are Brazil, Vietnam, and Colombia, which produce approximately 66% of the world's coffee (ICO 2020). More than 125 million people depend on coffee for their livelihood (Osorio 2002). Coffee is planted on ~11 million hectares worldwide, producing 9 million tons of consumable coffee annually (ICO 2013). In the last three decades, global production of coffee has increased by 45% (ICO 2020). The coffee trade includes green beans, soluble, roasted and ground coffee.

The coffee berry borer (CBB) (*Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae, Scolytinae)) is widely considered the most damaging pest of coffee, estimated to cause over $500 million in annual losses worldwide (LePelley 1968, Vega et al. 2002, Vega et al. 2015). CBB is a small bark beetle (~2 mm in length) native to Africa but has invaded nearly all coffee-producing countries except for Australia and Nepal (Vega et al. 2015, Johnson et al. 2020). This insect pest is challenging to control given that most of the life cycle occurs inside the coffee berry, where it is protected from pesticide sprays. Strategies commonly used for CBB management in many countries include cultural (e.g., post-harvest sanitation, pruning), biological (e.g., parasitoid wasps, *Beauveria bassiana* entomopathogenic fungus) and chemical (e.g., endosulfan, chlorpyrifos) control methods (Aristizábal et al. 2017, Infante 2018, Johnson et al. 2020).

The female CBB initiates infestation by boring a hole into the coffee fruit (often called as a "berry"), where she builds galleries for reproduction. Over 11–40 days, the female will lay multiple clusters of eggs (Vega et al. 2015). As the larvae develop, they feed on the endosperm tissue, causing further damage to the coffee seed or "bean" (Vega et al. 2015). The ratio of female to male offspring can vary greatly, although many studies report an average of around 10:1 (Vega et al. 2015, Mariño et al. 2016, Johnson et al. 2019). Siblings mate within their natal berry. The males (which have vestigial wings) remain inside the berry (Jaramillo et al. 2006, Vega et al. 2015) while the mated females emerge to search for a new berry to infest. The female CBB is capable of flying continuously for 30 m up to 3 h (Baker 1984, Baker 1999). The average migration range is reported to be 5–10 m, with longer distance dispersal likely occurring infrequently during periods of strong winds (Gil et al. 2015). Observations of flight behavior in the field suggest CBB tend to fly close to the ground (< 2 m in altitude; Ruiz-Diaz and Rodrigues 2021, M. Johnson, pers. obs.), making long distance dispersal less likely.

CBB was first detected in the Kona coffee-growing district on Hawaii island in 2010 (Burbano et al. 2011) and quickly spread to all ~800 small farms on the island. Although quarantine restrictions were put into place by the Hawaii Department of Agriculture (HDOA) to limit the movement of unroasted coffee between islands, CBB was later detected on the neighboring islands of Oahu (2014), Maui (2016), Lanai (2020), and Kauai (2020). Currently, coffee plants, coffee plant parts, green coffee beans, and used coffee bags are prohibited from entry into Hawaii unless a permit is issued following the regulations set by HDOA (HDOA 2020). Green coffee beans must be fumigated with methyl bromide before entering Hawaii to prevent the introduction of pests and diseases. Although improper fumigation is possible, accidental transport by migrant workers has been cited as a more likely pathway into Hawaii based on phylogenetic evidence that suggests the source of the initial introduction was Latin America (Chapman et al. 2015). Most seasonal workers on coffee plantations in Hawaii are from Latin American countries, followed by Micronesia and the Philippines. In addition, a variety of nonindigenous plants and plant pests have been intercepted from baggage carried by travelers at the U.S. ports of entry (POE) (McCullough et al. 2006). To determine if transport by air passengers (e.g., tourists, seasonal workers, and travelers) was a likely means of entry into the state, we evaluated current CBB distributions and the risk of passengers bringing CBB-infested materials from foreign countries. We also evaluated possible pathways of CBB dispersal between the Hawaiian Islands based on commercial flight frequency, flight direction and the number of passengers.

Methods

CBB distribution and host species. The current CBB distribution and coffee-growing countries were mapped using FAOSTAT (FAO 2020). Although several potential host plants have been suggested in earlier studies, coffee is the only known host in which CBB can complete their life cycle (Messing 2012, Vega et al. 2012, Vega et al. 2020).

CBB climate suitability in Hawaii.The lower and upper temperature thresholds for CBB development are reported as 18°C and 30°C, respectively (Jaramillo et al. 2009, Azrag et al. 2020). We classified coffee-growing areas within this temperature range as optimal and determined the average number of months per year that the temperature stays between 18°C and 30°C using tools within the Spatial Analytic Framework for Advanced Risk Information Systems (SAFARIS) and Daymet version 3 weather data from 2000 to 2019 (ORNL 2021, SAFARIS 2021). Months with optimal temperature conditions were determined by counting the number of days with a mean daily minimum temperature above 18°C and mean daily maximum temperature below 30°C and then dividing by 30.

Number of air passengers traveling to Hawaii from CBB-occurring countries. We collected data on air passengers traveling from CBB-occurring countries to Hawaii from the Department of Transportation (DOT) BTS T100 Segment and Market datasets (US DOT 2020). However, given that the BTS T100 datasets had missing data we could only obtain partial information. For example, annual passenger numbers from Brazil and Mexico to the Hawaiian Islands were available, but annual passenger numbers from any African countries to Hawaii were unavailable. We, therefore, estimated the number of people traveling to Hawaii from CBB-occurring countries by subtracting the passengers from countries where CBB does not occur from total annual foreign visitors, using monthly statistics from the State of Hawaii Department of Business, Economic Development and Tourism (DBEDT 2020).

Inspection rates and CBB detections at the U.S. port of entry. The Custom and Border Protection (CBP) agriculture specialists and CBP officers at the U.S. POE inspect passengers' baggage to prevent the entry of pests and diseases that could be harmful to Hawaii's agricultural industry. The inspection rate at the Honolulu International Airport was estimated from the 2010 to 2019 data using United States Department of Agriculture – Animal and Plant Health Inspection Service (USDA-APHIS) Agricultural Quarantine Activity Systems (AQAS) to calculate the number of air passengers inspected from CBB occurring countries each year.

USDA-APHIS keeps records of pest interceptions at U.S. ports of entry through the PestID database. This database contains interception date, inspection location, pathway (e.g., airport, maritime), origin, destination, pest type, scientific pest name (often at the genus level, but some are identified to species), inspected host species, inspected host part (e.g., seed, leaf, fruit, flower), where inspected (e.g., mail, permit cargo, baggage), and the number of pests found. The number of CBB detections from air passengers was obtained from PestID.

CBB dispersal pathways between the Hawaiian Islands. Currently, CBB is known to occur on the Hawaiian Islands of Kauai, Oahu, Maui, Lanai and Hawaii Island. We collected data on the number of passengers traveling between these islands to determine the probability of inter-island CBB movement. We obtained the number of inter-island passengers by using DOT BTS T100 datasets (US DOT 2020). Based on passenger traveling patterns and the current CBB distributions in Hawaii, we defined seven inter-island dispersal pathways within Hawaii: 1) between Oahu and Kauai, 2) between Maui and Kauai, 3) between Hawaii island and Kauai, 4) between Oahu and Maui, 5) between Oahu and Lanai, 6) between Oahu and Hawaii island, and 7) between Maui and Hawaii island.

Quantitative modeling. We developed a probabilistic model that estimated the likelihood of passengers bringing CBB-infested materials from foreign countries to Hawaii. We then developed probabilistic models to estimate the likelihood of CBB dispersal via air passengers traveling between the Hawaiian Islands. These models describe one of the most critical CBB pathways to new locations. The parameters used in these models are associated with quantities or probabilities (e.g., what is the likelihood that a passenger is bringing infested material? What is the estimated number of passengers from CBB-occurring countries? How many people are traveling between the Hawaiian Islands?).

The number of passengers was projected based on the traveler information from 2010 to 2019 using a PERT distribution. The number of passengers from CBB-occurring countries increased overtime; therefore, we used linear regression to determine the distribution for the incoming passenger numbers from CBB-occurring countries. We used the extrapolated value for the next year as the most likely value in a PERT distribution. The minimum and the maximum number of passengers were the lower and upper prediction intervals (α=5%) for the predicted value (via JMP, SAS Institute Inc., Cary, NC, USA).

For modeling inter-island pathways, we estimated the probability of CBB dispersal in both directions with the same model parameters, given that the numbers of incoming and outgoing passengers were similar between two islands (e.g., from Hawaii island to Maui, and from Maui to Hawaii island). We used the average number of annual passengers from 2010 to 2019 as the most likely value and selected the minimum and maximum passenger values using the data for both directions, except for the pathways between Maui and Kauai, between Hawaii island and Maui, and between Hawaii island and Kauai. The pathways between Hawaii island and Maui and between Maui and Kauai exhibited a significant increase in the number of passengers from 2010 to 2019 ($p<0.05$); therefore, we fitted a linear regression line to extrapolate the most likely value and estimated confidence intervals (α=5%) for the most likely value as the minimum and the maximum passenger values (via JMP, SAS Institute Inc., Cary, NC, USA). There was also a significantly larger number of passengers traveling between Kauai and Hawaii Island at the beginning of 2017 due to the addition of direct flights between these islands; therefore, we only used the passenger data from 2017 to 2019 to parameterize the model. We excluded the pathway assessment from Maui to Lanai because the number of travelers from Maui to Lanai was too low to model.

Instead of using averaged values to determine the overall likelihood, variability in biological systems is best represented by a distribution of values. Four probability distribution types (i.e., the Beta, binomial, negative binomial and PERT) were used in these models to capture uncertainties, including variability. The Beta, binomial and negative binomial distributions comprise the binomial process, which describes a stochastic system where probability and randomness are associated with an event, and there are *n* independent trials (Vose 2000). The binomial process is well suited for CBB pathway analysis since multiple independent passengers arrive at ports with a probability of infestation. We used the PERT distribution due to its objectivity and resistance to the effects of extreme values. We used the software @Risk 7.5 Professional (Palisade Corporation, Newfield, NY, USA), which uses Monte Carlo simulation to run the model. We used Latin Hypercube sampling with a fixed random generator seed of one and 10,000 iterations to run the model simulation.

Results

CBB distribution and host species. CBB has been reported in almost every coffee-producing country except for Australia and Nepal (Figure 1; Appendix 1). CBB is distributed throughout Central Africa, Southeast Asia, Central America, and northern South America.

CBB climate suitability in Hawaii. All Hawaiian Islands were observed to have areas with optimal conditions for CBB development (mean daily temperatures from 18°C to 30°C) based on data from 2000 to 2019 (Figure 2). High elevation areas on Hawaii island had no optimal temperature days. Mountain regions on Kauai, Maui and Molokai had less than one month (30 days) of optimal temperatures. All remaining areas had more than six months of optimal development conditions. These results indicate that Hawaii provides very favorable conditions for CBB development throughout the year.

Number of passengers traveling to Hawaii from CBB-occurring countries. Approximately 3 million international passengers per year have entered Hawaii since 2010 (DBEDT 2020). In 2019 alone, over 10 million air passengers entered Hawaii, with more than 3.3 million of these being international visitors. More than 65% of passengers to Hawaii are from the mainland United States (DBEDT 2020). Travelers from Japan and Canada are also some of the most frequent visitors to Hawaii. Travelers from those three countries comprise over 87% of visitors to Hawaii.

To estimate the number of passengers traveling to Hawaii from the CBB-occurring countries, we subtracted the number of visitors from Japan, Canada, Europe, China, Taiwan, South Korea, Australia, and New Zealand from 2010 to 2019. These countries accounted for 87–92% of the total international travelers to Hawaii. Most international travelers enter Hawaii through the Honolulu International Airport on the island of Oahu. We estimated that the number of passengers from CBB-occurring countries increased from 2010 (308,817 passengers) to 2019

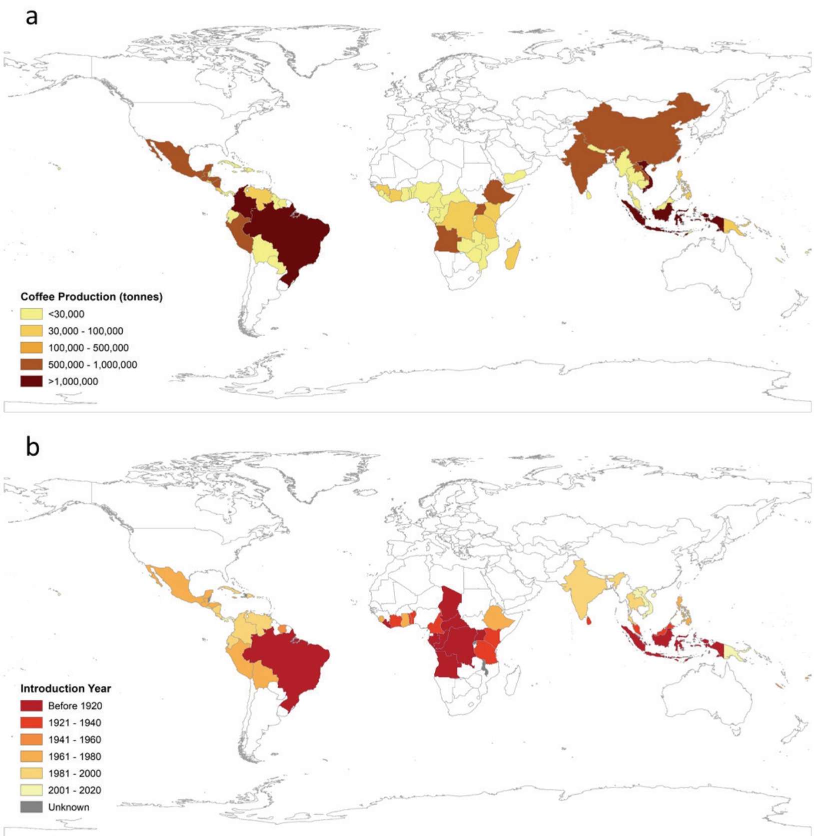

Figure 1. World coffee production with CBB world distribution: a) 2019 coffee production (FAO 2020); b) CBB distribution by introduction year (Vega et al. 2015).

(408,179 passengers) (Table 1). There were over 3.3 million visitors from CBB-occurring countries to Hawaii from 2010 to 2019. CBB was detected for the first time in China in 2019 (Sun et al. 2020); however, we did not include China as a CBB-occurring country in 2019, given that it was observed to be restricted to Hainan. We assumed the number of people coming from Hainan to Hawaii was a small proportion of passengers compared to the other areas of China.

Inspection rates and CBB detections at U.S. ports of entry. The estimated annual inspection rate varied each year from 4.2% to 10% (Table 1). The annual inspection rate was highest in 2011 and lowest in 2019 (Table 1). Using these inspection rates, we estimated the number of passengers from CBB-occurring countries who were inspected at the U.S. POE. We estimated that 238, 237 passengers from CBB-occurring countries were inspected from 2010 to 2019.

There were 31 CBB detection records since 1985 on air passengers from foreign countries at U.S. airports. In addition, there were 11 pre-departure detections in Puerto Rico (10 records) and Hawaii (1 record). The pre-departure inspection

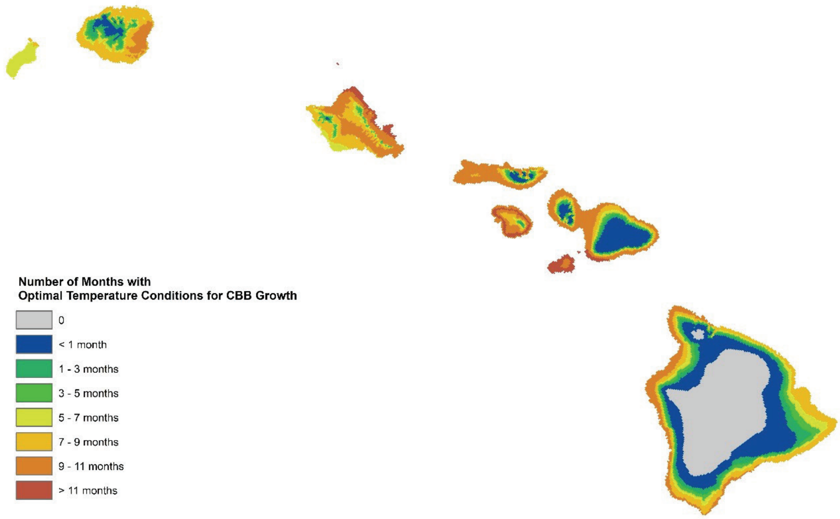

Figure 2. Number of months per year with optimal temperature conditions for CBB growth. The optimal temperature conditions were determined by evaluating the area where daily minimum temperature was above 18°C and daily maximum temperature was below 30°C.

Table 1. Annual number of passengers traveling to Hawaii from CBB-occurring countries, the number of passengers inspected at U.S. POE, and the inspection rate.

	Passengers from CBB-occurring countries		
Year	**Number**	**Number inspected**	**Inspection rate**
2010	308,817	28,411	0.092
2011	278,287	27,829	0.100
2012	343,215	32,949	0.096
2013	237,489	20,187	0.085
2014	321,273	25,381	0.079
2015	327,728	20,647	0.063
2016	333,683	21,356	0.064
2017	406,122	23,961	0.059
2018	415,780	20,373	0.049
2019	408,179	17,144	0.042
Total	**3,380,573**	**238,237**	

program prevents the introduction of harmful and invasive pests from Hawaii, Puerto Rico, and U.S. Virgin Islands to the continental United States. Those inspections happen at the departure airports for passengers flying to the continental United States. There have been no CBB detections at Hawaii airports on passengers arriving from foreign countries.

CBB dispersal pathways between the Hawaiian Islands. The numbers of people traveling between the Hawaiian Islands

Table 2. Number of passengers traveling by air between the five Hawaiian Islands with confirmed CBB populations from 2010 to 2019

Origin	Destination	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2010 –2019 Average
Oahu	Hawaii	1,208,499	1,216,069	1,255,631	1,260,834	1,217,745	1,209,172	1,244,185	1,306,274	1,143,947	1,229,953	1,229,231
	Maui	1,088,551	1,060,128	1,110,688	1,104,750	1093,907	1,063,992	1,069,823	1,114,316	1,081,867	1,118,715	1,090,674
	Kauai	755,263	702,156	689,184	683,463	650,101	664,390	699,196	720,866	650,906	644,398	685,992
	Lanai	41,850	41,966	37,702	37,060	48,517	36,644	41,613	37,214	41,058	48,447	41,207
Hawaii	Oahu	1,209,171	1,202,963	1,239,385	1,245,130	1,204,780	1,196,328	1,228,332	1,302,952	1,146,224	1,228,539	1,220,380
	Maui	141,554	146,936	171,553	199,703	206,055	225,227	242,760	234,515	224,579	193,063	198,595
	Kauai[2]	2,213	2,323	859	-[1]	-	-	-	28,934	46,572	39,140	38,215
Maui	Oahu	1,113,658	1,077,184	1,107,916	1,108,416	1,097,248	1,063,892	1,065,650	1,110,109	1,083,644	1,123,522	1,095,124
	Hawaii	127,199	137,974	164,651	183,140	197,216	217,261	230,471	226,503	205,950	182,303	187,267
	Kauai	29,583	36,840	85,933	107,214	116,324	139,765	142,749	135,218	135,048	124,465	105,314
Lanai	Oahu	43,370	43,447	44,780	43,503	49,311	37,530	39,760	35,762	41,268	48,070	42,680
Kauai	Oahu	736,311	682,806	691,662	682,910	652,678	665,947	694,052	730,197	664,488	644,523	684,557
	Hawaii[2]	2,938	3,077	1,185	117	-	-	-	28,380	43,960	38,694	37,011
	Maui	59,362	71,343	90,994	109,483	117,826	138,469	146,839	136,672	136,783	125,867	113,364

[1] Dash mark (-) indicates that no passenger data was available.
[2] Due to significant passenger pattern changes between Hawaii and Kauai, the average was calculated using 2017 to 2019 data.

of Kauai, Oahu, Maui, Lanai and Hawaii from 2010 to 2019 are displayed in Table 2. The numbers of incoming and outgoing passengers between the islands were similar. For example, there were 41,207 passengers traveling from Oahu to Lanai, compared to 42,680 passengers traveling from Lanai and Oahu (Table 2). Each year, more than 1 million passengers were traveling in both directions between Oahu and Hawaii island and between Maui and Oahu (Table 2). Fewer passengers were observed traveling between Kauai and Oahu, Maui and Kauai, Maui and Hawaii island, Kauai and Hawaii island, and Oahu and Lanai. Oahu is the main dispersal pathway to all other islands based on the mean annual number of passengers traveling between islands. (Figure 3).

Quantitative modeling. Given that there were zero CBB detections on visitors from foreign countries at airports in Hawaii, we used this number (zero) to estimate the probability of the passengers from foreign countries bringing CBB-infested materials into Hawaii (Table 3). The number of trials (n) was determined by the number of passengers from CBB-occurring countries who were inspected at the U.S. POE in Hawaii. In addition, we used the same approach to estimate the likelihood of CBB dispersal between the Hawaiian Islands. The parameters used in the model to determine the probability of CBB arriving to Hawaii from CBB-occurring countries and the probability of CBB dispersal between the Hawaiian Islands

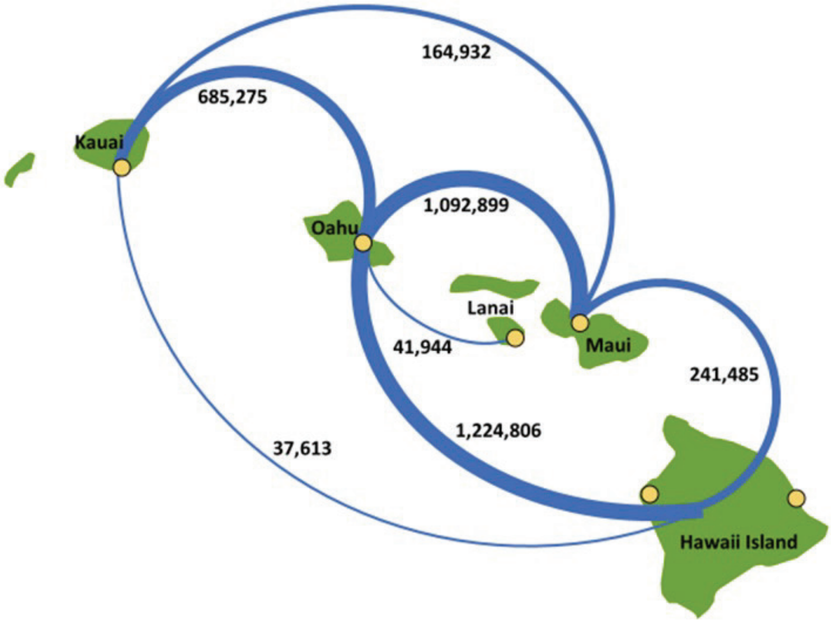

Figure 3. Mean annual number of air passengers traveling between the Hawaiian Islands. Dispersal pathways are shown for those islands that are confirmed to have coffee berry borer. Thicker blue lines indicate higher numbers of passengers.

Table 3. Probability model parameters.

Model parameters	Description
Probability of a passenger carrying CBB-infested materials	We used the Beta distribution to determine the probability. $\beta(s+1, n-s+1)$ s = 0 (number of CBB detections on foreign passengers) n = 238,237 (number of people inspected at the airport)
Number of visitors	**PERT**
from CBB-occurring countries to Hawaii	(311,502; 420,267; 529,032)
between Hawaii island and Oahu	(1,143,947; 1,224,806; 1,306,274)
between Hawaii island and Maui	(185,152; 241,485; 297,819)
between Hawaii island and Kauai	(28,380; 37,613; 46,572)
between Oahu and Kauai	(644,398; 685,275; 755,263)
between Oahu and Lanai	(35,762; 41,944; 49,311)
between Oahu and Maui	(1,060,128; 1,092,899; 1,123,522)
from Maui to Kauai	(117,816; 164,932; 212,047)

Table 4. Mean probability of at least one passenger bringing CBB-infested materials, annual number of passengers with CBB-infested materials, and number of years until at least one person brings CBB-infested materials to Hawaii from CBB-occurring countries and between Hawaiian Islands.

Origin	Destination	Annual probability of at least one person with CBB	Annual number of passengers with CBB-infested materials			Number of years until at least one person arrives with CBB		
			5th	Avg.	95th	5th	Avg.	95th
Foreign countries	Hawaiian Islands	0.64	0	2	6	1	1.6	3
Hawaii	Oahu	0.84	0	5	16	1	1.2	2
Hawaii	Maui	0.50	0	1	4	1	2.0	5
Hawaii	Kauai	0.14	0	0.2	1	1	7.4	21
Oahu	Kauai	0.75	0	3	10	1	1.3	3
Oahu	Lanai	0.15	0	0.2	1	1	6.5	19
Oahu	Maui	0.82	0	5	15	1	1.2	2
Maui	Kauai	0.41	0	0.7	3	1	2.5	6

were summarized in Table 3.

The model predicted that there was a 64% chance of one or more passengers arriving with CBB-infested materials in Hawaii each year (Table 4a). The annual number of passengers bringing infested materials was predicted to be two passengers (Table 4; Figure 4a). The mean number of years for at least one person coming to Hawaii with infested materials was 1.6 years. The annual probability of at least one person bringing CBB-infested materials on inter-island flights ranged from 0.14 to 0.84. The highest probabilities of dispersal were between Hawaii and Oahu, Oahu and Maui, and Oahu and Kauai while the lowest probabilities were between Hawaii and Kauai and Oahu and Lanai (Table 4).

Summary and Discussion

The climate suitability assessment indicated that all the Hawaiian Islands could support CBB development. Optimal temperature conditions for CBB development occur at low to mid-elevations year-round, while high-elevation regions support development within a very limited time frame (0–3 months). This indicates that when air passengers carry CBB-infested materials, it is highly likely that CBB would find suitable areas to survive and reproduce, especially given the abundance of feral coffee plants that exist on all islands. The high ratio of female to male offspring also increases the likelihood of CBB survival during the initial colonization of new environments. This evidence indicates that there is high likelihood of establishment if CBB enters into Hawaii.

There are approximately 410,000 visitors from CBB-occurring countries to Hawaii each year in recent years. Visitors entering the United States have carried CBB-infested materials in their baggage, and there have been 31 detections at U.S. POE since 1985. However, CBB has never been detected on visitors from foreign countries at the U.S. POE in Hawaii. We constructed probabilistic models using historical data to estimate the likelihood of CBB introduction to the Hawaiian Islands via air passengers traveling from foreign countries. The model suggested a 64% probability of at least one passenger bringing CBB-infested

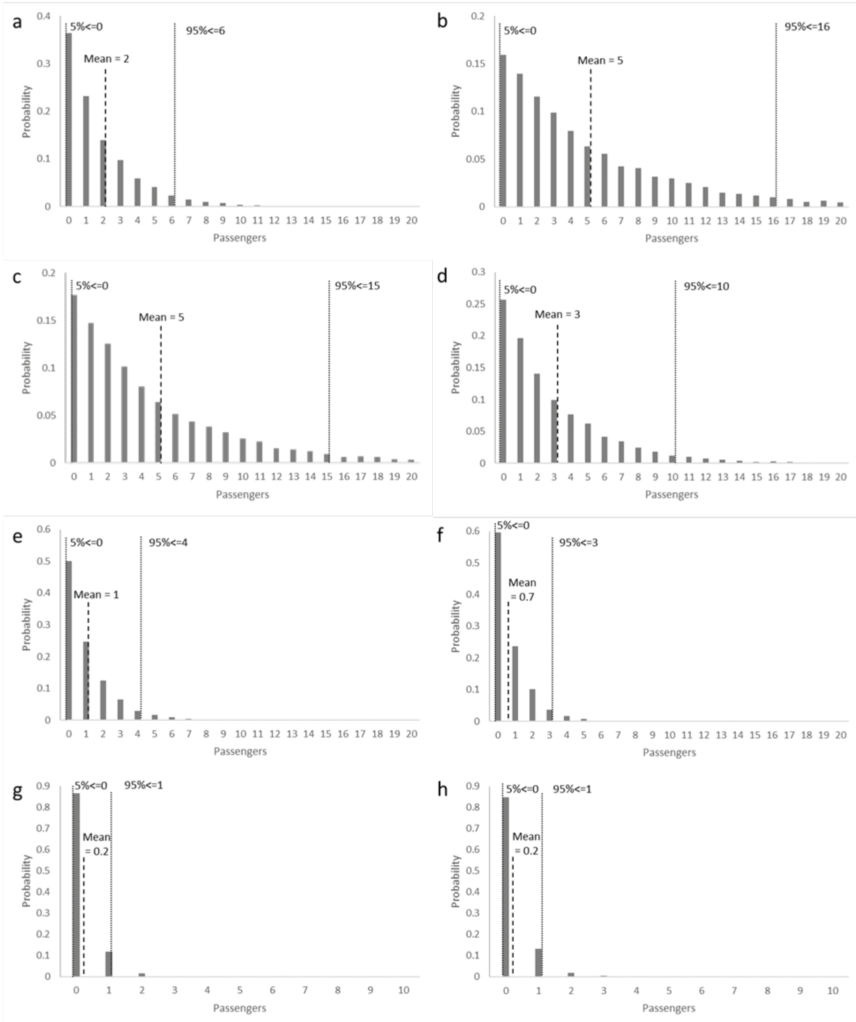

Figure 4. Probability for the estimated annual passenger entries with CBB-infested materials: (a) to Hawaii from CBB-occurring countries; (b) between Hawaii island and Oahu; (c) between Oahu and Maui; (d) between Oahu and Kauai; (e) between Hawaii island and Maui; (f) between Maui and Kauai; (g) between Hawaii island and Kauai; (h) between Oahu and Lanai.

materials to Hawaii from foreign countries each year. One critical point to note is that we estimated the number of visitors from CBB-occurring countries by subtracting the major visitor countries with no CBB occurrence (e.g., Japan, Canada, Europe, China, Taiwan, South Korea, Australia, and New Zealand). Given that this method may have overestimated the number of foreign visitors from CBB-occurring countries, leading to a lower approach rate estimation, it is possible that we underestimated the number of passengers that might be traveling with infested materials than is suggested by the model.

Our results are based on the numbers of passengers traveling between islands and the quantitative model probabilities can be used to predict the order of CBB dispersal between the Hawaiian Islands. With an initial colonization of Hawaii island, our findings suggest that the most likely dispersal pathway for CBB across the island chain was from Hawaii island to Oahu, Oahu to Maui, Oahu to Kauai, and Oahu to Lanai. Interestingly, the order of CBB detection in the Hawaiian Islands seems to coincide with this prediction: CBB was first detected on Hawaii island in 2010, Oahu in 2014, Maui in 2016, and Kauai and Lanai in 2020. Together, these results suggest that Oahu is the most likely gateway for human-mediated dispersal of new coffee pests and diseases once they have entered Hawaii.

We expect that the models presented here may be expanded to encompass other agricultural pests and diseases with a high capacity for human-mediated transport. For example, a similar approach was used to assess potato pest introduction into Mexico (Fowler et al. 2014) and Asian longhorned beetle (*Anoplophora glabripennis* (Motschulsky)) introduction outside of quarantine areas (Auclair et al. 2005). A coffee pest not yet present in Hawaii but is anticipated to cause major damage to the industry if established is coffee leaf miner (CLM, *Leucoptera coffeellum* (Guérin-Méneville)), a micromoth whose larvae makes tunnels in the coffee leaves and cause reduced photosynthesis and eventual defoliation. This insect pest is found in the Americas, although other leaf miner species exist as pests in Africa and Asia. CLM could be transported illegally by passengers coming to Hawaii on the leaf material of coffee plants used for propagation. Future pathway analysis of this nature could focus on the passengers from the countries with climates similar to Hawaii since they would likely to pose a greater risk of introducing CLM.

An exception to the ability of our model to predict human-mediated dispersal pathways includes those plant pests and diseases that are also easily wind-dispersed. An example is *Hemileia vastatrix* Berkeley & Broome, the fungus that causes Coffee Leaf Rust (CLR) and is one of the most devastating coffee diseases worldwide. Unlike CBB, CLR has a much greater capacity to disperse long distances by wind (potentially thousands of miles), such that the pathways for human-mediated dispersal described in the present study may be difficult to apply in cases such as this. CLR was first detected on Maui in October 2020 and was then reported shortly thereafter on Hawaii Island in November 2020, on Oahu and Lanai in January 2021, Molokai in June 2021, and Kauai in July 2021. However, observations of disease progression and spores detected in traps suggest that CLR was likely on the islands for many months (possibly even a year or more) prior to detection (L. Keith, pers. comm.), making it difficult to determine the order of island colonization and dispersal.

Conclusions

The present study characterized the probability of entry and dispersal of CBB to Hawaii by air passengers. Our quantitative model suggested a 64% probability that passengers could bring CBB-infested materials from foreign countries to Hawaii and that further dispersal between the Hawaiian Islands was also likely occurring through this pathway. However, since the predicted number of passengers bringing infested materials into Hawaii is small compared to the annual number of international visitors, detecting passengers with infested materials may be challenging.

We, therefore, suggest implementing more focused inspection protocols at U.S. POE, targeting inspection of passengers traveling from countries with pests and diseases that are a high risk to Hawaii's agricultural industry and/or native biodiversity. This may include countries with a tropical or subtropical climate similar to Hawaii, which would indicate a higher likelihood of pests and diseases from these countries finding suitable climates and hosts upon arrival. We also suggest a pre-boarding inspection program for inter-island travelers to limit the possibility of pest and disease dispersal between islands, particularly for those passengers departing from Oahu to neighboring islands. Ultimately, these focused inspection protocols at Hawaii's airports will help mitigate the likelihood of new pest and disease introduction via air passengers and reduce the economic costs associated with eradication programs.

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Appendix 1. List of Countries where CBB has been Detected

Country	Data sources
Angola	Morstatt 1912, Corbett 1933
Belize	Williams et al. 2013
Benin	Hesse 1925, Vega et al. 2002b
Bolivia	Rogg 1997, Bustillo 2002
Brazil	Berthet 1913, Neiva 1928, Vega et al. 2002b, Benavides et al. 2005, Benavides et al. 2006, Benavides Machado et al. 2007, Gauthier 2010, Chapman et al. 2015
Cameroon	Mbondji 1988, Vega et al. 2002b, Gauthier 2010
Central African Republic	Chevalier 1947
Republic of Chad	Chevalier 1947
People's Republic of China (Hainan)	Sun et al. 2020
Colombia	Cárdenas and Bustillo 1991, Bustillo 2002, Vega et al. 2002b, Benavides et al. 2005, Benavides et al. 2006, Benavides Machado et al. 2007
Costa Rica	Staver et al. 2001, Benavides et al. 2005, Benavides et al. 2006, Benavides Machado et al. 2007, Gauthier 2010
Côte d'Ivoire	Beille 1925, Gauthier 2010
Cuba	Hernández 2002, Vega et al. 2002a
Republic of Congo	Fleutiaux 1901
Democratic Rep. of Congo	Leplae 1928
Dominican Republic	Serra 2006, Gauthier 2010
Ecuador	Klein-Koch 1990, Vega et al. 2002b, Benavides et al. 2005, Benavides et al. 2006, Benavides Machado et al. 2007
El Salvador	Vega Rosales and Romero 1985, Bustillo 2002, Vega et al. 2002b
Ethiopia	Davidson 1967, Gauthier 2010, Chapman et al. 2015
Fiji	Anonymous 1979, Jackson 2020
Gabon	Beille 1925, Ndoutoumou et al. 2015

Appendix 1 (continued)

Country	Data sources
Ghana	Padi 1984, Padi 1999
Guatemala	Hernández Paz 1972, Bustillo 2002, Gauthier 2010, Chapman et al. 2015
Haiti	Ryckewaert and Lenteren 2020
Honduras	Muñoz 1985, Bustillo 2002, Vega et al. 2002b
India	Kumar et al. 1990, Gauthier 2010, Chapman et al. 2015
Indonesia	Hagedorn 1910, Chapman et al. 2015
Jamaica	McPherson 1978, Reid 1983, Chapman et al. 2015
Kenya	Wilkinson 1928, 1929, Gauthier 2010, Chapman et al. 2015
Laos	CABI 2008
Liberia	Hopkins 1915
Malaysia	Corbett 1933
Malawi	Lee 1971
Mariana Islands	Wood 1960
Martinique	Dufour 2013
Mexico	Baker 1984, Bustillo 2002, Vega et al. 2002b, Gauthier 2010
Mozambique	De Ingunza S. 1966
New Caledonia	Bugnicourt 1950, Gauthier 2010, Chapman et al. 2015
Nicaragua	Monterrey 1991, Vega et al. 2002b, Gauthier 2010, Chapman et al. 2015
Nigeria	Idown 1980
Panama	Inwood 2005
Papua New Guinea (Independent State of)	Tlozek 2017, Johnson et al. 2020
Peru	de Ingunza 1964, Benavides et al. 2005, Benavides et al. 2006, Benavides Machado et al. 2007
Philippines	Gandia and Boncato 1964
Pohnpei	Wood 1960, SPC 2015
Rwanda	Bigirimana et al. 2019
São Tomé and Principe (Democratic Republic of)	Kaden 1930
Sierra Leone	Taylor 1973
Sri Lanka	Hutson 1936, Perera et al. 1985
Surinam	Van Dinther 1960, Kairo et al. 2003
Tahiti	Johnston 1963
Thailand	Onishi et al. 2017
Timor-Leste	SPC 2015
Togo	Gauthier 2010, Wegbe 2012, Chapman et al. 2015
Uganda	Gowdey 1911, Gauthier 2010, Chapman et al. 2015
United Republic of Tanzania	Ritchie 1925, Jaramillo et al. 2006, Magina et al. 2007, Aristizábal et al. 2017
USA (Hawaii)	Burbano et al. 2011
USA (Puerto Rico)	Osorio 2007, Aristizábal et al. 2017
Venezuela (Bolivarian Rep.)	Rosales Mondragón et al. 1998, Torres 2005
Vietnam	Beaver and Lan-Yu 2010

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